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Relationship between structural and functional aspects of microbial and macrofaunal communities in different areas of the North Sea

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ABSTRACT: Spatial similarities of structural and functional (trophic) aspects of microbial and macrofaunal community patterns were studied in relation to sediment parameters in the German Bight, the Oyster Ground, the Dogger Bank, eastern North Sea, the Skagerrak, and northern Kattegat in May and September 1999 and 2000. Spatial patterns of microbial and macrofaunal communities were congruent. Differences in spatial distribution of communities were caused by utilisation of the different food sources available in the different areas. In the German Bight, the communities were correlated significantly with chlorophyll *a* (chl *a*) concentrations in the sediments, an indicator of fresh nitrogen-rich organic matter. In contrast, communities in the Skagerrak and Kattegat were correlated with total organic carbon (TOC) and mud concentrations, indicating the presence of more refractory organic matter for the microbial and macrofaunal organisms. For the communities in the Oyster Ground, the eastern North Sea and the Dogger Bank, no such significant correlations were found. The community in the Oyster Ground was characterised by the ophiurid *Amphiura filiformis* foraging on relatively refractory macrofloculate organic matter from the benthic boundary layer. Preferred substrates of the microbial communities in this area were macrofaunal excretion products. The Skagerrak and Kattegat stations were also characterised by the *A. filiformis* community, indicating lower food supply than in the German Bight. Although microbial community patterns were similar to those in the German Bight, lower chl *a* concentrations also suggested the presence of relatively refractory organic matter. Reflected by the dominance of sand-licking species, macrofaunal communities at the Dogger Bank and in parts of the eastern North Sea seem to rely on benthic primary production. Here, microbial communities were adapted to hydrodynamically induced stress, sediment disturbance and limited food supply. Our results revealed that in areas with high food supply such as the German Bight, no competition for food between microorganisms and macrofauna occurs. But in areas with less or limited food supply from the water column, macrofauna provides the microorganisms with organic matter or microorganisms utilise macrofaunal excretion products and are physiologically adapted to the exposed environment.

KEY WORDS: Microorganisms · Macrofauna · Community structure · Trophic relationships · Food availability · Phytopigments · North Sea

INTRODUCTION

Macrofaunal communities in the North Sea have been intensively studied since 1920 (see review by Kröncke & Bergfeld 2003). The various macrofaunal communities occurring in different areas of the North Sea have been described in numerous publications (e.g. Salzwedel et al. 1985, Kröncke 1992, Künitzer et al. 1992, E. Rachor & P. Nehmer unpubl. data). In contrast, very little information is available on bacteria and microorganisms living in the North Sea benthic system (Billen et al. 1990). Van Duyl et al. (1993) and van Duyl

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& Kop (1994) studied benthic bacterial biomass and production in sediments of different areas of the North Sea and found that both parameters were significantly related to pigment concentrations in sediments. Temperature and phytopigment concentration accounted for major percentages of seasonal and spatial variations in bacterial production. Upton et al. (1993) and Osinga et al. (1996) compared the benthic mineralisation rates of different sediment types in different areas of the southern North Sea. They found differences in oxygen uptake, sulphate reduction and bacterial production due to variability in carbon supply and hydrodynamics. Upton et al. (1993) stated that, on average, benthic mineralisation was equivalent to 17–45% of the total net primary production.

The relationship between structural and trophic aspects of microbial and macrofaunal communities has mainly been studied experimentally (Aller 1982, 1988, Alongi & Hanson 1985, Alongi & Tenore 1985, Sundbäck et al. 1990), *in situ* in the intertidal (Kristensen et al. 1985, Andersen & Kristensen 1988, 1991, 1992, Kristensen 1988) or in the deep-sea (Rowe & Deming 1985, Rowe et al. 1991, Rowe & Pariente 1992, Rowe 1996, Kröncke et al. 2000), but not in the offshore North Sea. The experimental and intertidal studies revealed that bioturbation by macrofauna stimulates both the aerobic and anaerobic decomposition processes, causing benthic metabolism to increase 1.5 to 3 times in the presence of burrowing macrofauna. Regarding competition for food, Kristensen (2000) showed that the polychaete *Nereis* (*Hediste*) *diversicolor* competes with microorganisms for high-quality food and microbial activity generally decreases in the presence of the polychaete.

To obtain more insight into the relationship between microbial and macrofaunal communities, we studied microorganisms and macrofauna from the same box cores during 4 cruises in 1999 and 2000 in different areas of the North Sea (German Bight, the eastern North Sea, Dogger Bank, Skagerrak and northern Kattegat) (Stoeck & Kröncke 2001, Stoeck et al. 2002, 2003, present study). These areas were chosen because they are known to be different in terms of primary production, sedimentation rates and hydrodynamics (Eisma & Kalf 1987, Kröncke & Knust 1995, de Haas & van Weering 1997, Puls et al. 1997).

The results on microbial communities of our interdisciplinary study have already been published (Stoeck & Kröncke 2001, 2002, 2003). In our 2001 study we emphasized the influence of particle mixing on verticle profiles of chl *a* and bacterial biomass. Our 2002 study focused on phospholid fatty acid profiles at depositional and non-depositional sites, and our 2003 study examined functional profiles of microbial communities in relation to organic substrates.

In this paper, we compare macrofaunal and microbial data sets, with special emphasis on the following: (1) Is microbial and macrofaunal spatial distribution congruent? (2) What role does the food availability play on microbial and macrofaunal communities? (3) Do microbial and macrofaunal communities compete for food?

MATERIALS AND METHODS

Study sites. The study sites in the German Bight (Stns TS 2 to 5), the Oyster Ground (Stns TS 6 to 8) and the Dogger Bank area (Stns TS9, DB9, DB11 and DB12) were sampled in May and September 1999; those in the eastern North Sea (Stns EN1 to EN5), the Skagerrak (Stn SK) and northern Kattegat (Stn KT) in May and September 2000 (Table 1, Fig. 1).

Sampling. Samples were taken during cruises with RV 'Senckenberg' using a 0.1 m^2 USNEL box corer equipped with a closing lid to prevent any disturbance of the sediment surface. Three cores per station were sub-sampled for macrofauna, microbes and sediment analyses.

For microorganisms and sediment analyses 5 PVC tubes (40 cm long, 5 cm inner diameter) were taken per core. All cores were sliced at 2, 5 and 10 cm. Only data

Table 1. Coordinates, depth, bottom-water temperature and salinity at study sites (Fig. 1) in May and September 1999 and 2000

Study site	Latitude (N)	Longitude (E)	Depth (m)	Temp (°C) May/Sep	Salinity May/Sep
German Bight					
TS2	54° 02′	008° 02′	25	11.6/18.5	32.6/33.2
TS4	54° 00′	007° 50′	34	11.1/18.5	33.8/34.4
TS5	54° 06′	007° 24′	33	11.6/18.1	34.2/34.1
TS6	54° 25′	006° 16′	37	11.4/17.9	34.6/34.9
TS7	54° 49′	005° 35′	41	10.7/16.9	35.1/36.5
TS8	55° 06′	005° 01′	37	9.7/13.8	35.1/35.8
TS9	55° 29′	004° 10′	29	10.6/15.0	35.3/35.7
Dogger Bank					
DB9	55° 33′	002° 59′	42	10.2/12.2	36.2/36.3
DB11	55° 01′	003° 00′	23	12.6/16.7	36.3/35.4
DB12	54° 37′	003° 00′	34	11.7/14.9	35.9/36.5
Eastern North Sea					
EN1	54° 40′	007° 40′	19	12.2/16.8	33.7/32.3
EN2	55° 00′	007° 20′	28	11.2/16.5	34.8/33.6
EN3	55° 40′	007° 00′	30	10.5/16.2	35.2/34.8
EN4	56° 00′	006° 20′	44	9.6/14.8	35.4/35.2
EN5	56° 30′	007° 20′	35	10.2/15.3	35.8/34.8
Skagerrak (SK)					
	57° 49′	009° 10′	140	10.0/10.8	32.5/35.8
Kattegat (KT)					
	57° 38′	010° 58′	28	11.8/15.8	22.0/23.0

from the surface sediments are presented here (for details of sampling see Stoeck & Kröncke 2001). All subsamples taken at each station were pooled and mixed to prevent selective sampling. Mixed samples were frozen at –20°C.

Macrofauna samples were taken using 10 cm diameter plastic tubes; 2 to 3 tubes were taken per core. All cores were sliced at 2, 5 and 10 cm, but abundances of all depths were pooled because the main percentage of fauna was found in the upper 2 cm. Thus, values are related to a sample area of 10 cm diameter. Samples were sieved through 0.5 mm sized mesh and the animals retained were fixed in 4% buffered formalin.

Sample treatment. The mud concentration (<63 µm) at each station was analysed using the laser particle sizer 'Analysette 22 Economy' (Fritsch) as described in detail by Stoeck et al. (2000).

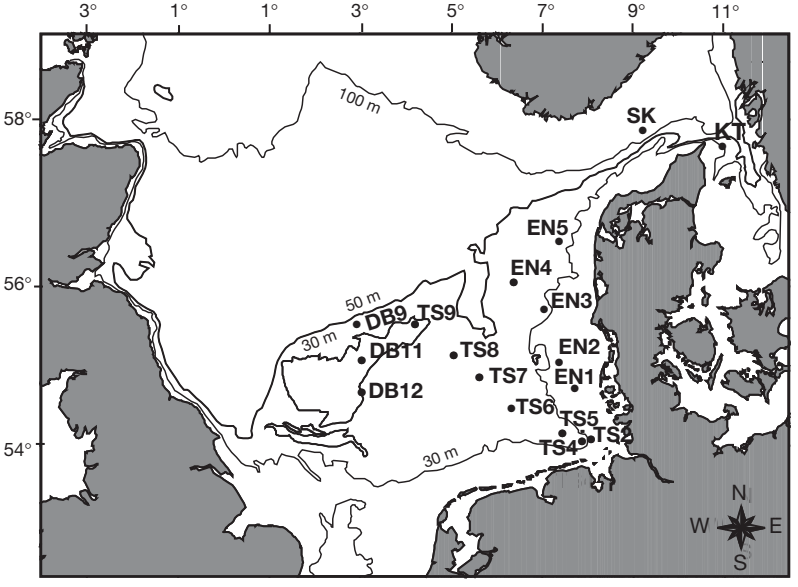

Fig. 1. Map with stations in the German Bight and Oyster Ground (TS), at the Dogger Bank (DB), in the eastern North Sea (EN) and in the Skagerrak (SK) and Kattegat (KT)

Analyses of sediment total organic carbon (TOC) and total nitrogen were determined on freeze-dried samples that had been finely powdered and homogenised. An aliquot of 10 to 30 mg was combusted at 1010°C in an Heraeus C/N analyser following acidification with concentrated HCl in a desiccator to remove inorganic carbonates (Hedges & Stern 1984).

The redox gradients of 3 undisturbed sediment cores were measured on board ship using a GAT Ionode IH30 (GAT) together with a Portamess 651-2 Microprocessor (Knick).

Chl *a* was extracted from 5 g sediment with 5 ml 90% acetone. After incubation of the suspension for 1 h at 4°C in darkness it was mixed for 1 min, followed by ultrasonication in a water bath for 3 min at medium power. To remove particles the suspension was centrifuged for 25 min at 1745×*g* at 0°C. Chl *a* was analysed in the supernatant by high performance liquid chromatography (HPLC) as described by Wallerstein & Liebezeit (1999).

Total bacterial counts (TBC) were determined after staining with the fluorescent dye bisbenzimid H33342 (Sigma) according to the method of Stoeck & Albers (2000). Briefly, immediately after sampling, fresh sediment (0.2 g) was mixed with 5 ml sterile seawater containing EDTA and formol to a final concentration of 5 mM and 3.7%, respectively, and stored in darkness at 4°C until further processing. In the laboratory, the sample was ultrasonicated for 30 s with an Ultrasonic Processor (Soniprep 150, MSE) and the suspension was mixed for 1 min. The procedure of ultrasonication and mixing was repeated 3 times. Subsequently, the suspension was centrifuged at 500×*g* for 15 min. A 5 ml aliquot of the supernatant was stained with the fluorescent dye Hoechst 33342 (Sigma) for 90 min at 37°C, and filtered on a black polycarbonate membrane filter (0.2 µm, 25 mm, Costar). Blue-stained bacteria were counted with an epifluorescence microscope (Zeiss Axiophot) using an excitation of 395 nm and an emission of 420 nm.

Microbial biomass and activity was determined as sediment DNA and RNA concentration, respectively, according to Stoeck et al. (1998). Because the cellular RNA concentration is significantly related to the metabolic activity of the respective cell(s), the cellular RNA concentration is considered to be a measure of microbial activity for single cells and cultures, as well as communities (Dortch et al. 1983, Frantzis et al. 1992, 1993). These analyses detect not only bacterial biomass and activity, but included also protists and small fauna. Nucleic acid measurements were performed using a high-performance liquid chromatography (HPLC) technique as described by Stoeck et al. (1998). A subsample of the homogenised sediment was frozen at –20°C and freeze-dried. An aliquot of 0.2 g of the dried sediment (3 replicates) was transferred into 1 ml of Tris-HCl buffer containing 0.2% sodium dodecyl sulphate and 0.4% EDTA. The mixture was sonicated (Soniprep 150 MSE) 3 times for 10 s at 1 min intervals. After sonication, the samples were centrifuged for 5 min at 3000×*g*. To remove particulate material the supernatant was filtered over a 0.45 µm pore size cellulose acetate filter. In accordance with Copella et al. (1987), we used a urea buffer with a KCl gradient for

HPLC analysis. DNA-C, i.e. the carbon biomass on the basis of DNA, was calculated using a C:DNA ratio of 83 (Holm-Hansen et al. 1968).

Phospholipid fatty acids (PLFA) were analysed at certain stations only. Until now, only few PLFAs have been identified as markers for certain bacteria or microbial groups (described in detail by Stoeck et al. 2002). Because analysis of phospholipid fatty acids is time- and cost-intense, samples for a reduced number of stations were analysed: TS2, TS7, DB9, DB11, DB12 in May and September 1999; EN5, SK, KT in May and September 2000. PLFA analyses were performed according to Frostegård et al. (1993) and Palojärvi et al. (1997), with slight modifications. Lipid extractions and fractionations were carried out from 8 g (samples from Stns GB, KT and SK) or 16 g (samples from all other stations) of freeze-dried sediment (for details see Stoeck et al. 2002). The nomenclature used to describe fatty acids was as follows. The number before the colon indicates the number of carbon atoms in the fatty acid, the number after the colon the degree of unsaturation (= the number of carbon carbon double bonds). The position of the first double bond is indicated by the number of carbon units from the methyl (or aliphatic; 'ω') end of the molecule of the monounsaturated fatty acid (MUFA). In the polyunsaturated fatty acid (PUFA) 'ω' is followed by the position of the first double bond from the terminal methyl end of the molecule. When the exact position of the double bond was unknown, the 'ω' was omitted. The suffixes '*c*' and '*t*' indicate *cis* and *trans* geometry. The prefixes '*i*' and '*a*' refer to *iso* and *anteiso* branching; '*br*' indicates unknown methyl branching position. Other methyl branching is indicated by the position of the additional methyl carbon from the carboxyl end followed by 'Me' (10Me18:0). The number before the prefix 'OH' indicates the position of a hydroxy group from the carboxyl end (3-OH14:0). Cyclopropane fatty acids are designated by the prefix '*cy*'.

Macrofaunal organisms were identified in the laboratory, to species level where possible. Data for subsamples of each core and station were summed and then calculated m^{-2}. Biomass was determined as wet weight, which was converted into Ash Free Dry Weight (AFDW) using conversion factors on a faunal class level given by Rumohr et al. (1987) and Ricciardi & Bourget (1998). Feeding modes were determined according to Fauchald & Jumars (1979), Lincoln (1979), Hartmann-Schröder (1996) and Dauwe et al. (1998).

Statistics. We used the PRIMER v5 program package to perform cluster analyses of macrofaunal and microbial (PLFA) abundance data to reveal similarities between stations (Clarke & Warwick 1994). Similarities were calculated using the Bray-Curtis coefficient. Square-root transformation was used for faunal abundance, none for PLFAs. The average group-linkage method was used to calculate dendrograms. Similarity percentage analysis (SIMPER) was used to analyse dominance of species.

Table 2. Sediment, microbial and macrofaunal parameters at stations in different areas of North Sea in May and September 1999 and 2000. Original data of sediment contents and microbial parameters in Stoeck & Kröncke (2001) and Stoeck et al. (2002) were converted to volume-specific concentrations using equations of Delafontaine et al. (1996) and Flemming & Delafontaine (2000). TOC: total organic carbon; Eh: redox potential; Chl *a*: chlorophyll *a*; TBC: total bacteria counts; DNA-C: microbial biomass; PLFA: phospholipid fatty acids; station abbreviations as in Table 1; –: no data

Stn	Mud ($kg\ m^{-2}$)		TOC ($g\ m^{-2}$)		Eh (mV)		Chl *a* ($mg\ m^{-2}$)		TBC-× $10^{14}\ m^{-2}$		DNA-C ($g\ m^{-2}$)	
	May	Sep	May	Sep	May	Sep	May	Sep	May	Sep	May	Sep
TS2	13.65	14.55	431.21	518.03	–115	–170	61.95	29.74	2.87	1.89	209.13	54.55
TS4	8.9	9.73	241.63	271.62	–53	–122	69.40	31.56	3.09	1.46	48.78	103.46
TS5	4.5	5.72	156.46	178.91	–46	0	55.87	28.61	2.53	1.18	52.84	147.34
TS6	5.68	6.39	178.13	192.18	192	100	28.11	28.18	2.94	0.96	38.97	69.69
TS7	4.58	5.16	157.87	168.39	193	–106	30.27	30.39	1.92	1.17	30.95	109.28
TS8	0.92	0.81	101.98	100.49	193	180	28.08	32.04	1.51	1.02	48.71	72.95
TS9	0.24	0.31	93.35	94.21	145	274	45.94	33.53	2.71	2.59	42.57	52.32
DB9	0.31	0.20	94.29	92.96	7	60	26.07	33.18	2.2	0.58	32.85	52.9
DB11	0.29	0.28	93.98	93.9	186	179	21.02	43.74	1.31	0.56	42.34	56.49
DB12	1.48	1.63	109.36	111.48	267	227	30.55	36.67	1.23	1.43	56.56	89.42
EN1	2.05	1.71	117.53	112.58	126	180	32.26	18.64	0.82	0.96	30.21	42.38
EN2	7.1	6.8	206.94	200.5	230	16	26.6	31.51	0.67	0.61	57.40	107.30
EN3	–	4.88	–	163.29	–	22	–	24.83	–	0.64	–	72.96
EN4	10.57	4.53	296.74	157.09	–14	–65	29.09	32.06	0.68	0.99	28.44	52.22
EN5	0.85	1.81	101.04	113.99	215	105	32.43	28.85	0.61	0.31	23.82	39.73
SK	14.42	14.54	499.27	516.78	–16	–31	20.94	21.17	1.43	1.25	72.77	57.87
KT	11.04	12.56	873.72	802.99	–33	–91	11.57	10.38	0.9	0.88	50.83	49.62

A canonical correspondence analysis (CCA, Microcomputer Power) was applied to reveal relationships between the macrofaunal and microbial community patterns and sediment-bulk parameters. This ordination technique, developed for community analysis (ter Braak 1986), differs from other 2-step ordination techniques in that CCA allows direct analysis of the effect of specific environmental variables because ordination axes are constrained to be linear combinations of environmental variables (ter Braak & Verdonschot 1995). We used a Monte Carlo permutation test (ter Braak & Smilauer 1998) to check the statistical validity of the association between environmental variables and variance in the community pattern.

RESULTS

Mud, total organic carbon (TOC), Eh and chl *a*

Mud, TOC and chlorophyll *a* concentrations in the southern North Sea were highest in the inner German Bight and decreased towards the Oyster Ground to the Dogger Bank (Table 2). At Dogger Bank Stn DB12, TOC and chl *a* concentrations were similar to those at the eastern North Sea stations EN2 and EN5, but mud concentrations were lower. In the eastern North Sea the lowest mud and TOC concentrations were found at Stns EN1 and EN5, but chl *a* concentrations were similar to those at Stns EN2 to EN4. At the deep Skagerrak station (SK) mud and TOC concentrations were similar to those in the inner German Bight Stn TS2, but TOC and chl *a* concentrations were lower. The Kattegat station had the highest TOC concentration of all sites, but the lowest chl *a* concentrations. In general, no significant differences in mud and TOC concentrations occurred between May and September. Chl *a* concentrations were higher in May than in September in the inner German Bight and half of the eastern North Sea and in the Kattegat and vice versa in September at the Dogger Bank stations. Negative Eh values were only found in the inner German Bight, at Stn EN4 and at the Skagerrak and Kattegat stations.

Total bacterial counts (TBC) and microbial biomass (DNA-C)

The bacterial abundance (TBC) and microbial biomass patterns were similar to those of the sediment parameter (Table 2). In the North Sea, the highest TBCs were found in the inner German Bight and decreased towards the Dogger Bank. Lowest counts were found at the eastern North Sea stations. Maximum concentrations of microbial biomass were also found in the inner German Bight and the Skagerrak and Kattegat stations, but concentrations at the remaining stations were fairly homogeneously distributed. TBCs and microbial biomass at the Skagerrak and Kattegat stations were similar to those in the eastern and Dogger Bank stations. TBCs were generally higher in May, microbial biomass was generally higher in September.

Table 2 (continued)

RNA ($g\ m^{-2}$)		No. PLFA (g sediment)$^{-1}$		PLFA biomass (mmol m^{-2})		Macrofauna					
						Species (no. 0.04 m^{-2})		Abundance (ind. m^{-2})		Biomass (g C m^{-2})	
May	Sep	May	Sep	May	Sep	May	Sep	May	Sep	May	Sep
0.69	1.27	34	36	1.76	2.11	35	46	7770	14476	4.92	8.69
0.98	0.76	–	–	–	–	40	49	9380	6258	7.31	4.54
0.47	0.99	–	–	–	–	13	24	2898	3885	0.1	0.65
0.33	0.39	26	25	0.69	1.00	39	31	2408	3486	5	0.53
0.64	0.62	–	–	–	–	32	40	2254	2128	6.12	6.83
0.26	0.35	–	–	–	–	29	34	3066	4214	22	8.58
0.39	0.14	27	29	0.74	1.04	21	40	2226	3122	0.15	1.39
0.15	0.26	22	22	0.44	0.78	16	41	2814	3262	0.25	0.75
0.27	0.25	22	25	0.44	0.68	29	46	13356	3808	4.66	0.46
0.37	0.5	24	27	0.96	1.56	29	37	1932	2562	4.73	1.54
0.16	0.3	–	–	–	–	29	39	1484	5264	1.2	2.13
0.52	0.78	–	–	–	–	18	32	504	44478	0.49	9.97
–	0.64	–	–	–	–	–	39	–	8085	–	0.69
0.2	0.35	–	–	–	–	29	31	4774	6237	0.82	1.02
0.17	0.34	27	22	0.76	0.51	23	28	2884	3759	11.02	1.77
0.54	0.55	34	33	1.31	1.17	33	24	5096	9310	1.33	1.87
0.37	0.32	36	35	1.14	1.07	49	42	13622	4816	1.53	9.91

Table 3. Significant correlations (*: 5% level) between microbial, macrofaunal and sediment-bulk parameters. Abbreviations as in Table 2

	TBC	RNA	DNA	Macrofaunal abundance
May				
Chl *a*	*	*		
TOC		*	*	*
Mud		*	*	*
September				
Chl *a*				
TOC				
Mud		*		

Microbial activity (RNA)

Microbial activity did not follow the patterns of sediment parameters, TBC and DNAC. Highest microbial activity occurred at the German Bight and the eastern North Sea stations EN2 and EN3 (Table 2). Values in the Oyster Ground were similar to those measured in sediments from the eastern North Sea (EN1, EN4 and EN5) as well as the Skagerrak and Kattegat stations.

Correlations between sediment, bacterial and microbial bulk parameters

In May, TBCs and microbial activity correlated significantly with chl *a* concentrations, while microbial activity and biomass were also both correlated with TOC and mud concentrations. Macrofaunal abundance correlated with mud and TOC concentrations. In September, only microbial activity was significantly correlated with mud concentrations (Table 3).

Abundance and biomass of phospholipid fatty acids (PLFAs)

We identified 36 PLFAs in North Sea sediments (Stoeck et al. 2002). The majority is considered to be of bacterial origin, because fatty acids in the range of C_{12} to C_{19} are known to be characteristic of bacteria (Lechevalier 1977). Additionally, fatty acids were detected which are known to be present in protists and microeukaryotes. More than 30 different fatty acids and the highest PLFA biomass were found in depositional areas such as the German Bight, Skagerrak and Kattegat. Hardly any seasonal differences were found in PLFA numbers, but biomass was higher in September at the southern stations (Table 2).

Microbial community structure = PLFA composition

Cluster analysis revealed high spatial similarities (>80%) of PLFA distribution at the study sites (Fig. 2) in regard to total number (as well as in the relative proportion of single fatty acids published in detail by Stoeck et al. 2002). The Skagerrak, Kattegat and inner German Bight Stn TS2 appeared in 1 cluster in both May and September. Another cluster was observed for Stns TS7, DB12 and EN5 in May. In September, Stn EN5 joined the third cluster of stations (DB9, DB11 and TS9) from the more northern Dogger Bank area.

Saturated, monounsaturated (MUFA), polyunsaturated (PUFA), branched (br), cyclopropyl (cy) and

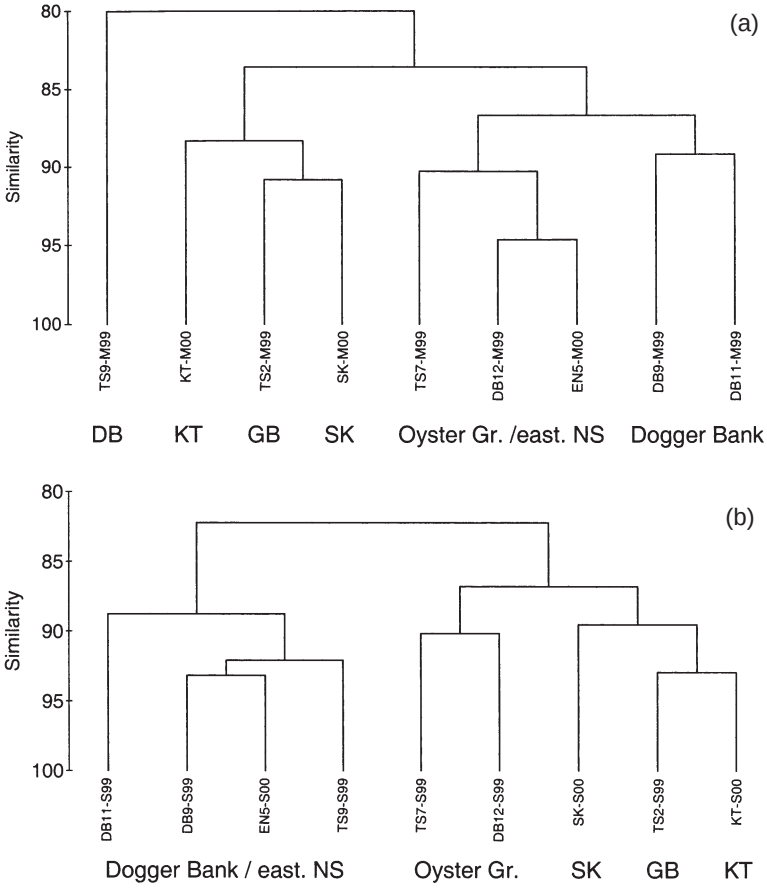

Fig. 2. Dendrograms for microbial communities (composition of PLFAs) in (a) May and September 1999 and 2000 (b) in the German Bight (GB), Oyster Ground, at the Dogger Bank (DB), in the eastern North Sea (EN) and in the Skagerrak (SK) and Kattegat (KT)

hydroxy (OH) fatty acids in the range of C_{12} to C_{24} were identified. The majority of PLFAs is considered to be of bacterial origin (C_{12} to C_{19}) and the major percentage of the total PLFA at all stations were found for 14:0, i15:0, a15:0, 16:1ω7c, 16:0 and 18:ω17.

Of the 36 fatty acids, 14 fatty acids (12:0, 13:0, 3-OH12:0, 3-OH14:0, 16:1ω5 (marker for the *Cytophaga-Flavobacterium-Bacteroides* phylum), 17:1, 10Me18:0 (marker for *Actinomycetes* spp.), cy19:0 (marker for *Desulfobacter* spp.) and all PLFAs $>C_{20}$ (marker for eukaryotes) were significantly more abundant in the German Bight, the Skagerrak and the Kattegat than in all other areas; 7 additional fatty acids (i14:0, br17:0, 10Me16:0 [marker for *Desulfobacter* spp.], cy17:0 [marker for *Desulfobacter* spp.], 17:0, $18:1_b$ and 18:0) were also present in significantly higher quantities in these areas compared with the remaining sites. Also, 4 fatty acids (i14:0, 16:1ω5, a17:0 and 18:1ω9c) were significantly more abundant in the Oyster Ground and southern Dogger Bank Stn DB12 than in the Dogger Bank and the eastern North Sea stations.

In addition to the marker fatty acids 24:0, 10Me18:0 and 16:1ω5, the relative contribution of PUFA (marker for microeukaryotes), cyclopropyl fatty acids (marker for *Desulfobacter* spp.) and saturated fatty acids $>C_{20}$ (marker for eukaryotes) were significantly higher in the German Bight, the Skagerrak and the Kattegat compared to the other sites. The relative contribution of 10Me16:0 (marker for *Desulfobacter* spp.) decreased from the German Bight towards the open and eastern North Sea, where MUFAs (marker for aerobic prokaryotes) and *trans* fatty acids (marker for physiological stress) were highest.

Macrofauna species number, abundance and biomass

The macrofaunal distributions differed from the sediment and microbial patterns (Table 2). Species numbers and abundance were highest in the inner German Bight (Stns TS2 and TS4) in May and September and in the Kattegat in May, but lowest at Stn TS5 in May and September. A decreasing trend from the German Bight towards the Dogger Bank was only found for species numbers in May. The remaining stations in both months displayed fairly similar species numbers.

In the southern North Sea, maximum abundance was found in the inner German Bight (Stns TS2 and TS4) (Table 2). Abundance decreased abruptly at Stn TS5 and remained stable towards the Dogger Bank, except at Stn DB11 in May. Abundance in the eastern North Sea was generally lower in May than in September. Highest variability in abundance was at Stn EN2, where the lowest abundance in this region was found in May and the highest in September, when it exceeded even values for the inner German Bight. Abundance in the Skagerrak and Kattegat were comparable with that in the inner German Bight in May and September as well as with the eastern North Sea in September only.

Biomass did not show any regular pattern (Table 2). In May, biomass was high in the inner German Bight, the Oyster Ground, and at Stns DB11 and DB12 and EN5 compared to the remaining stations. In September, the inner German Bight and Stns TS4, TS7, TS8, EN2 and KT also displayed the highest biomass.

Macrofaunal abundance correlated significantly with mud and TOC concentrations in May, and with biomass in September (Table 3).

Macrofaunal community structure

Although only 0.04 m^2 of the communities were sampled per station and month, the species given in Table 4 represent the dominant or characteristic species of well-known communities documented in several earlier studies (Salzwedel et al. 1985, Kröncke & Rachor 1992, E. Rachor & P. Nehmer unpubl. data). The *Nucula nitidosa* community occurs in the German Bight, the *Amphiura filiformis* in the Oyster Ground and the Skagerrak and Kattegat, the *Fabulina fabula* community in the eastern North Sea, and the *Bathyporeia-Fabulina* community on the Dogger Bank (Fig. 3).

In this study, the *Nucula nitidosa* community (Stns TS2-TS6) (Table 4) was dominated in May by the subsurface deposit-feeding polychaete *Scalibregma inflatum*, juvenile bivalves and asteroids, as well as juvenile *Echinocardium* spp. and *N. nitidosa*. In September 1999, this community extended over the whole Oyster Ground including Stns TS7 and TS8, as well as Stn DB 12 on the southern border of the Dogger Bank due to high numbers of juveniles of ophiurids, *N. nitidosa*, *Abra* spp., *Echinocardium* spp., *Fabulina fabula* and *Ensis* spp. (for feeding modes see Table 4). In contrast, the Oyster Ground is known to be inhabited by the *Amphiura filiformis* community dominated by the ophiurid *A. filiformis* and it's commensal bivalve *Mysella bidentata*.

The *Fabulina fabula* community in the eastern North Sea (Stns EN1 to EN5) was dominated in May 2000 by the small episammic browsing echinoid *Echinocyamus pusillus*, juvenile asteroids, the deposit-feeding bivalve *Corbula gibba*, as well as nemerteans and several polychaete species such as *Pholoe balthica*, *Chaetozone setosa*, *Spiophanes bombyx* etc. (Table 4). In September, a dramatic increase in phoronids occurred found with maximum numbers of 44 478 m^{-2} at Stn EN2. Additionally, juvenile *F. fabula*, ophiurids,

Table 4. Mean abundance, N (no. m^{-2}) of dominant species and feeding types (Mode) of macrofaunal communities. IF: interface-feeder; SF: suspension-feeder; SD: surface deposit-feeder; SSD: subsurface deposit-feeder; P: predator; SL: sand-licker; G: grazer; station abbreviations as in Table 1

May			September		
Species	N	Mode	Species	N	Mode
***Nucula nitidosa* community (German Bight, Stns TS2–TS6)**			***Nucula nitidosa* + *Amphiura filiformis* communities (Stns TS2–TS8, DB12)**		
Scalibregma inflatum	1229	SSD	*Ophiura* juveniles	1147	SD
Bivalvia juveniles	851	SF	Hydrozoa	1072	IF/HP
Echinocardium juveniles	753	SD	*Nucula nitidosa*	376	SSD
Nucula nitidosa	284	SSD	*Abra* juveniles	341	SD
Asteroidea juveniles	182	P	*Mysella bidentata*	170	SF
Spiophanes bombyx	126	IF	*Echinocardium* juveniles	107	SD
Lanice conchilega	119	IF	*Spiophanes bombyx*	123	IF
Mysella bidentata	49	SF	*Fabulina fabula* juveniles	101	IF
Nephtys juveniles	42	P	*Ensis ensis*	99	SF
Eumida sanguinea	35	P	*Spio decorata*	60	IF
***Fabulina fabula* community (Eastern North Sea, Stns EN1-EN5, TS7)**			***Fabulina fabula* community (Eastern North Sea, Stns EN2-EN5)**		
Echinocyamus pusillus	552	SL	*Phoronis* spp.	13832	SF
Asteroidea juveniles	431	P	*Fabulina fabula* juveniles	868	IF
Corbula gibba juveniles	314	SF	*Ophiura* juveniles	714	SD
Nemertini	90	P	Nemertini	427	P
Pholoe balthica	64	P	*Spio* spp.	245	IF
Chaetozone setosa	59	SD	*Magelona filiformis*	238	IF
Spiophanes bombyx	56	IF	*Phaxas pellucidus* juveniles	217	SF
Magelona filiformis	53	IF	*Spiophanes bombyx*	161	IF
Phoronis spp.	39	SF	*Chamelea gallina* juveniles	140	SF
Fabulina fabula juveniles	28	IF	*Magelona johnstoni*	119	IF
***Bathyporeia-Fabulina* + *Amphiura filiformis* communities (Dogger Bank border, Stns TS8, DB9, DB12)**			***Bathyporeia-Fabulina* community (Dogger Bank, Stns TS9, DB9, DB11)**		
Hydrozoa	467	IF	*Spiophanes bombyx*	536	IF
Spiophanes bombyx	331	IF	*Bathyporeia* juveniles	302	SL
Bivalvia juveniles	294	SF	*Bathyporeia elegans*	280	SL
Bathyporeia elegans	280	SL	Nemertini	126	P
Mysella bidentata	215	SF	*Ophiura* juveniles	98	SD
Magelona johnstoni	131	IF	*Urothoe poseidonis*	81	SL
Nemertini	84	P	*Spio decorata*	76	IF
Amphiura filiformis	70	IF	*Fabulina fabula* juveniles	70	IF
Urothoe poseidonis	70	SL	*Perioculodes longimanus*	53	SL
Magelona filiformis	56	IF	*Lanice conchilega*	50	IF
***Bathyporeia-Fabulina* community (DB Tail End + centre, Stns TS9, DB11)**					
Echinocardium juveniles	7581	SL			
Spiophanes bombyx	723	IF			
Bathyporeia elegans	114	SL			
Magelona filiformis	102	IF			
Hydrozoa	93	IF			
Nemertini	84	P			
Lagis koreni	70	SSD			
Lanice conchilega	63	IF			
Urothoe poseidonis	35	SL			
Spio decorata	30	IF			
***Amphiura filiformis* community (Skagerrak/Kattegat)**			***Amphiura filiformis* community (Skagerrak/Kattegat)**		
Ophiura juveniles	1939	SD	*Myriochele* spp.	2118	IF
Mysella bidentata	616	SF	*Mysella bidentata*	1050	SF
Pholoe balthica	224	P	*Phoronis* spp.	618	SF
Amphiura filiformis juveniles	224	IF	*Ophiura* juveniles	497	SD
Nemertini	189	P	*Pholoe balthica*	399	P
Amphiura filiformis	168	IF	*Amphiura filiformis* juveniles	390	IF
Diplocirrus glaucus	105	SD	Nemertini	173	P
Spio spp.	84	IF	Oligochaeta	89	SSD
Tanaidacea	56	SD	*Diplocirrus glaucus*	42	SD
Levinsenia gracilis	49	SSD	Gastropoda indeterminate	42	G

Nemertini, *Spio* spp., *Magelona filiformis* and *M. johnstoni* were present.

On the Dogger Bank, the typical *Bathyporeia-Fabulina* community was found, represented by dominant species such as the interface-feeding polychaetes *Spiophanes bombyx*, *Magelona johnstoni* and *M. filiformis*, the sand-licking amphipod *Bathyporeia elegans*, and other amphipods such as *Urothoe poseidonis*, and *Perioculodes longimanus* (Table 4). In May, the Dogger Bank stations were divided into different communities due to extremely high abundances of juvenile *Echinocardium* spp.

The Skagerrak and Kattegat stations were also inhabited by the *Amphiura filiformis* community, and were clearly separated from the other areas in both May and September (Fig. 3). In May, The communities were dominated by juvenile ophiurids and the commensal bivalve *Mysella bidentata* (Table 4). Juvenile and adult *A. filiformis* occurred also in high mean abundances. *Pholoe balthica* and other small surface- and subsurface-feeding polychaetes such as *Diplocirrus glaucus*, *Spio* spp. and *Levinsenia gracilis* were also found in these communities. In September, *Myriochele* spp. dominated the communities. Minor abundant species were again *M. bidentata*, *Phoronis* spp. and oligochaetes (Table 4).

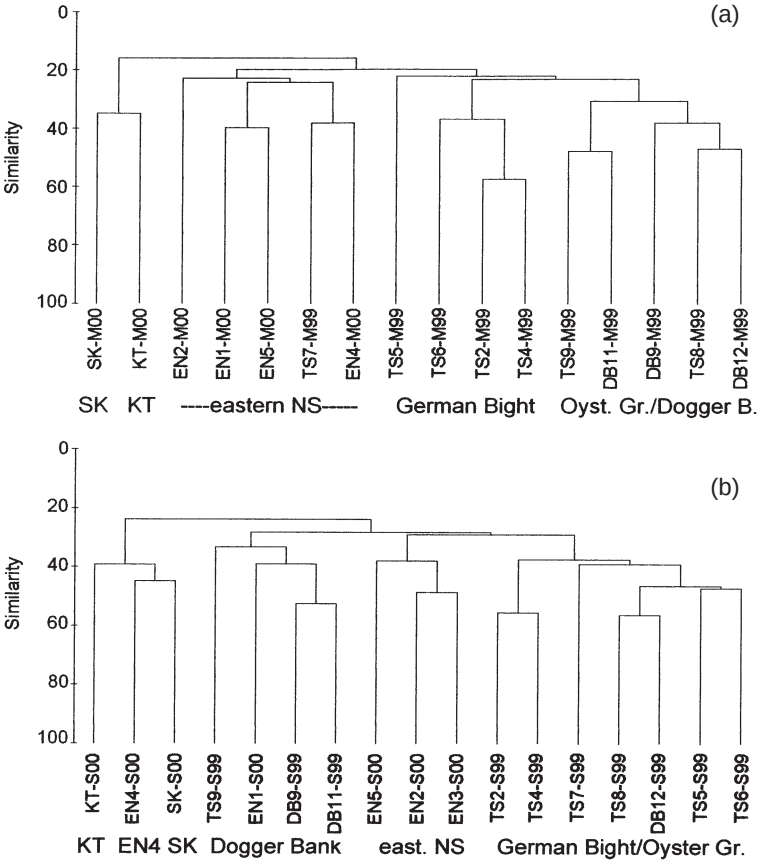

Fig. 3. Dendrograms for macrofaunal communities (abundance) in May (a) and September (b) 1999 and 2000 in the German Bight (GB), Oyster Ground, at the Dogger Bank (DB), in the eastern North Sea (EN) and in the Skagerrak (SK) and Kattegat (KT)

Macrofaunal abundance related to microbial and sediment parameters

We used canonical correspondence analyses (CCA) to analyse and demonstrate the relationship between sediment parameters, microbial and macrofaunal community structure and function. The CCA for May revealed that the first canonical axis is a significant function of a chl *a* gradient (r = 0.73) (Fig. 4). The stations related to the first axis were Stns TS2 to TS5 from the German Bight. The second axis is a function of RNA (r = −0.85) and mud concentrations (r = −0.79), with DNA-C biomass and bacterial abundance being further significant variables. The mud gradient was associated by the most muddy stations in the Kattegat, Skagerrak and Stn EN2 in the eastern North Sea.

A similar pattern was observed in September, with the Skagerrak and Kattegat stations again related to the mud gradient, and the German Bight stations to the RNA, chl *a* and DNA-C concentrations gradients. The environmental gradients explained 45% of the macrofaunal abundance pattern.

Macrofaunal biomass related to microbial and sediment parameters

Similar to abundance, the biomass of communities in the German Bight in both months and in the eastern North Sea in September was related to gradients of chl *a*, RNA and TBC. The environmental gradients explained 60% of the macrofaunal biomass pattern in May and 76% in September.

Relation between taxonomic groups and microbial and sediment parameters

A relationship between taxonomic groups and microbial and sediment parameters was not detectable in May or September. Phoronids and cumaceans showed a slight preference for the TOC gradient. It was obvious that groups whose food resources are not directly connected with the sediment (such as predatory decapods and anthozoa, hydrozoa, ophiurids and amphiurids) were poorly related to sediment parameters.

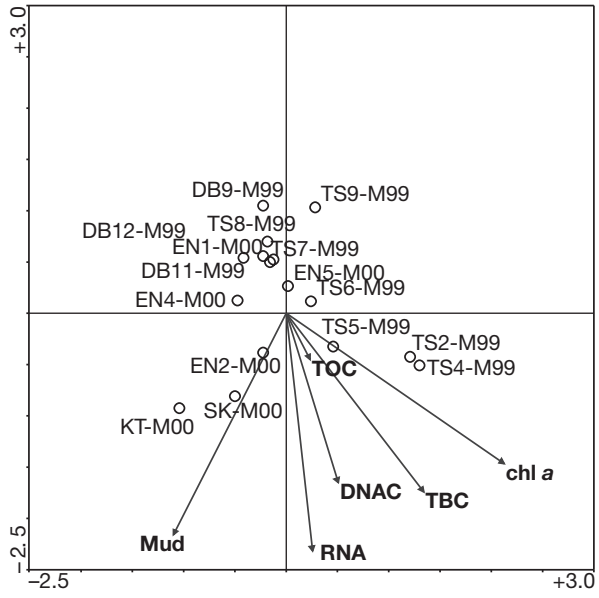

Fig. 4. CCA revealing relationship between macrofaunal community (abundance) and microbial and sediment parameters in May 1999 and 2000. Circles represent the station positions within the ordination space. Vector lines represent the relationship of significant environmental variables to the ordination axes, and their length is proportional to their relative significance. TOC: total organic carbon; chl *a*: chlorophyll *a*; TBC: total bacteria counts; DNA-C: microbial biomass; RNA: microbial activity; station abbreviations as in Table 1

Relation between feeding modes and microbial and sediment parameters

Using feeding modes instead of abundance, the CCAs revealed a closer relationship between all measured sediment and microbial parameters and subsurface-feeders and to lesser extent surface deposit-feeders as well as suspension-feeders and omnivores. Sand-lickers, interface-feeders and predators displayed no relationship with any gradient (Fig. 5).

Relation between macrofaunal and microbial community structure

Despite co-linearity, all PLFAs were included in the CCAs to achieve a preliminary insight into the relationship between microbial (PLFA) and macrofaunal community structure. However, PLFA data were not available for all stations sampled for macrofauna, and thus, the statistical analyses are restricted to Stns TS2 (German Bight), TS7 (Oyster Ground), DB9, DB11, DB12 (Dogger Bank), EN5 (eastern North Sea), SK (Skagerrak) and KT (Kattegatt) for May and September 2000.

Macrofaunal abundance and PLFAs

Fig. 6 gives an example of the general relationship between macrofaunal and microbial (PLFA) community patterns in May (Fig. 6a) and September (Fig. 6b). Both axes explain 37 to 41% of the macrofaunal abundance pattern in May and September. The first species axis were significantly explained by the PLFAs 10Me16:0 = sulphate reducing bacteria (r = 0.63) and 16:1ω5 = *Cytophaga-Flavobacterium-Bacteroides* phylum (r = 0.62), which were closely associated with the macrofaunal communities of the Skagerrak (SK) and Kattegat (KT) stations. The second axis was a function of most of the PLFAs, but faunal communities were not closely related to any of these gradients. However, communities of Stns TS2, TS7, TS9, EN5 and DB9-12 were associated with the gradients of PLFAs 16:00, 16:1ω7c, 18:1ω9c, 10Me17:0, 17:00, i17:00 and br17:0, which are characteristic for bacteria and reflect the general microbial and macrofaunal patterns and relationships revealed by the CCA in Fig. 4.

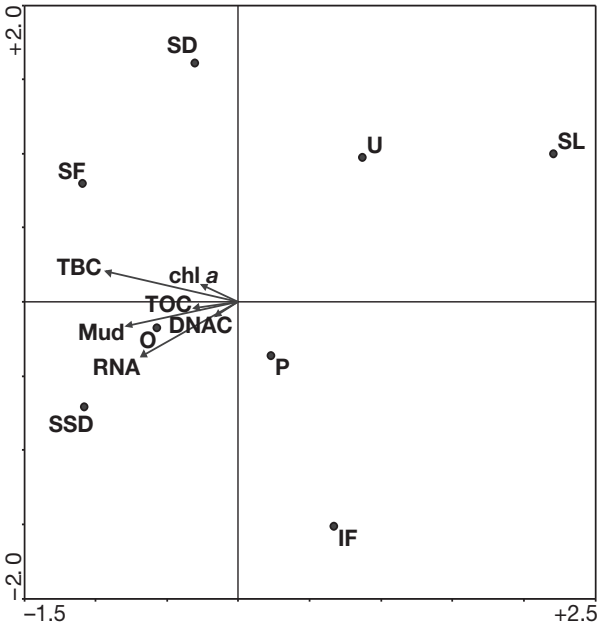

Fig. 5. CCA revealing relationship between macrofaunal feeding modes and microbial and sediment parameters. Dots represent the positions of feeding types contributing significantly to the biological variance. Vector lines represent the relationship of significant environmental variables to the ordination axes, and their length is proportional to their relative significance. TOC: total organic carbon; chl *a*: chlorophyll *a*; TBC: total bacteria counts; DNA-C: microbial biomass; RNA: microbial activity; IF: interface-feeder; SF: suspension-feeder; SD: surface deposit-feeder; SSD: subsurface deposit-feeder; P: predator; SL: sand-licker; O: omnivore; U: unknown

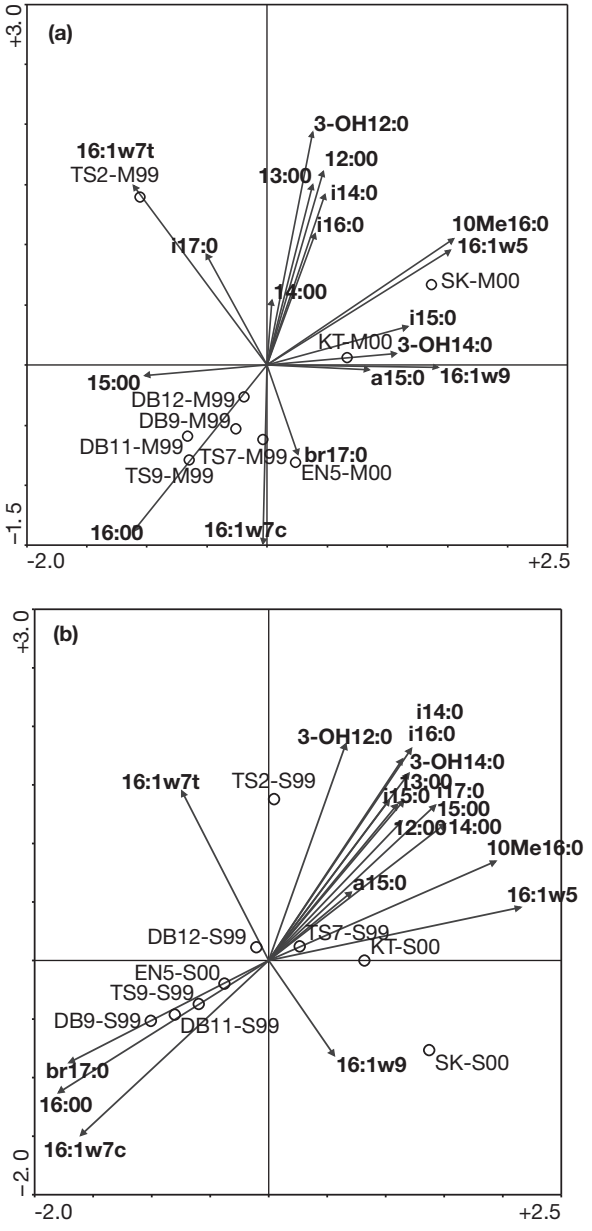

Fig. 6. CCA revealing relationship between macrofaunal (abundance) and microbial (PLFAs) community structure in May (a) and September (b) 1999 and 2000. Circles represent the station positions within the ordination space. Vector lines represent the relationship of significant PLFAs to the ordination axes, and their length is proportional to their relative significance; station abbreviations as in Table 1

Macrofaunal biomass and PLFAs

In terms of biomass (Fig. 7), the communities were structured mainly along the second axis, which was explained by the PLFA gradients 10Me16:0 (marker for *Desulfobacter* spp.) (r = −0.67), 17:00 (r = −0.6), a17:0 (r = −0.6), 17:01 (r = −0.5), 16:1ω5 (r = −0.45), 20:04 (r = −0.42), 15:00 (r = −0.47), i16:0 (r = −0.43), br17:0 (r = 0.49), cy17:0 (marker for *Desulfobacter* spp.) (r = −0.46) and associated with the communities of Stns SK, KT, DB11, EN5 and TS9. Only Stns DB9 and 12 were related to PLFAs 18:1ω9c and 16:1ω9. Both axes explain 66% of the macrofaunal biomass pattern in May and September.

Relation between taxonomic groups and sediment parameters

The most obvious relationship between macrofaunal feeding modes and the microbial PLFA pattern was that amphipods and decapods occurred at higher than average densities at PLFAs 16:00, 16:1ω7c and br17:0, 18:1ω7, recorded for the Dogger Bank Stns DB9 and DB12 and may thus be markers for amphipods or amphipod-related microbes or substrates. Bivalve, echinoids and gastropod occurrence was associated with most PLFAs (Fig. 8), while polychaetes occurred in higher average abundances at PLFAs 15:0, 15:00 and 20:00 and cy17:0. Abundance of cumaceans and nemerteans was not related to any PLFA.

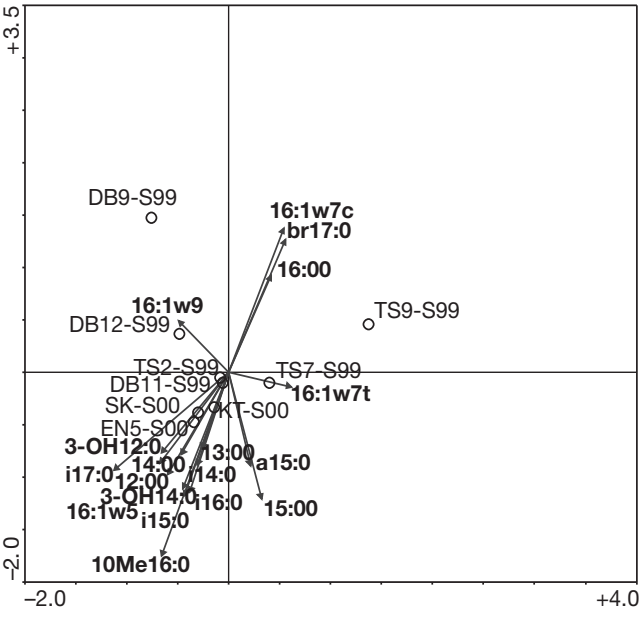

Fig. 7. CCA revealing relationship between macrofaunal (biomass) and microbial (PLFAs) community structure in September 1999 and 2000. Circles represent the station positions within the ordination space. Vector lines represent the relationship of significant PLFAs to the ordination axes, and their length is proportional to their relative significance; station abbreviations as in Table 1

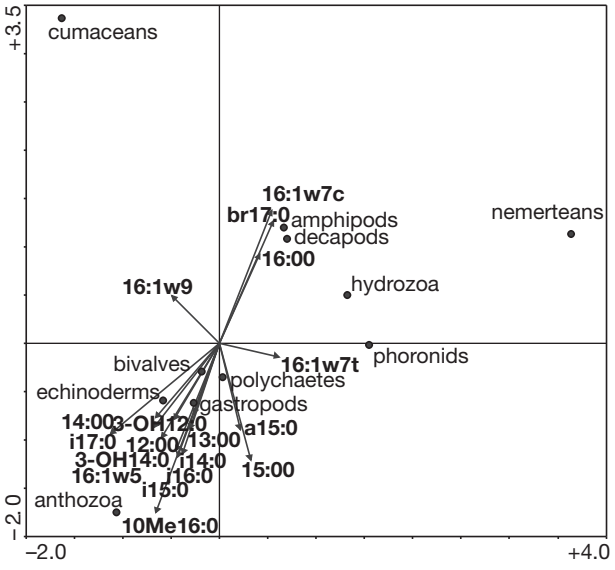

Fig. 8. CCA revealing relationship between taxonomic groups and microbial (PLFA) community structure. Dots represent the positions of taxonomic groups contributing significantly to the biological variance. Vector lines represent the relationship of significant environmental variables to the ordination axes, and their length is proportional to their relative significance; station abbreviations as in Table 1

DISCUSSION

The results of the first quantitative macrofaunal investigation in the eastern North Sea in the 1920s by Hagmeier (1925), the large-scale investigation in the 1970s by Salzwedel et al. (1985), the studies by Kröncke & Rachor (1992) and E. Rachor & P. Nehmer (unpubl. data) in 1990 and in 2000, and the present study, all suggest that the spatial distribution of macrofaunal communities has remained fairly stable over time. Our results show that the spatial distribution of the structure of microbial (PLFAs) and macrofaunal communities is congruent, generally due to functional (trophic) factors and is thus a function of food availability, since both microbial and macrofaunal communities were significantly correlated with chl *a* and TOC concentrations in the sediments (Josefson & Conley 1997, Josefson 1998). We shall therefore discuss differences in food availability in relation to the variability in environmental parameters at the different study sites (Table 5).

Gradients of environmental parameters

The decreasing gradients of mud, TOC and chl *a* concentrations from the German Bight towards the Dogger Bank result from differences in production and sedimentation of organic matter (Eisma & Kalf 1987, Joint & Pomroy 1993, Kröncke & Knust 1995, de Haas & van Weering 1997, Puls et al. 1997, Hickel 1998). A sediment map for the whole North Sea (Basford et al. 1993) revealed that most of the sediments are sands, indicating that in most parts of the North Sea little deposition occurs.

The highest mud and TOC concentrations recorded in this study confirm that the only depositional site in the southern North Sea is the inner German Bight (Figge 1981), where deposition is largely due to currents and morphological features (Aigner & Reineck 1982, Becker et al. 1992, Dippner 1993); the high loads of suspended matter and nutrients transported by the river Elbe into the German Bight (Eisma & Kalf 1987, de Haas et al. 1997, Puls et al. 1997, Dauwe & Middelburg 1998); and high primary production, especially in spring (Joint & Pomroy 1993, Hickel 1998, Stoeck & Kröncke 2001, H. Reiss & I. Kröncke unpubl. data). The net input of labile organic matter into the sediment is so high (de Haas & van Weering 1997) that large amounts of organic matter are buried into deeper sediments by bioturbation (Dauwe et al. 1998, H. Reiss & I. Kröncke unpubl. data). The organic matter deposited in the German Bight is rich in bioavailable nitrogen, and thus of high quality (Dauwe & Middelburg 1998).

In contrast, the Oyster Ground is assumed to be an area of low sedimentation rates and net deposition (Cadée 1984, Boon et al. 1999) due to stratification and currents. This results in lower mud and TOC concentrations than in the inner German Bight. Deposition and resuspension of aggregated organic matter occur in this area (Jones et al. 1998), and are related to the feeding modes of the dominant macrofaunal species. In the eastern North Sea, we measured TOC and chl *a* concentrations similar to those in the Oyster Ground and in the southern Dogger Bank Stn DB12, indicating similarities in currents, production and sedimentation.

The Dogger Bank is known to be an area strongly affected by hydrodynamics (Kröncke & Knust 1995, Wieking & Kröncke 2001, 2003). Sedimentation rates are low, resuspension rates high (Wirth & Wiesner 1988), and mud and TOC concentrations low. Thus, the benthic system only partially benefits from the high primary production observed throughout the year in the Dogger Bank area (Brockmann & Wegner 1985, Riegman et al. 1990, Joint & Pomroy 1993, Nielsen et al. 1993, Stoeck & Kröncke 2001, Wieking & Kröncke 2003). Since chl *a* concentrations on the Dogger Bank were similar to those measured for the Oyster Ground and the eastern North Sea, benthic primary production seems to be important in this shallow area, where light penetration reaches the sea floor and sufficient nutrients are available in the water column throughout the year (Riegman et al. 1990, Nielsen et al. 1993). No data on benthic primary production are available, but Wieking & Kröncke (2001,

2003) inferred from the dominance of amphipods (which browse on microalgae on sand grains) that benthic primary production comprises a major food source for this community (Wieking & Kröncke in press).

The Skagerrak is the major sink for particles produced and resuspended in the North Sea (van Weering et al. 1993, Josefson et al. 1993, de Haas & van Weering 1997) as reflected by the high mud concentrations recorded in the present study. Similar or higher TOC but lower chl *a* concentrations in the Skagerrak than in the German Bight reflect that the POC deposited in the Skagerrak is highly refractory (Dauwe & Middelburg 1998, Dauwe et al. 1999) with up to 20% being of terrestrial origin (Liebezeit 1987, Anton et al. 1993, Meyenburg & Liebezeit 1993, de Haas & van Weering 1997) compared to the fresh nitrogen-rich POC in the German Bight or the Oyster Ground (Dauwe & Middelburg 1998, Dauwe et al. 1999).

Microorganisms, macrofauna and environmental parameters

In May, bacterial counts as well as microbial biomass and activity were significantly correlated with mud, TOC and chl *a* concentrations, indicating that the

Table 5. Characteristics of study sites and communities. Abbreviations as in Table 2

Parameter	German Bight	Oyster Ground	Dogger Bank	Eastern North Sea	Skagerrak/Kattegat
Chl *a*	High	Moderate	Moderate	Moderate	Moderate
TOC	High	Moderate	Low	Moderate	High
Mud	High	Moderate-low	Low	Moderate	High
TBC	High	Moderate	Moderate to low	Low	Moderate to low
DNA	High	Moderate	Moderate	Moderate to high	Moderate
RNA	High	Moderate	Moderate	Moderate	Moderate
No. PLFAs	High	Moderate	Low	Low	High
Biomass of PLFAs	High	Moderate	Moderate	Moderate	High
Marker PLFAs for bacteria	High	Moderate	Low	Low	High
Marker PLFAs for microeukaryotes	High	Low	Low	Low	High
Marker PLFAs for sulphate-reducing bacteria, *Desulfobacter*	High	Moderate	Moderate	Moderate	High
Marker PLFAs for the genera *Cytophaga-Flavobacterium-Bacteroides*, *Actinomycetes* (organic enriched, macromolecules)	High	Low	Low	Low	High
Marker PLFAs for physiological stress, food limitation	Moderate	Low	High	High	Moderate
Preferred utilised substrate	Amino acids, carbohydrates	Glycogen	Amino acids, carbohydrates, dextrin		
Macrofauna					
Species	High	High	High	Moderate	High
Abundance	High	Moderate	Low to high	Low to high	High
Biomass	High	High	Low to high	Low to high	Low to high
Feeding types	Subsurface-deposit-, surface-deposit and interface feeders, predators	Interface-, and surface-deposit feeders	Sand-licker, interface-, and surface-deposit feeders	Sand-licker, suspension feeders, interface feeders, surface-deposit feeders	Interface feeders, surface-deposit feeders, suspension feeders
Food competition (microbes vs macrofauna)	None: sufficient food	Yes, macrofauna provides microbes with food, microbes utilise macrofaunal excretion products	Yes	Yes	No for amount of organic matter, yes for fresh organic matter
Macrofaunal community	***Nucula nitidosa***	***Amphiura filiformis***	***Bathyporeia-Fabulina***	***Fabulina fabula***	***Amphiura filiformis***

abundance of microbial organisms is generally controlled by food supply, as also found by van Duyl et al. (1993), Upton et al. (1993), van Duyl & Kop (1994), Osinga et al. (1996) and Stoeck & Kröncke (2001).

Macrofaunal abundance was significantly correlated with mud and TOC concentrations in May. Wieking & Kröncke (2003) showed that the abundance of the sea urchin *Echinocardium cordatum* at the Dogger Bank was also significantly correlated with TOC concentrations, but that growth was correlated with chl *a* concentrations. Thus, the amount of particulate organic matter is the first-order parameter controlling macrofaunal abundance (Sibuet et al. 1989), since carbon is essential for metabolic (calorimetric) requirement and even refractory organic matter seems sufficient to meet energetic needs (Tenore 1983, Tenore & Chesney 1985). In contrast, the quality of the organic matter seems to be essential for recruitment and growth (Wieking & Kröncke 2003).

However, for the German Bight stations, the CCAs revealed a significant relationship between macrofaunal abundance and biomass, as well as between microbial activity and biomass and chl *a* concentration. The latter is an indicator of fresh, and high-quality food (Boon & Duineveld 1998). Thus, high-quality food from the water column seems to be a key factor in structuring both macrofauna and microbial communities. The quick and direct response of microorganisms to an input of fresh organic matter has been described in many studies for different marine areas (Aller & Yingst 1980, Middelburg et al. 1993, Boetius & Lochte 1994, Kristensen et al. 1995). In contrast, at the community level, the CCA revealed a relationship between chl *a* concentration and macrofaunal species abundance and biomass, which seems to be related to the dominance of juvenile macrofaunal species. This indicates a response to the enhanced supply of fresh nitrogen rich food in the form of recruitment and growth, as confirmed by monthly samples of H. Reiss & I. Kröncke (unpubl. data) in the same area.

The CCAs did not show this relationship for the other regions, where other factors may be more important. For example, the abundances of the macrofaunal communities at the Skagerrak and Kattegat stations were associated with the mud and TOC gradients in both months (May and September) and with a chl *a*/RNA gradient in May only. This indicates that the microbial and macrofaunal community structures were generally related to the presence of mud and the quantity of organic matter (TOC), with the input of fresh organic matter (chl *a*) being important for the community structure in spring only. Because of the greater depth of the Skagerrak and Kattegat stations, chl *a* concentrations were significantly lower than in the German Bight, but microbial biomass and activities were similar. This indicates that microbes in the Skagerrak and northern Kattegat may utilise more refractory organic matter for remineralisation because of the higher amounts of this food source in this area (Dauwe & Middelburg 1998).

Community structure, trophic modes and environmental parameters

The *Nucula nitidosa* community in the inner German Bight (E. Rachor & P. Nehmer unpubl. data) was to a large extent dominated by juvenile bivalves and echinoderms. These species forage as surface deposit or suspension feeders (Bridges et al. 1994, Marsh & Tenore 1990) and may benefit from the high amounts of fresh organic matter produced in the water column. High chl *a* concentrations, which are markers of fresh and nitrogen-rich organic matter (Boon & Duineveld 1998), reflect the availability of fresh organic matter for both macrofaunal and microbial communities (Stoeck et al. 2003). Thus, microbial parameters were higher in this area than in the open North Sea. High amounts of the *Cytophaga-Flavobacterium-Bacteroides* phylum represented e.g. by PLFA 16:1ω5 and *Actinomycetes* by PLFA 10Me18:0 are known to occur in organic enriched sediments and are able to degrade complex macromolecular substrates (McCarthy 1989) such as artificial carbon polymers transported by the river Elbe (Dauwe & Middelburg 1998). Also higher concentrations of $>C_{20}$ PLFAs in this area (characteristic of microeukaryotes: Vestal & White 1989) indicate a greater food supply (Stoeck et al. 2003).

The inner German Bight was the only area of those studied, where subsurface deposit-feeders such as the polychaete *Scalibregma inflatum* and the bivalve *Nucula nitidosa* also occurred in high abundance. In a depositional area such as the German Bight, the net input of labile organic matter into deeper sediment layers by sedimentation and bioturbation is extremely high (de Haas & van Weering 1997, Dauwe et al. 1998, H. Reiss & I. Kröncke unpubl. data). Subsurface deposit-feeders as well as microorganisms benefit from this food source (Osinga et al. 1996, Kristensen 2000). Both bacterial biomass and particulate organic matter can be used as food by subsurface deposit-feeding macrofauna (Rice & Rhoads 1989, Kemp 1990, Marsh & Tenore 1990). Generally, microorganisms are able to mineralise also more refractory organic matter, which is normally found in deeper sediment layers (Kristensen et al. 1995). Thus, high bacterial production (van Duyl & Kop 1994) and mineralisation rates of organic matter are responsible for the extremely anoxic sediments in the German Bight, common in this area (Hickel et al. 1989, Duineveld et al. 1990, Niermann et al. 1990). The anoxic sediment conditions in

the German Bight are also responsible for the presence of the typical marker PLFAs for sulphate reducing bacteria of the genus *Desulfobacter* (e.g. 10Me16:0) (for details see Stoeck et al. 2002).

The macrofaunal community in the Oyster Ground belong to the *Amphiura filiformis* community (E. Rachor & P. Nehmer unpubl. data). In this study, this community was separated from the *Nucula nitidosa* community in May only, since in September the whole area was dominated by juvenile ophiurids and bivalves as well as hydrozoans. Moderately high chl *a* concentrations in May and September across the Oyster Ground hint at a high availability of fresh organic matter, which might favour growth, as indicated by the fairly high biomass observed in autumn, and recruitment throughout the year (also found by H. Reiss & I. Kröncke unpubl. data).

The dominant species in this community was the brittlestar *Amphiura filiformis*, which forages as an interface feeder in areas with moderate currents (Otto et al. 1990, Wieking & Kröncke 2001, 2003). *A. filiformis* captures macroflocculate organic matter from the water column — available in the Oyster Ground from tidal or wave resuspension (Jones et al. 1998). The originally organic-rich aggregates are only of moderate nutritious quality because of scavenging of inorganic and refractory compounds (Dauwe et al. 1998, Jones et al. 1998). Also the lack of subsurface deposit-feeders such as *Nucula nitidosa* confirms the fact that the *A. filiformis* community occurs in areas with a lower burial of fresh organic matter than the German Bight.

Stoeck et al. (2002) showed that microbial communities associated with *A. filiformis* were not adapted to using fresh organic matter as food source but utilised glycogen, a sugar polymer originating from zooorganisms such as meio- and macrofauna. Thus, the higher microbial biomass and activity in September than in May (confirmed by Osinga et al. 1996), may be related to higher macrofaunal abundance at most stations in autumn. On the other hand, H. Reiss & I. Kröncke (unpubl. data) found an additional increase in diatom-derived fucoxanthin in autumn in the Oyster Ground due to mixing of the water column, which provided an additional food supply to both the microbial and macrofaunal communities.

The stations in the Skagerrak and northern Kattegat are both inhabited by the *Amphiura filiformis* community (Josefson et al. 1993) despite differences in water depth (140 and 28 m). Although mean macrofaunal abundance was similar to that in the German Bight, a lower biomass (except in September in the Kattegat), and the dominance of interface feeders such as *A. filiformis* and the polychaetes *Myriochele* spp. and suspension-feeders such as *Phoronis* spp. indicate that sedimentation and burial of fresh organic matter is lower in these areas than in the German Bight. Thus, the communities are more dependent on lateral transport of organic matter in this area (Rosenberg 1995). In contrast to the *A. filiformis* community, which occurs in the Oyster Ground, microbial parameters in the Skagerrak and Kattegat were typical for depositional sites, but the microbes seemed to use different food sources (e.g. more refractory organic carbon) than the microbial community in the German Bight.

For the Dogger Bank, an area strongly affected by hydrodynamics (Kröncke & Knust 1995), Wieking & Kröncke (2001, 2003) described the *Bathyporeia-Fabulina* community as being dominated by interface-feeding polychaetes and sand-licking amphipods that clean off the microalgae from each sand grain (Nicolaisen & Kanneworff 1969, Sundbäck & Persson 1981, Herman et al. 2000, Wieking & Kröncke 2003). The dominance of sand-licking amphipods indicate benthic primary production as described for other shallow areas (Cahoon et al. 1993, Nelson et al. 1999). Benthic primary production at the Dogger Bank is supported by sufficient nutrients (Brockmann et al. 1990, Bo Pedersen 1994) and considerable light penetration down to 40 m depth (Riegman et al. 1990, Nielsen et al. 1993, Jones et al. 1998). Fairly high chl *a* concentrations and microbial substrate preference of amino acids and a phytosugar polymer in this area (Stoeck et al. 2003) confirm the role of benthic primary production for the nutrition of benthic Dogger Bank communities. Our own (unpubl.) data comparing phytopigment concentrations of total and decanted Dogger Bank sediments have revealed that the sand fraction provides a pattern of chl *a*, chl *c* and fuxoxanthin concentrations characteristic for benthic microalgae, as also found by Cahoon et al. (1993) and Nelson et al. (1999). And we saw benthic microalgae adhering to the sand grains using electron microscopy.

Concerning microbes, the presence of marker PLFAs for aerobic microeukaryotes and bacteria, associated with strategies for survival during physiological stress (probably hydrodynamical and food-related) (Stoeck et al. 2002) confirms that the Dogger Bank is a hydrodynamically affected area.

The eastern North Sea is inhabited by the *Fabulina fabula* community (Niermann 1997, Rachor & Nehmer unpubl. data). In the present study, the community was dominated by the small echinoid *Echinocyamus pusillus* in May; this species forages as a sand-licker (Ghiold 1982). As for amphipods at the Dogger Bank, this feeding mode indicates benthic primary production as an important food resource for the macrofauna. The further presence of suspension- and interface-feeding species indicates that the area is strongly affected by hydrodynamics and thus lateral transport of organic matter. Phoronids dominated the community in Sep-

tember and were found in maximum abundances of about 45 000 individuals m^{-2} at Stns EN2 and EN3. The baffling behaviour of the phoronids led to high mud concentrations at these stations. Hickel et al. (1989) and Niermann (1997) also found the highest abundance of phoronids in the same area. Hickel et al. (1989) and Bauerfeind et al. (1990) also measured high chl *a* and phytoplankton carbon concentrations in the bottom water of this area indicating that the phoronids are directly favoured by the high food supply. On the other hand, the presence of phoronids may cause microbe-phoronid interactions since settling and metamorphosis of *Phoronis* spp. is known to be related to biofilms (Herrmann 1995).

Food competition and role of hydrodynamics in food availability

On a eutrophic shelf sea such as the North Sea food supply should not be a limiting factor. Kristensen (2000) found reduced microbial activity in surface sediments in the presence of the polychaete *Nereis diversicolor*. Beside direct competition for food at the surface, bioturbation enhances microbial remineralisation of organic matter and thus sediment chemistry in deeper sediment layers (Kristensen & Blackburn 1987, Aller 1988, van Duyl & Kop 1994, Forster et al. 1995, Osinga et al. 1996, Ziebis et al. 1996, Kristensen 2000). Sediment chemistry may influence the structure and function of microbial and macrofaunal communities.

However, our results indicate that microbial and macrofaunal communities in the depositional area of the inner German Bight seem to receive enough fresh and nitrogen-rich food to obviate any need for competition. The surplus of food not used by organisms in surface sediments is buried in deeper sediment layers, where it becomes available to subsurface-feeding macrofauna and microbes. This indicates a benthic food web structure based on sufficient food supply and low food competition.

In the other depositional areas, the Skagerrak and Kattegat, the situation is different. Macrofaunal feeding modes hint at a stronger influence of hydrodynamics, and sediment parameters and CCAs reveal a sedimentation of more refractory organic matter (TOC) that is utilised by microbial and macrofaunal communities.

In areas with stronger hydrodynamics and a low deposition of organic matter such as the Oyster Ground and the eastern North Sea, the dominance of interface- and suspension-feeders such as brittlestars and phoronids reflects the fact that in most parts of the North Sea advection (hydrodynamics) controls the availability of food (Wieking & Kröncke 2003, Wieking & Kröncke in press). In such areas, macrofauna, which feed in the benthic boundary layer, are essential for the transport of organic matter produced in the water column to the benthic system. Our data show that in such areas microbial communities are also dependent on macrofaunal excretion products.

On the Dogger Bank, hydrodynamics are so strong that hardly any sedimentation of organic matter takes place. Thus, food for the dominant sand-licking amphipods is derived from benthic primary production (Wieking & Kröncke 2003). The poor correlation between microbial/macrofaunal and sediment parameters indicates that the microbial and macrofaunal communities are nutritionally independent and use different food sources, and suggests the existence of food chains similar to those under food limited conditions in the deep sea (Kröncke et al. 2000).

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