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Evidence for an enriched hyperbenthic fauna in the Frisian front (North Sea)

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Abstract

The hyperbenthos of the Frisian front, an enriched benthic area of the southern North Sea, and surrounding waters was investigated along two cross-frontal transects in August 1994 and April 1996. A total of 111 species was recorded, mainly peracarid crustaceans and decapods. On average, *Calanus* spp. (Copepoda), *Schistomysis ornata* (Mysidacea) and *Scopelocheirus hopei* (Amphipoda) represented more than 40% of the total density, while *S. ornata* constituted 30% of the biomass. Community structure differed strongly between the two months, as shown by the species composition and the much lower densities and biomasses in April. In August, the density of the holohyperbenthic fraction reached pronounced peaks in the Frisian front area: densities for chaetognaths, copepods, amphipods and mysids were one order of magnitude higher than in the surrounding waters. Diversity was also highest at the Frisian front. The high abundances may be explained by active migration and/or by passive transport to the food-enriched area. Merohyperbenthic species showed a less distinct increase in density in the front zone, but a clear south-to-north change in community structure was observed. These species are more heavily subjected to the prevailing tidal flow. The Frisian front fauna seems to be transitional between two merohyperbenthic communities established in late summer, one belonging to the environmentally different sandy Southern Bight to the south, the other to the silty Oyster Ground to the north. In spring, no such hyperbenthic enrichment over the Frisian front was observed. This is most probably due to the strong seasonality of the hyperbenthic fauna and the low water temperature, suggesting that production and subsequent recruitment had not started yet. Alternatively, winter storms could have resuspended particulate organic matter, followed by a rapid migration of the motile hyperbenthos to more northern depositional areas and thus leading to a temporal density decline. We conclude that the Frisian front is an enriched area for the hyperbenthos at the end of summer, as has already been reported for the benthic system. © 2002 Published by Elsevier Science B.V.

Keywords: Hyperbenthos; Peracarida; Community structure; Biodiversity; Benthic boundary layer; North Sea; Frisian front

1. Introduction

The hydrodynamic regime of the North Sea is to a large extent reflected in its sediment granulometry, with a marked discontinuity between the sandy shallow Southern Bight and the silty deeper Oyster Ground. At this boundary, tidal current velocity drops below a critical value, enabling fine-grained material to settle from the water column (Creutzberg and Postma, 1979; Creutzberg et al., 1984). Favourable conditions generate a vigorous spring phytoplankton bloom and a locally stronger primary production during summer (Baars et al., 1991), resulting in high sedimentation

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of organic matter and leading to an enriched bottom fauna. This enriched benthic zone is referred to as the "Frisian front" and is located between the − 30 and − 40 m isobaths, as first reported by Creutzberg et al. (1984). The area has been found to act as a boundary between northern and southern communities, as described for macrobenthos and epibenthos (Baars et al., 1991). More recently, the focus has been on the quality and quantity of the near-bottom particulate organic matter and its degradation and incorporation into the sediment (Boon and Duineveld, 1996, 1998; Boon et al., 1998; Dauwe and Middelburg, 1998; Dauwe et al., 1998, 1999).

Additionally, the Frisian front approximately coincides with the transition between the permanently mixed southern North Sea and the stratified water masses of the central North Sea during summer (Creutzberg, 1985). Tidal fronts occur in these boundary areas in a series of more or less fixed geographical locations and are characteristic of the summer regime on the northwestern European continental shelf (Simpson et al., 1978; Bowers and Simpson, 1987; Brown et al., 1999).

To date, no information is available on the hyperbenthos of the Frisian front. The hyperbenthos is the faunal element of the benthic boundary layer, i.e. the fauna living in the lower strata of the water column and dependent on the proximity of the bottom (Mees and Jones, 1997). Hyperbenthic animals possibly signify a major link in coastal food webs as consumers of detritus, algae and zooplankton and as prey for demersal fish (in particular for postlarval and juvenile life stages) and adult shrimp (Mauchline, 1980; Mees and Jones, 1997; Beyst et al., 1999a; Hostens and Mees, 1999; Pedersen, 1999; Oh et al., 2001). The highly motile hyperbenthic organisms (mainly peracarid crustaceans and early life history stages) often reach high densities in regions with a strong input of organic matter to the bottom environment (Sorbe, 1984; Buhl-Jensen and Fosså, 1991; Dauvin et al., 1994; Mees and Jones, 1997). The elevated carbon flux at the Frisian front can thus be expected to attract hyperbenthic species, resulting in an increased density and biomass in comparison with surrounding waters.

The aims of this study were (1) to describe the hyperbenthic fauna of the Frisian front during a spring and summer situation in terms of species composition, density, biomass and diversity; (2) to investigate structural characteristics of the hyperbenthic community along a cross-frontal gradient in order to discover a possible shift in community structure at the Frisian front.

2. Material and methods

2.1. Sampling

The Frisian front (15 km wide) is approximately located between 53°30′ N–4°E and 54°N–5°E and between the − 30 and − 40 m isobaths (Baars et al., 1991). Sampling was done along two parallel south-to-north transects (transects A and B) perpendicular to the isobaths and covering the front and the surrounding waters. Six sites were selected along transect A (from site A1 to A6); only four sites were sampled along the shorter transect B (from site B1 to B4). Four sites were situated in the Frisian front zone, three to the south and three to the north. All sites were sampled on two occasions: on 30 August 1994, and on 16 April 1996 (except sites B1 and B4, which were sampled on 25 August). In April 1996, two additional sites (sites A7 and B5) north of the study area were sampled. A total of 22 samples were assessed; the geographical position of the sampling sites is presented in Fig. 1.

Sampling was done from the RV *Belgica* with a modified hyperbenthic sledge after Sorbe (1983). Two nets (1 mm mesh size, 3 m long, 71 cm wide) fixed on the sledge sampled the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (which measures the towing distance, for details see Sorbe, 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was carried out during daytime, against the current and at an average ship speed of 1.5 knot relative to the bottom. In August each towing lasted 5 min; in April towing duration was doubled to 10 min because of poor catches. Average towing distance was 258 ± 16.0 m in August and 503 ± 27.0 m in April; the volume filtered per net amounted to 100 ± 5.3 m^3 and 184 ± 17.8 m^3, respectively. The catches from the upper and lower net were rinsed separately over a 1-mm mesh size sieve and preserved in a buffered formaldehyde solution (7% final concentration).

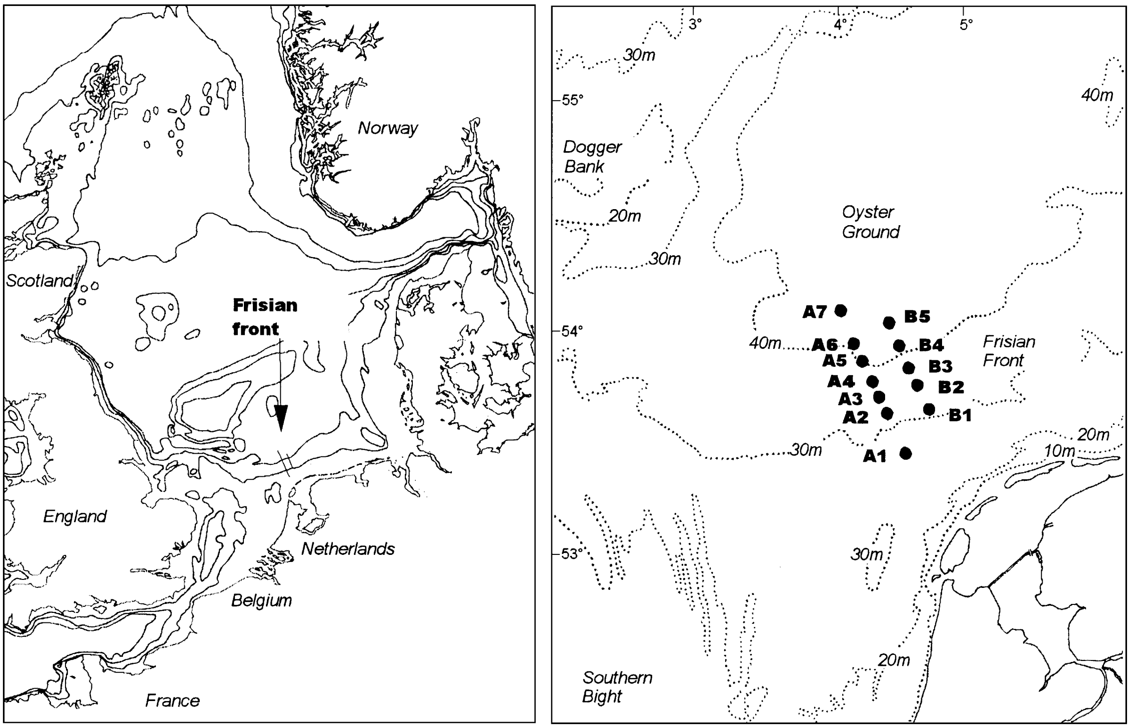

Fig. 1. Study area and position of transects A and B with indication of sampling sites.

Surface temperature and salinity (thermosalinograph *Sea-bird SBE21*) and in situ depth were registered. Additionally, but only in August, box-core (*Reineck*) samples of the sediment were taken at each site, the upper 2 cm being sampled for grain fraction analysis (particle-size analyser *Coulter LS 100*). Median grain size and percentage mud (< 63 μm, consisting of the organic and the inorganic fraction) were calculated for each site.

2.2. Data acquisition

After sorting, all organisms were identified to species level, if possible. For certain taxa, further classification was done based on the life history stage, such as the distinction between zoea, megalopa and postlarval stage for decapods. All animals were counted at species and stage levels. In case of uncertain identification, specimens were reported on a higher taxonomic level (indicated as "spp." and further called "species"). All brachyuran zoeae, most of them probably belonging to the genus *Liocarcinus*, were reported as Brachyura spp. (except for *Rhitropanopeus harrisii*). *Calanus helgolandicus* and *C. finmarchicus* were lumped together as *Calanus* spp. Cumaceans of the genus *Diastylis* (for the most part juvenile specimens) were grouped as *Diastylis* spp., mainly being a mixture of *Diastylis bradyi* and *D. laevis*.

Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans and from the tip of the lower jaw to the end of the notochord for fish larvae) and their biomass was derived from regressions relating standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60 °C for 5 d) and ash weight (650 °C for 2 h) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular length, an average biomass value was assigned per stage or per species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage. Both the regressions and the assigned biomass values were partly determined using animals from this study and partly from previous research (Beyst et al., 1999a; Dewicke et al., unpubl. data).

After identification of all species, non-hyperbenthic species were removed from the "catch-dataset", i.e. all animals that were caught by the Sorbe-hyperbenthic sledge and which were retained on a 1-mm sieve. Thus, juvenile and adult decapods and fish, polychaetes (except Tomopteridae), scyphozoans, echinoderms, fish eggs and all sedentary organisms were excluded. Additionally, the hyperbenthos was divided into its holo- and merohyperbenthic representatives. Holohyperbenthos is defined as animals that spend variable periods of their adult life in the hyperbenthic zone (Mees and Jones, 1997). It comprises a group of taxa which have small body sizes throughout their development (generally <20 mm), such as all peracarids, copepods, chaetognaths and hydromedusae. The merohyperbenthos consists of early life history stages, generally originating from larger animals, and is mainly represented by decapod larvae (<10 mm) and postlarval fish (<20 mm) (modified after Mees and Jones, 1997). The resulting species list of all hyperbenthos is presented in Appendix A. Density and biomass data were calculated as numbers of individuals and mg ADW per 100 m^2. Since the catch efficiency of sledges remains largely unknown (Mees and Jones, 1997), all densities and biomass values are considered to be minimum estimates.

2.3. Data analysis

Seasonal differences and spatial trends along the cross-frontal gradient were investigated. The two extra April samples north of the study area were omitted from the dataset, except for examining the total species composition. Holo- and merohyperbenthos were considered separately for describing species composition, density, biomass and diversity. Hill's diversity numbers N_0, N_1 and N_2 were calculated per sample (Hill, 1973). N_0 is equal to the number of species, N_1 is the inverted natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of Simpson's dominance index. Hurlbert's modification of Sanders' rarefaction curves (Hurlbert, 1971) was used to calculate diversity for standardised sample size, allowing comparison between different sites and seasons: $E(S_{100})$ determines the expected number of species present in a sample of 100 individuals. Species reported on a higher taxonomic level were treated as a single species if no other representative of the same taxonomic level was present or if they were distinctly different. Thus, the diversity estimates given here are minimum values.

Additionally, raw density data were fourth root transformed (Field et al., 1982; Legendre and Legendre, 1998) and ordination techniques were performed, using the program package CANOCO 4 (Ter Braak and Smilauer, 1998). First, an exploratory Detrended Correspondence Analysis (DCA) was performed for estimating the gradient lenght (g.l.) of species turnover in standard deviation units (s.d.), which gives an indication of the expected underlying model for species response curves (unimodal or linear) (Ter Braak and Prentice, 1988; Van Wijngaarden et al., 1995). Indirect techniques were further applied to detect any gradients in community structure. Principal Components Analysis (PCA) (linear method) was applied on the holohyperbenthos data (g.1. 2.370 s.d.) and Correspondence Analysis (CA) (unimodal method) was used for merohyperbenthos (g.1. 3.283 s.d.). Spearman rank's correlation coefficient (r_s) (Sokal and Rohlf, 1995) was calculated between the abundance of the most common species and some environmental variables.

3. Results

The Frisian front is considered to be the area between the -30 and -40 m isobaths, with geographical co-ordinates as described by Baars et al. (1991). The median grain size ranged from 99 to 296 μm. Along both transects, medium sandy sediments in the south were gradually displaced by very fine sands towards the north. Total mud fraction increased with depth from 0 to nearly 40% (see Section 3.2.2.). Surface temperature was on average 17.4 ± 0.12 °C in August and 5.4 ± 0.20 °C in April; mean values for surface salinity were 34.2 ± 0.08 psu and 34.2 ± 0.15 psu, respectively.

3.1. Seasonality

The number of species encountered in the hyperbenthic zone was slightly higher in August (84 species) than in April (70 species); 111 species were recorded in total (see Appendix A). The holohyperbenthos showed a strong overlap in species composition between both months, except for hydromedusae (Table 1). Amphipods were the most diverse group: 36 species were recorded in total. Other species mainly belonged to the Mysidacea (9 species), the Cumacea (6 species) and the Copepoda (6 species). The merohyperbenthos community was much poorer in species numbers in April (14 species) than in August (30 species). Nearly all decapod species caught in April (8 species) were also present in August (21 species). This was not so for fish larvae, of which only postlarval Ammodytidae were reported in both months.

In August, average total density and biomass for holohyperbenthos amounted to 1019 ± 303.4 ind 100 m^{-2} and 195 ± 55.3 mg ADW 100 m^{-2}, respectively. Hydromedusae (mainly *Mitrocomella* spp.) were numerically dominating (40%) (Fig. 2A). Subdominant taxa, i.e. amphipods, chaetognaths, mysids and copepods, each contributed for approximately 15% (or 150 ind 100 m^{-2}) of the total density. The gravimetrical composition of the total biomass was quite different, yet more than 62% was accounted for by the mysid fauna alone (mainly *Schistomysis ornata*). Density and biomass mean values for merohyperbenthos were much lower (152 ± 29.6 ind 100 m^{-2} and 139 ± 35.5 mg ADW 100 m^{-2}, respectively). The merohyperbenthos consisted of nearly 90% decapod larvae in August (mainly postlarval Processidae). Yet, its biomass was dominated by fish larvae (66%) with postlarval gobies as main representatives.

Average density and biomass of the holohyperbenthos were nearly one order of magnitude lower in April (132 ± 23.3 ind 100 m^{-2} and 30 ± 4.6 mg ADW 100 m^{-2}, respectively). Dominance among major taxonomic groups also changed (Fig. 2B). The dominant taxa in terms of density were the ctenophores (39%), the copepods (29%) and the mysids (15%). As in August, mysids dominated the total biomass (70%), but in April the greatest share was contributed by *Schistomysis spiritus*. Also for the merohyperbenthos, much lower density (19 ± 2.8 ind 100 m^{-2}) and biomass values (8 ± 1.4 mg ADW 100 m^{-2}) were reported in April. Fish larvae (mainly postlarvae of *Merlangius merlangus* and Ammodytidae) were the most important taxa, both for density and for biomass. Decapod abundance was low in April and most individuals were still in the zoea stage.

3.2. Community structure along the south-to-north gradient

3.2.1. Density

Total density for holohyperbenthos in August was clearly higher at the front sites and reached a maximum value of 3093 ind 100 m^{-2} at site A4 (Fig. 3). Several taxa contributed to this increased abundance at sites A3

Table 1
The number of species recorded per taxonomic group. A distinction is made between species numbers that were only reported in August, only reported in April and encountered in both months. The last column refers to the total number of species per taxonomic group

	Only in August	Only in April	In both months	In total		Only in August	Only in April	In both months	In total
Holohyperbenthos					Merohyperbenthos				
Hydromedusae	3	7	1	9	Polychaeta	0	1	0	1
Ctenophora	1	1	1	1	Cephalopoda	1	0	0	1
Polychaeta	1	0	0	1	Caridea	8	2	2	8
Chaetognatha	2	2	2	2	Thalassinidea	2	2	2	2
Copepoda	5	3	2	6	Anomura	5	3	2	6
Nebaliacea	1	1	1	1	Brachyura	6	1	1	6
Euphausiacea	1	1	1	1	Pisces	8	5	1	12
Mysidacea	8	7	6	9					
Cumacea	6	5	5	6					
Amphipoda	24	28	15	36					
Isopoda	2	0	0	2					
Pycnogonida	0	1	0	1					
Total	54	56	34	75	Total	30	14	8	36

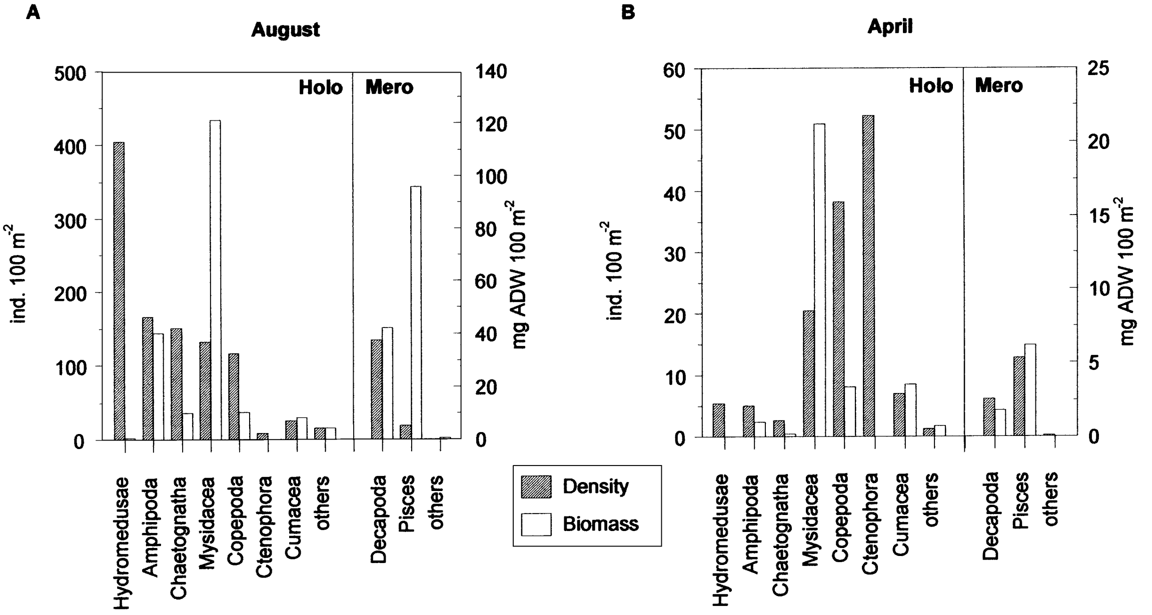

Fig. 2. Mean density (left axis) and biomass (right axis) for the major taxonomic groups in (A) August, (B) April; holohyperbenthos (holo), merohyperbenthos (mero).

and A4: the chaetognaths *Sagitta setosa* and *S. elegans* (max. 1013 ind 100 m^{-2} for all arrow worms together), the copepod *Calanus* spp. (max. 727 ind m^{-2}), the amphipod *Scopelocheirus hopei* (max. 508 ind 100 m^{-2}), and the mysid *Schistomysis ornata* (max. 238 ind 100 m^{-2}). Such a trend was absent for *Mitrocomella* spp. ; this hydromedusa reached its highest density at site A2. In April, species distribution patterns were more erratic. The density of *Pleurobrachia pileus* peaked at site A3 (max. 160 ind 100 m^{-2}), *Calanus* spp. (max. 57 ind 100 m^{-2}) showed an increase in numbers towards the north. *Schistomysis spiritus* was the most abundant mysid (max. 37 ind 100 m^{-2}), other mysid species being quite uniformly represented although in low numbers.

In August, the merohyperbenthos showed a rather weak increase in abundance towards sites A4 and A5; its density ranged from 5 to 285 ind 100 m^{-2} (Fig. 4). Highest densities were reached by postlarval Processidae, probably exclusively a mixture of *P. modica* and *P. nouveli* subsp. *holthuisi* (max. 160 ind 100 m^{-2} for all postlarval Processidae together), megalopae of *Liocarcinus holsatus* (max. 92 ind 100 m^{-2}) and postlarval Gobiidae (max. 62 ind 100 m^{-2}). In April, densities decreased slightly from south to north. Note the nearly uniform distribution of fish larvae.

3.2.2. Biomass

Biomass for all hyperbenthos obviously peaked at the Frisian front sites in August, with a maximum value of 541 mg ADW 100 m^{-2} at site A4 (Fig. 5). This figure illustrates the substantial contribution of the mysids (max. 212 mg ADW 100 m^{-2}) to the total biomass at the Frisian front area. Smaller organisms such as amphipods, copepods and chaetognaths attained biomass values that were often one order of magnitude higher at the Frisian front than in the surrounding waters (max. 179 mg ADW 100 m^{-2}, 68 mg ADW 100 m^{-2} and 67 mg ADW 100 m^{-2}, respectively). A different trend was found for merohyperbenthic taxa. The biomass for decapod larvae was only slightly higher at the front sites (max. 80 mg ADW 100 m^{-2}), highest biomass for fish larvae was reached at site A5 (330 mg ADW 100 m^{-2}). In April, the total biomass varied between 18 and 68 mg ADW 100 m^{-2} without any conspicuous changes along the transect (not figured).

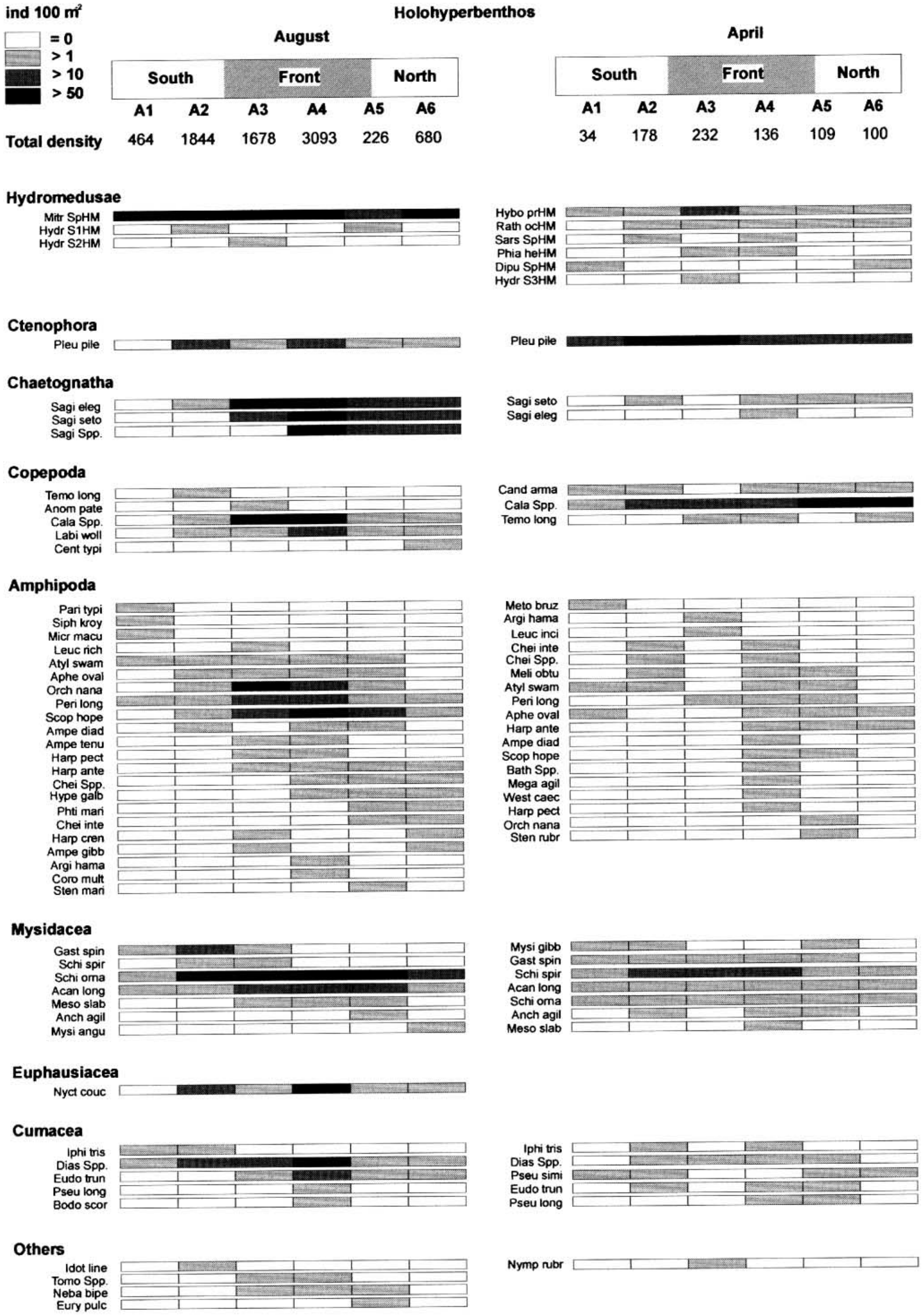

Fig. 3. Distribution patterns for all holohyperbenthic species along transect A in August (left) and April (right), representing gross density classes; total density is expressed as ind 100 m^{-2}. Abbreviations of species names are given in Appendix A.

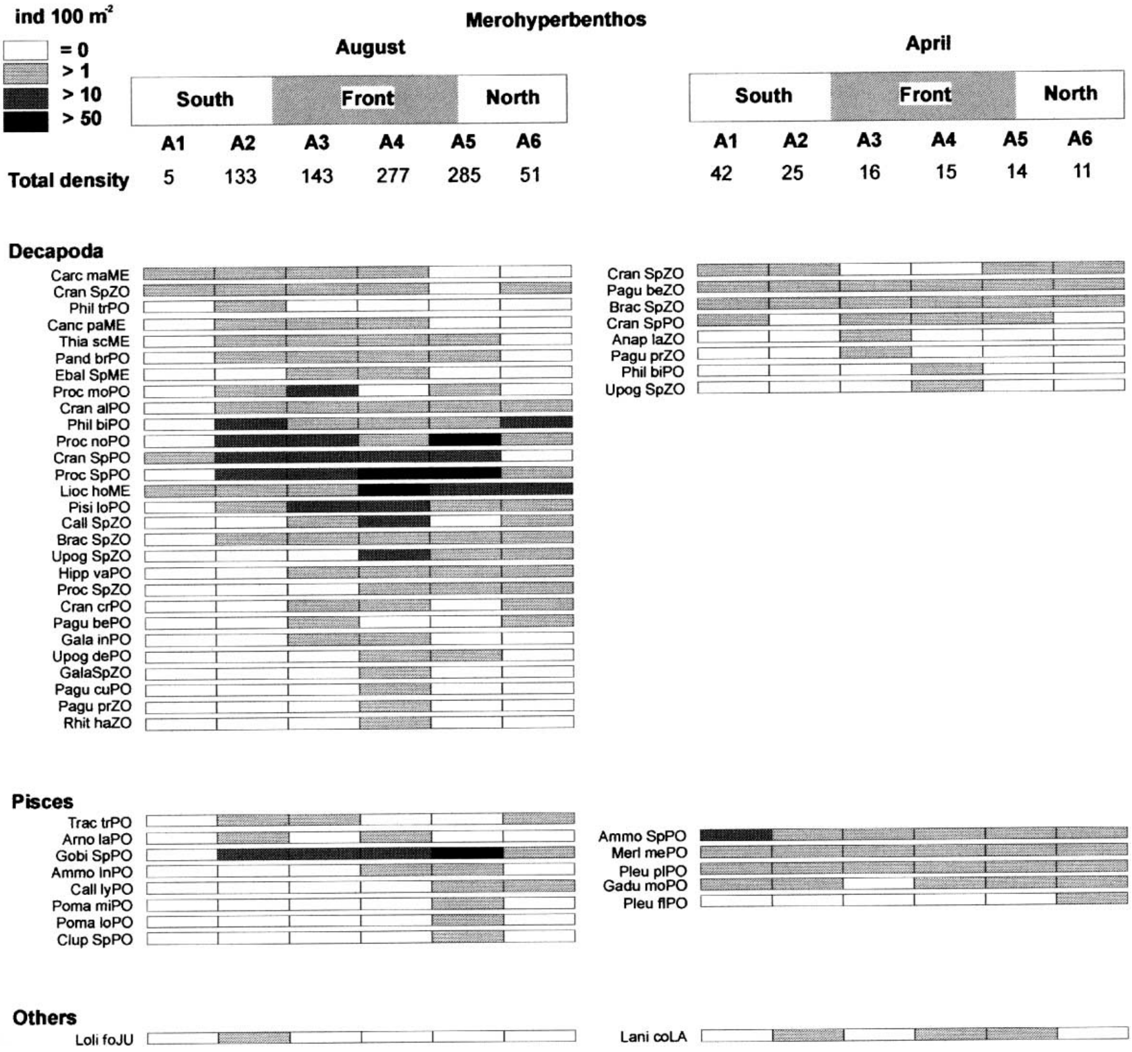

Fig. 4. Distribution patterns for all merohyperbenthic species along transect A in August (left) and April (right), representing gross density classes; total density is expressed as ind 100 m^{-2}. Abbreviations of species names are given in Appendix A.

3.2.3. Diversity

In August, diversity of the holohyperbenthos increased towards the front sites judging both from species richness (N_0) as from species diversity ($E(S_{100})$, N_1 and N_2) (Fig. 6). The diversity pattern along the transect in April was more erratic, but highest estimates for all indices were again noted at site A4. No seasonal differences in diversity existed in $E(S_{100})$, since the mean value for all sites (including the B transect) was 10.6 ± 1.28 in August and 11.7 ± 1.03 in April.

Also for merohyperbenthos, species richness (N_0) in August was highest at the front sites (Fig. 6). The distribution of $E(S_{100})$ was rather uniform along the transect and both N_1 and N_2 peaked at site A3. The diversity indices showed little variation in April. As in the holohyperbenthos, the average values of $E(S_{100})$ (including the B transect) were similar in August (12.7 ± 1.07) and April (11.6 ± 0.29).

3.2.4. Ordination

Eigenvalues for the PCA analysis performed on the holohyperbenthos density data were 0.489 for the first axis and 0.150 for the second axis. They display together 63.9% of the species variance (Fig. 7). Sea-

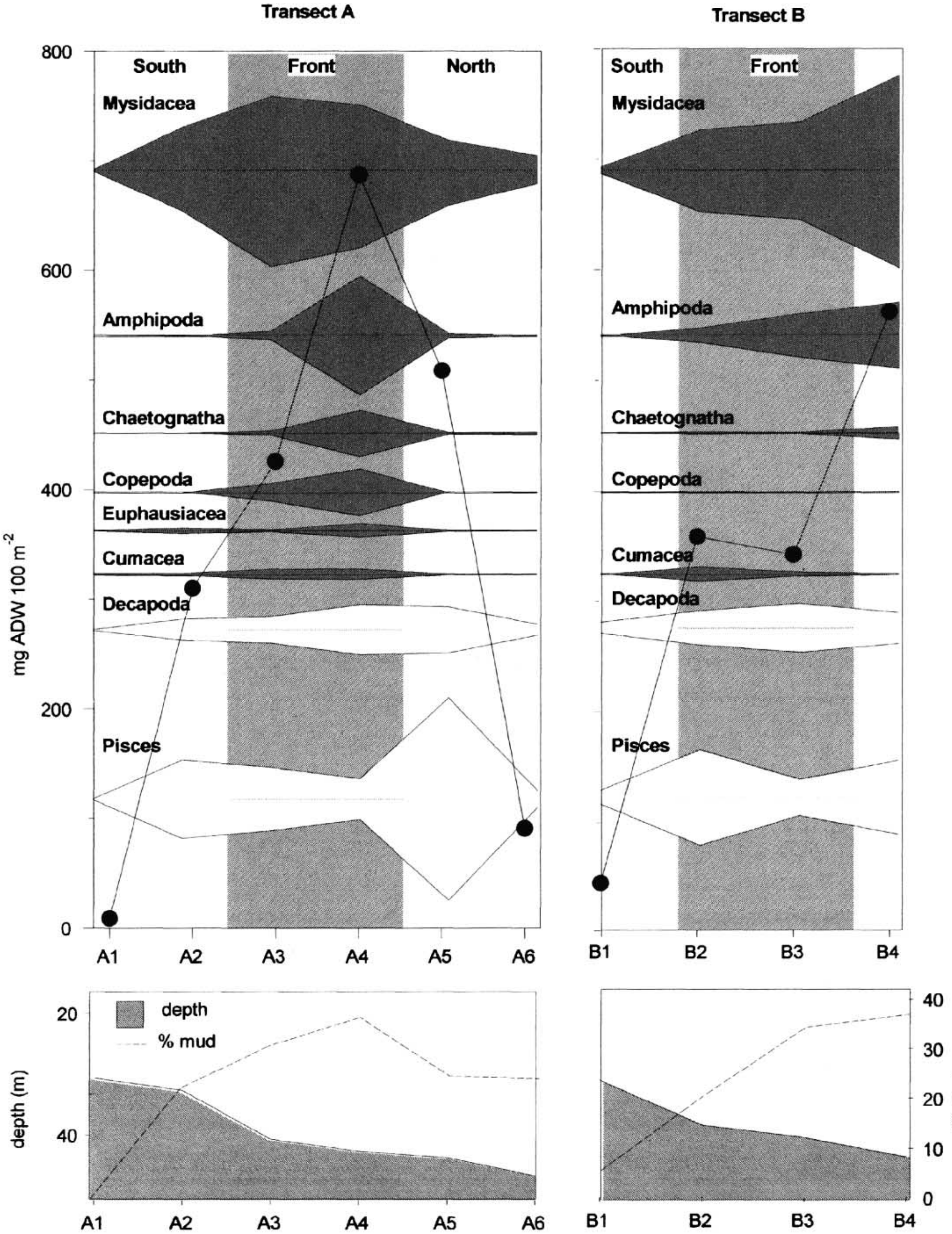

Fig. 5. The August biomass distribution along transects A (left) and B (right) for the total hyperbenthos and for the main taxonomic groups, together accounting for >97% of the total biomass. Total biomass corresponds with the y-axis and is represented by dots connected with a full line. Biomass per taxonomic group is shown as kite diagrams; the same scale was used for all taxa; for absolute values see the text. The shaded area represents the geographical position of the Frisian front between the −30 and −40 m isobaths. In situ depth (left axis) and % mud (<63 μm) (right axis) along both transects are also figured (bottom).

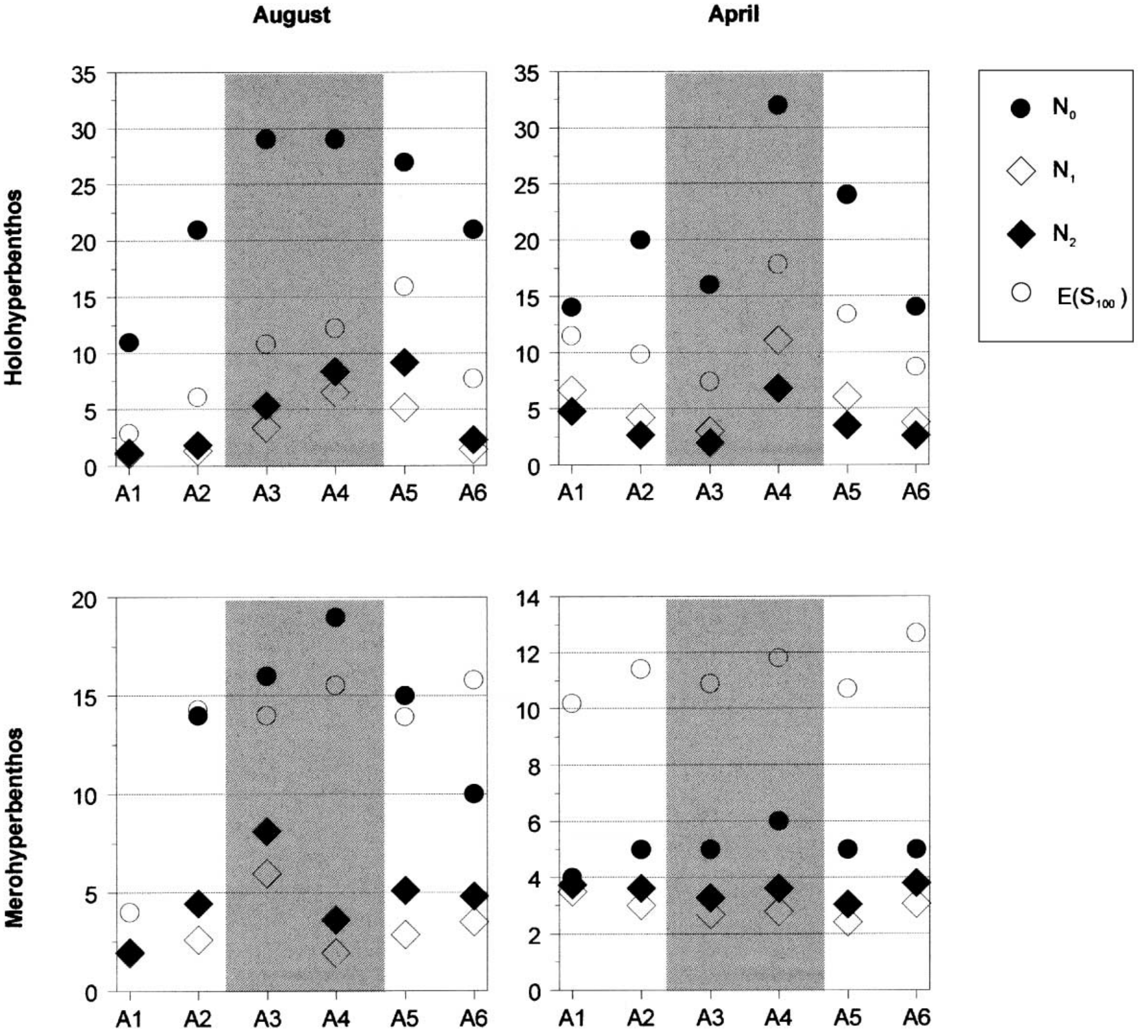

Fig. 6. Hill's diversity numbers N_0, N_1 and N_2 and the expected numbers of species $E(S_{100})$ along transect A, for holo- (top) and merohyperbenthos (bottom), separately presented for August (left) and April (right). The shaded area represents the geographical position of the Frisian front between the − 30 and − 40 m isobaths.

sonal patterns appear along the first axis since the April samples (left) are separated from the August samples (right). However, the August samples collected south of the Frisian front (A1 and A2) have a score on the first axis highly similar to that of the April samples.

Axis one (eigenvalue 0.719) and axis two (eigenvalue 0.183) of the CA analysis applied to merohyperbenthic densities together represent 49.3% of the species variance (Fig. 7). Judging from the much higher eigenvalue of the first axis than of the other axes, the seasonal separation shown in Fig. 7 is strong. Yet, a distinct and meaningful pattern did appear along the second axis. The August samples are spread according to their geographical position from south to north. No such pattern was found for April since all samples are lumped together.

4. Discussion

4.1. Seasonality

In April the hyperbenthos differed structurally from that of August. Species composition was differ-

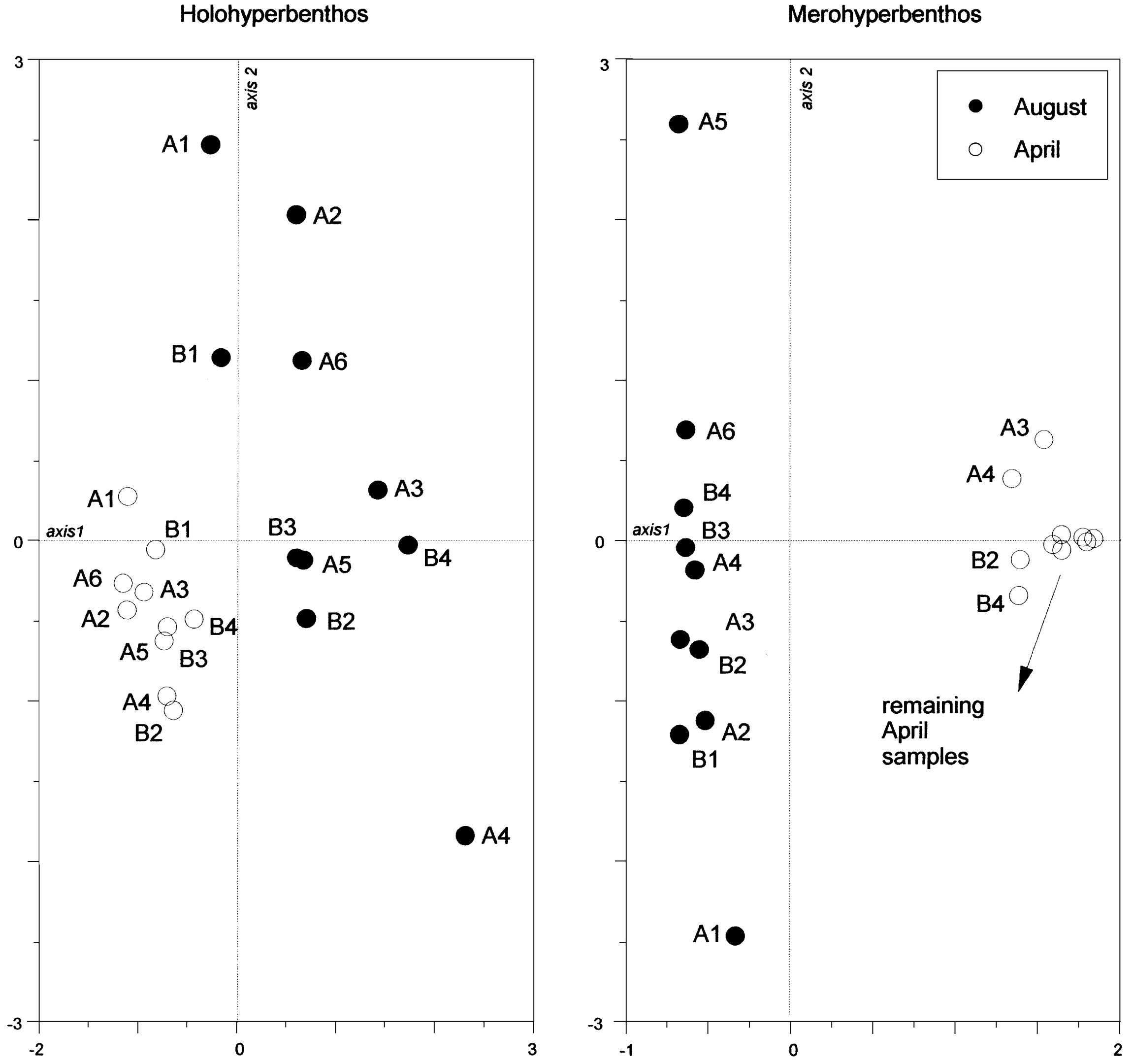

Fig. 7. Ordination diagrams resulting from the multivariate analyses performed on the holohyperbenthic (left) and merohyperbenthic (right) species densities. Eigenvalues for the PCA analysis on holohyperbenthos are 0.489, 0.150 and 0.183 for the first to third axis, respectively. Axes one and two together represent 63.9% of the species variance. CA analysis on merohyperbenthos has eigenvalues of 0.719 (axis one), 0.183 (axis two) and 0.173 (axis three). The diagram formed by the first and second axis represents 49.3% of the species variance.

ent, densities and biomasses were much lower and south-north related patterns were not prominently present. Note that the two surveys were not conducted during the same year: the August samples were taken in 1994 and the April ones in 1996. The hyperbenthos is often characterised by a strong seasonality in community structure, particularly in shallow waters (Sorbe, 1989; Mees and Jones, 1997; Cunha et al., 1999; Vallet and Dauvin, 1999; Beyst et al., 2001; Dewicke et al., unpubl. ms). The change in species composition was mainly due to the seasonal occurrence of planktonic groups such as hydromedusae and fish larvae (Table 1).

Temporal density fluctuations of mysids can be real, i.e. through recruitment, or apparent, i.e. caused by their migration and aggregation behaviour (Mauchline, 1971). *Schistomysis ornata* was the most common mysid in August and represented 59% of the total biomass. In April, this fraction was reduced to 14% and dominance was taken over by *S. spiritus* (52%). *S. ornata* is most frequently encountered in offshore and deeper waters. It is abundant on the Dogger Bank (Dewicke et al., unpubl. ms), in the English Channel (Zouhiri et al., 1998; Dauvin et al., 2000), in the Bay of Biscay (Sorbe, 1989) and off Portugal (Cunha et al., 1997). The most frequently caught mysid in April, *S. spiritus*, is typically common in shallow coastal areas (Sorbe, 1989; Mees et al., 1993a; Zouhiri et al., 1998; Dauvin et al., 2000; Dewicke et al., unpubl. ms), estuaries (Mees et al., 1993b) and sandy beaches (Beyst et al., 2001; Beyst and Mees, unpubl. ms). Both species were supposed to perform seasonal horizontal migrations (Mauchline, 1967, 1970). In the Bay of Biscay, Sorbe (1989) reported highest densities for *S. ornata* at 91 m depth during April and encountered it at a deeper site (126 m depth) only during summer. San Vicente and Sorbe (1995) suggested reverse migration behaviour fo *S. spiritus* in the same area, from a 30-m-deep site towards shallower coastal grounds during summer.

The general composition of the mysid fauna seems to be transitional between the more southern shallow Belgian coast (e.g. dominance of *Schistomysis kervillei* and *S. spiritus*) and the offshore Dogger Bank (e.g. dominance of *S. ornata* and *Erythrops elegans*) situated north-west to the study area (Dewicke et al., unpubl. mss). All mysids caught during this study were also reported from the English Channel by Zouhiri et al. (1998), who investigated the shallow coastal waters and offshore regions down to 75 m depth.

Seasonality of amphipods and cumaceans in the hyperbenthic water layer is even more difficult to assess. These often patchily distributed taxa can be dependent on conditions both in the water column and the bottom, where they are sometimes buried (Kaardvedt, 1986).

According to Lindley (1987, 1998), seasonal occurrence of decapod larvae is much more related to temperature than are seasonal cycles of holoplankton (e.g. copepods, chaetognaths). Data from the continuous plankton records in the North Sea showed an increase in species numbers of decapod larvae through the year from January (no larvae) to August (30 species) (Lindley, 1998). Average temperature recorded in April at the Frisian front was only 5.4 °C, which is probably still too low for most decapod species to start reproduction and subsequent larval recruitment. This therefore most likely explains their low densities.

Larval Processidae were the most common decapods encountered in August. This taxon is less common in the nearby southern Dutch and Belgian coastal waters, where *Crangon crangon* larvae are dominant (Hamerlynck and Mees, 1991; Dewicke, unpubl. ms). Larvae of *Philocheras bispinosus* are dominant around the Dogger Bank at that time of the year (Dewicke et al., unpubl. ms).

Fish larvae were markedly more abundant at the Frisian front during summer than on the Belgian coast and the Dogger Bank; postlarval gobies were the dominant fish in these three areas (Dewicke et al., unpubl. mss). Temporal distribution of fish larvae is often sharply restricted to a certain period of the year, which is species-specific and mostly very short (Beyst et al.,1999b; Beyst et al., 2001; Dewicke et al., unpubl. ms). This is illustrated in this study by the big difference in species composition for fish larvae between August and April.

Thus, it is postulated that the observed seasonal pattern results from a complex variety in species-specific ecology and life history traits of the hyperbenthic fauna, in addition to density fluctuations caused by the production of offspring.

4.2. August

4.2.1. Holohyperbenthos

The summer holohyperbenthos showed drastic changes in community structure in the Frisian front area. Between the − 30 and − 40 m isobaths, several species attained maximum densities that were often one order of magnitude higher than those recorded for surrounding waters. Increased abundances were mainly caused by holohyperbenthic species as concluded from their distribution along the transect; only the hydromedusae of the genus *Mitrocomella* showed a reverse pattern (Fig. 3). The Frisian front thus seems to attract a variety of species that most probably take advantage of the increased food supply. The bottom enrichment of the Frisian front that was first described by Creutzberg (1985) was still a fact in August 1994, as confirmed by Boon and Duineveld (1996), Dauwe and Middelburg

(1998) and Dauwe et al. (1998), who conducted field campaigns in this month. High sedimentation of particulate organic matter occurred and the incorporation of chlorophyll-a into the sediment was >10 times higher than at the Broad Forteens (located south of the Frisian front) (Dauwe et al.,1998). Macrofaunal biomass was also reported to be 7 times higher (Dauwe and Middelburg, 1998).

The abundance of several species was significantly correlated with the percentage of mud in the sediment, as indicated for the mysid *Schistomysis ornata* ($r_s = 0.85$, $p < 0.005$). As mysids are good swimmers and omnivores (Mauchline, 1980), it is suggested that *S. ornata* actively migrates to the food-enriched area. This species also reached highest abundances at the more muddy sites of the Dogger Bank (Dewicke et al., unpubl. ms). Likewise, the high densities reported for the lysianassid amphipods *Scopelocheirus hopei* ($r_s = 0.84$, $p < 0.005$, for density vs. % mud) and *Orchomenella nana* ($r_s = 0.68$, $p < 0.05$, for density vs. % mud) — typical scavengers and less dependent on burrowing into the sediment (Vallet and Dauvin, 1998) — may be linked with their motile behaviour. Mysids and amphipods constituted the major part (83%) of the total biomass at the Frisian front. Most mysids utilise organic detritus to a considerable extent (Kost and Knight, 1975; Jansen, 1985; Fockedey and Mees, 1999) and may therefore add to the remineralisation of refractory organic matter. Since they often contribute substantially to the diet of juvenile demersal fish (Mees and Jones, 1997), their presence may be significant in sustaining the rich fauna at the Frisian front system.

The density of the planktonic taxa *Sagitta* spp. and *Calanus* spp. was also significantly correlated with the mud content of the bottom ($r_s = 0.85$, $p < 0.005$ and $r_s = 0.78$, $p < 0.01$, respectively). Both taxa showed a striking increase in density at the front sites: their density was respectively 22 and 85 times higher than at the surrounding sites. Despite their planktonic behaviour, copepods can maintain themselves within one area by tide-related vertical migration (Wooldridge and Erasmus, 1980; Kimmerer and McKinnon, 1987; Hough and Nayler, 1991). They may respond to the elevated summer primary production at the Frisian front as previously reported by Kuipers et al. (1991) and/or to the enhanced carbon flux. Chaetognaths are strictly carnivorous, mainly feeding on copepods (Stuart and Verheye, 1991; Alvarez-Cadena, 1993; Frid et al., 1994; Baier and Purcell, 1997; Froneman et al., 1998). Hourly sampling data revealed that their vertical migration closely follows that of large calanoid copepods (Stuart and Verheye, 1991).

A response of the hyperbenthic fauna to increased inputs of organic matter to the bottom environment has already been noted by several authors (e.g. Sorbe, 1984; Buhl-Jensen and Fosså, 1991; Dauvin et al., 1994; Mees and Jones, 1997), but the particular relation with primary production and/or degraded organic matter often remains unclear. This is mainly due to a lack of knowledge on the trophic structure of the fauna thriving in the hyperbenthic zone. Chevrier et al. (1991) found highest densities for hyperbenthic amphipods in areas of high primary production, but scavengers and predators had a similar success in less productive areas. According to Vallet and Dauvin (1998), peracarids and decapods occurring in the hyperbenthos are relatively independent of primary production, reaching highest biomasses in eutrophic conditions. Hamerlynck and Mees (1991) also noted highest densities in sheltered areas where organic matter may settle. Obviously, a high swimming ability enables hyperbentic animals to forage more efficiently (Mees and Jones, 1997; Vallet and Dauvin, 1998) and therefore to respond more quickly to available food sources than sedentary benthic animals. A rapid reaction to the extensive food supply at the Frisian front was also suggested for *Amphiura filiformis* (Ophiuroidea), which is a suspension feeder and, to a lesser extent, a deposit feeder (Duineveld and Van Noort, 1986).

4.2.2. Merohyperbenthos

The merohyperbenthos showed a smoother density increase along the transects with highest values at the northern part of the Frisian front. This fauna has a more planktonic way of life and is thus more vulnerable to the prevailing currents. The gradually changing community structure along the south-to-north gradient, judging from the ordination analysis, was conspicuous (Fig. 7). This indicates that the Frisian front harbours a transitional community between the two communities established in late summer in the environmentally different Southern Bight (south of the Frisian front) on the one hand and the Oyster Ground (north of the area) on the other. A similar trend was observed for macrobenthic communities in the study area. Holtmann et al. (1996) identified three macrobenthic communities: a Frisian front community, an Oyster Ground community and a Southern Bight community, with the Frisian front community characterised by highest densities and biomasses. Benthic species even showed a marked zonation from south to north corresponding with a succession in feeding types (Creutzberg et al., 1984). A change in species composition was also found for the epibenthos (Baars et al., 1991). Less evidence is available for the pelagic environment. Only Boon et al. (1998) mentioned a shift in algal families south and north of the Frisian front.

Additionally, hydrodynamic processes related to tidal fronts — a summer phenomenon occurring in the study area (Simpson et al., 1978; Bowers and Simpson, 1987; Van Aken et al., 1987; Bo Pederson, 1994; Tett and Walne, 1995) — may affect the distribution of planktonic organisms. In this view, two different water masses, each characterised by a distinct merohyperbenthic community, possibly meet at the approximate location of the Frisian front. Such a community transition has been reported for the tidal front off the east coast of England by Lindley and Williams (1994). These authors found a close relation between the position of the tidal front and the geographical division between plankton assemblages. However, data from the present study are too few to assess this complex phenomenon. Yet, such fronts are known to act as community boundaries (Longhurst, 1998) and are thought to be biological 'hot spots', with a significant change in productivity, structure and diversity at the higher trophic levels in the pelagic food web (Nielsen and Munk, 1998).

4.3. Early spring situation

The temporary disappearance of the summer enrichment discussed above can be explained in several ways, which might even act in concert. First, the low April temperature suggests that the benthic area will still be low in production and biological activity. Food supply for the holohyperbenthos is therefore believed to be much more pronounced during summer. The absence of a south-north related structure for the merohyperbenthos is most probably due to its poor development early in the year. Another possible explanation appears from the extra sites sampled in April (sites A7 and B5 north of the study area; Fig. 1). The holohyperbenthos reached a density peak of more than 600 ind 100 m^{-2} at site A7, and a less distinct density peak of 230 ind 100 m^{-2} at site B5, while more southern densities were on average 75 ± 10.9 ind 100 m^{-2}. The abundances at these northern sites were in the same order as the ones reported in August for the waters surrounding the Frisian front. Enhanced abundance was not due to a sudden increase in one or a few species, but was an overall feature. The most abundant species at site A7 were *Calanus* spp. (242 ind 100 m^{-2}), *Schistomysis ornata* (99 ind 100 m^{-2}) and *Diastylis* spp. (84 ind 100 m^{-2}), which were all frequently caught during the August campaign. Apart from the seasonal migration patterns as discussed for S. *ornata* and S. *spiritus*, one might suppose that the enrichment in the hyperbenthic layer has temporarily shifted to a more northern position. The motile hyperbenthos may respond quickly to local variations in food supply either by active migration to more favourable feeding areas (i.e. where suspended matter is deposited), or by being transported there with the prevailing currents. In fact, sedimentation processes in the area have a seasonal character as mentioned by Van Raaphorst et al. (1998). Suspended matter originates from the turbidity plume from south-east England and is transported by the residual current in a north-easterly direction, settling in the calmer waters of the Frisian front during spring and summer. Resuspension processes occur during autumn and winter and the material is ultimately deposited in the Skagerrak and Norwegian Channel area (Eisma and Kalf, 1987; Van Raaphorst et al. 1998). And finally — although the sampling interval of this study was less than two years — the possibility of a long-term decline cannot be excluded such as recorded for the macrobenthos community of the area during the nineties (Friese Front 1999).

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Appendix A

Species list of all hyperbenthos caught with indication of holo- (H) and merohyperbenthos (M), and with abbreviation of species names; hydromedusa (HM), juvenile (JU), larva (LA), megalopa (ME), postlarva (PO), zoea (ZO).

Species	H/M	Abbreviation	Species	H/M	Abbreviation
Phylum Cnidaria			**Superordo Peracarida**		
Subphylum Medusozoa			**Ordo Mysidacea**		
Classis Hydroidomedusae			**Subordo Mysida**		
Rathkea octopunctata HM	H	Rath ocHM	*Anchialina agilis*	H	Anch agil
Dipurena spp. HM	H	Dipu SpHM	*Gastrosaccus spinifer*	H	Gast spin
Sarsia tubulosa HM	H	Sars tuHM	*Mysidopsis angusta*	H	Mysi angu
Hybocodon prolifer HM	H	Hybo prHM	*Mysidopsis gibbosa*	H	Mysi gibb
Mitrocomella spp. HM	H	Mitr SpHM	*Acanthomysis longicomis*	H	Acan long
Phialidium hemisphaericum HM	H	Phia heHM	*Mesopodopsis slabberi*	H	Meso slab
Hydroidomedusae species 1 HM	H	Hydr S1HM	*Schistomysis ornata*	H	Schi orna
Hydroidomedusae species 2 HM	H	Hydr S2HM	*Schistomysis spiritus*	H	Schi spir
Hydroidomedusae species 3 HM	H	Hydr S3HM	*Heteromysis microps*	H	Hete micr
			Ordo Cumacea		
Phylum Ctenophora			*Bodotria scorpioides*	H	Bodo scor
Pleurobrachia pileus	H	Pleu pile	*Iphinoe trispinosa*	H	Iphi tris
			Eudorella truncatulla	H	Eudo trun
Phylum Annelida			*Pseudocuma longicomis*	H	Pseu long
Classis Polychaeta			*Pseudocuma similis*	H	Pseu simi
Tomopteridae spp.	H	Tomo spp.	*Diastylis* spp.	H	Dias Spp.
Lanice conchilega LA	M	Lani coLA	**Ordo Amphipoda**		
			Subordo Caprellidea		
Phylum Chaetognatha			*Pariambus typicus*	H	Pari typi
Sagitta elegans	H	Sagi eleg	*Phtisica marina*	H	Phti mari
Sagitta setosa	H	Sagi seto	**Subordo Gammaridea**		
Sagitta spp.	H	Sagi Spp.	*Ampelisca diadema*	H	Ampe diad
			Ampelisca gibba	H	Ampe gibb
Phylum Mollusca			*Ampelisca tenuicornis*	H	Ampe tenu
Classis Cephalopoda			Aoridae spp.	H	Aori Spp.
Loligo forbesii JU	M	Loli foJU	*Argissa hamatipes*	H	Argi hama
			Atylus swammerdami	H	Atyl swam
Phylum Arthropoda			*Apherusa ovalipes*	H	Aphe oval
Subphylum Crustacea			*Corophium multisetosum*	H	Coro mult
Classis Copepoda			*Siphonoecetes kroyeranus*	H	Siph kroy
Ordo Calanoida			*Microprotopus maculatus*	H	Micr macu

Candacia armata	H	Cand arma
Centropages typicus	H	Cent typi
Anomalocera patersoni	H	Anom pate
Labidocera wollastoni	H	Labi woll
Temora longicomis	H	Temo long
Calanus spp.	H	Cala Spp.
Classis Malacostraca		
Subclassis Phyllocarida		
Ordo Nebaliacea		
Nebalia bipes	H	Neba bipe
Subclassis Eumalacostraca		
Superordo Eucarida		
Ordo Euphausiacea		
Nyctiphanes couchi	H	Nyct couc
Ordo Decapoda		
Subordo Pleocyemata		
Infraordo Caridea		
Hippolyte varians PO	M	Hipp vaPO
Processa modica PO	M	Proc moPO
Processa nouveli subsp. *holthuisi* PO	M	Proc noPO
Processa spp. PO	M	Proc SpPO
Processa spp. ZO	M	Proc SpZO
Pandalina brevirostris PO	M	Pand brPO
Crangon allmanni PO	M	Cran alPO
Crangon crangon PO	M	Cran crPO
Crangon spp. PO	M	Cran SpPO
Philocheras bispinosus PO	M	Phil biPO
Philocheras trispinosus PO	M	Phil trPO
Crangonidae spp. ZO	M	Cran SpZO
Infraordo Thalassinidea		
Callianassa tyrrhena PO	M	Call tyPO
Callianassa spp. ZO	M	Call SpZO
Upogebia deltaura PO	M	Upog dePO
Upogebia spp. ZO	M	Upog SpZO
Infraordo Anomura		
Galathea intermedia PO	M	Gala inPO
Galathea spp. ZO	M	Gala SpZO
Pisidia longicomis PO	M	Pisi loPO
Anapagurus laevis PO	M	Anap laZO
Pagurus bernhardus PO	M	Pagu bePO
Pagurus bernhardus ZO	M	Pagu beZO
Pagurus cuanensis PO	M	Pagu cuPO
Pagurus prideauxi ZO	M	Pagu prZO
Paguridae spp. PO	M	Pagu SpPO
Infraordo Brachyura		
Thia scutellata ME	M	Thia scME
Cancer pagurus ME	M	Canc paME
Photis longicaudata	H	Phot long
Leucothoe incisa	H	Leuc inci
Leucothoe lilljeborgi	H	Leuc lill
Leucothoe procera	H	Leuc proc
Orchomenella nana	H	Orch nana
Scopelocheirus hopei	H	Scop hope
Tryphosites longipes	H	Tryp long
Megaluropus agilis	H	Mega agil
Cheirocratus intermedius	H	Chei inte
Cheirocratus spp.	H	Chei Spp.
Melita obtusata	H	Meli obtu
Monoculodes carinatus	H	Mono cari
Perioculodes longimanus	H	Peri long
Pontocrates altamarinus	H	Pont alta
Westwoodilla caecula	H	West caec
Harpinia antennaria	H	Harp ante
Harpinia crenulata	H	Harp cren
Harpinia pectinata	H	Harp pect
Dyopedos monacantha	H	Dyop mona
Bathyporeia spp.	H	Bath Spp.
Metopa bruzelii	H	Meto bruz
Stenothoe marina	H	Sten mari
Stenula rubrovittata	H	Sten rubr
Urothoe elegans	H	Urot eleg
Subordo Hyperiidea		
Hyperia galba	H	Hype galb
Ordo Isopoda		
Subordo Flabellifera		
Eurydice pulchra	H	Eury pulc
Subordo Valvifera		
Idotea linearis	H	Idot line
Subphylum Chelicerata		
Classis Pycnogonida		
Nymphon rubrum	H	Nymp rubr
Phylum Chordata		
Subphylum Vertebrata		
Classis Actinopterygii		
Clupeidae spp. PO	M	Clup SpPO
Gadus morhua PO	M	Gadu moPO
Merlangius merlangus PO	M	Merl mePO
Trachurus trachurus PO	M	Trac trPO
Ammodytidae spp. PO	M	Ammo SpPO
Callionymus lyra PO	M	Call lyPO
Pomatoschistus lozanoi PO	M	Poma loPO
Pomatoschistus microps PO	M	Poma miPO
Gobiidae spp. PO	M	Gobi SpPO

Liocarcinus holsatus ME	M	Lioc hoME	*Amoglossus latema* PO	M	Arno laPO
Carcinus maenas ME	M	Carc maME	*Limanda limanda* PO	M	Lima liPO
Rhithropanopeus harrisii ZO	M	Rhit haZO	*Pleuronectes platessa* PO	M	Pleu plPO
Ebalia spp. ME	M	Ebal SpME	*Pleuronectes flesus* PO	M	Pleu flPO
Brachyura spp. ZO					

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