Benthic-pelagic coupling
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CHAPTER 6

• Benthic organic matter supply and metabolism in depositional and non-depositional areas in the North Sea •

6.1. Introduction

The close relation between detrital supply to sediments and benthic metabolism has been demonstrated in the deep sea (Smith Jr 1978, Thiel et al. 1988) as well as continental seas (Smetacek 1984, Kanneworff & Christensen 1986, Boon et al. 1998). Boon & Duineveld (1998) demonstrated in the southern and central North Sea an annual balance between the amount of fresh detrital carbon supplied to and mineralised in the sediments. Although the sites in the latter study were all located in non-depositional areas in the North Sea, a substantial part of primary production was buried and subsequently degraded in these sediments.

Pertaining to this benthic organic matter cycling, the role of depositional areas within the North Sea is unclear. Are such areas, next to sinks for fine mineral particles and refractory carbon, also sinks for labile organic matter? And how do these areas compare to non-depositional areas with regard to the nature and amount of detritus and its mineralisation within sediments?

Other benthic studies in the North Sea have measured nutrient fluxes (Lohse et al. 1995) and bacterial production (Van Duyl & Kop 1994) in these depositional areas. However, studies on the amount and nature of labile organic matter in recent sediments in the North Sea are scarce and limited to particular areas (Liebezeit 1987, Kempe & Jennerjahn 1988, Wiesner et al. 1990, Anton et al. 1993). Moreover, they were not accompanied by benthic metabolic measurements.

To get insight into the above questions, this study focused at the sediment detritus composition and benthic metabolism in depositional and non-depositional areas during three cruises in 1994 at 4 locations in the southern and eastern North Sea. Stations were chosen on basis of their differences in depositional environment, depth and possible different origin of recent organic matter. Two stations were selected in acknowledged depositional areas, i.e. the German Bight and the Skagerrak (Eisma & Kalf 1987a, De Haas et al. 1997, Puls et al. 1997). As a comparison, the other 2 stations were located in non-depositional areas in the southern North Sea. These stations, at the Broad Fourteens and the Frisian Front, have been studied relatively extensively with regard to the supply of phytodetritus to the sediments and congruent benthic metabolism (Duineveld & Jenness 1984, Creutzberg 1985, Jenness & Duineveld 1985, Cramer 1990, Boon et al. 1998).

The nature and concentration of sedimentary labile organic matter were determined by down-core analyses of phytopigments and fatty acids. Benthic metabolism was assessed by measuring sediment oxygen demand in shipboard incubated cores and the depth-distribution of RNA and DNA in sediment cores.

Phytopigments have been widely used as markers for biomass and composition of algae in the water column (Lorenzen 1967, Gieskes & Kraay 1983). Because in most benthic habitats the major source of fresh organic matter in sediments consists of phytodetritus, phytopigments represent obvious markers for benthic food input (Gillan & Johns 1980, Relexans et al. 1992). There are numerous studies where the sedimentation of detritus on the sea-bed is successfully traced by means of pigments even down to the deep-sea floor (Billett et al.
Benthic organic matter supply and metabolism at depositional and non-depositional sites

Especially chlorophyll a, present in all algae, appears to be an appropriate indicator for the labile organic matter pool (Stephens et al. 1997, Boon & Duineveld 1998). Therefore, in this study, chlorophyll a is used to follow the temporal and spatial input of phytodetritus to North Sea sediments.

Fatty acids are important lipid components in all organisms. They are mainly part of the somatic and storage lipids, but may also have a physiological function as hormone precursors (Sargent et al. 1990). Since bacteria, algae and terrestrial plants have different biosynthetic pathways for fatty acids, these organism groups can be discriminated by their fatty acid composition (Gurr & James 1980, Arao & Yamada 1994). Due to this specificity in combination with the fact that they are relatively short-lived, fatty acids are important markers for the origin and nature of labile organic matter in water and sediments (Saliot et al. 1982, Reemtsma et al. 1990, Santos et al. 1994, Wolff et al. 1995). This study is a first description of fatty acid concentration and composition in recent North Sea sediments.

The metabolic response of the whole benthic community was measured using sediment oxygen consumption (Smith Jr. 1978, De Wilde et al. 1984). Furthermore, we used the RNA to DNA ratio as a proxy for the productivity of the group of small organisms (< 1 mm). So far, this ratio has been applied to cultured bacteria (Kerkhof & Ward 1993, Kemp et al. 1993) and metazoan organisms (Dortch et al. 1983, Mayrand et al. 1995). A positive correlation has been found between the RNA to DNA ratio or the RNA concentration and growth rate in bacterial cultures. (Kerkhof & Ward 1993, Kemp et al. 1993).

6.2. Methods

Description of study sites

The visited stations are indicated in Fig. 6.1. Two non-depositional stations were selected in the southern North Sea, station Broad Fourteens (BF) and station Frisian Front (FF). The third station is located in the German Bight (GB) and the last station is situated in the Skagerrak (SK), respectively in the south-eastern and north-eastern North Sea and are both depositional areas. In Table 6.1, an overview of some characteristics of the stations is given. Station BF (c. 30 m depth) has a sandy bottom which is poor in organic carbon (C_{org}), and displays relatively high near-bottom current velocities (max. ~45 cm.s^{-1}). Although fresh organic matter has been found in the sediments (Jenness & Duineveld 1985, Boon et al. 1998), no net deposition of particulate matter takes place (De Haas et al. 1997). More likely, it is a site with net erosion of sediments (Eisma & Kalf 1987a).

At station FF, at c. 40 m depth, near-bottom currents are lower than at stn BF, max. 25 cm.s^{-1} (Boon unpubl. res.), while the sediment consists of a mixture of fine sand and silt with an C_{org} content < 0.5% (De Haas et al. 1997). It is situated in a frontal area of two converging water masses, i.e. one that enters the North Sea from the south through the Channel, the other from the north around Scotland. Primary production at stn FF is often prolonged after the spring bloom and the sediment contains enhanced levels of phytodetritus compared to stations north and south of it (Creutzberg 1985, Baars et al. 1991). The local enrichment of stn FF is also apparent from the increased benthic biomass and sediment oxygen consumption (Creutzberg 1985, Cramer 1990).

At the third station, GB, near-bottom current velocities are close to those at stn BF (Boon & Duineveld 1996). Nevertheless, the sediment contains a relatively high concentration of C_{org} (1-2%) and silt. As a result of a net inflow of suspended matter and local eddy-forming, it is considered a depositional area (Eisma 1987). The sedimentation rate in this area could not be determined due to high bioturbation activity (De Haas et al. 1997). The last station, SK, is situated at the southern slope of the Skagerrak and is considerably deeper than the stations mentioned above, c. 270 m.
Near-bottom currents vary between 5 and 10 cm s\(^{-1}\) (Svansson 1975). At the sample site, the sediment consists of clayey and sandy silts, with a C\(_{\text{org}}\) content in the top layer between 1.5 and 2\% (De Haas 1997). The sedimentation rate in the area where the station is located varies between 2 and 4 mm yr\(^{-1}\) (see De Haas & Van Weering 1996). This area is believed to be the ultimate sink for about half of the refractory carbon produced in the North Sea. Calculations indicate that about \(10^6\) ton organic matter accumulates in the Skagerrak/northern Kattegat, of which 90\% is imported (De Haas & Van Weering 1997). This is at least ten times of the organic matter buried in the North Sea (De Haas et al. 1997), and underlines the importance of the Skagerrak area as a carbon sink.

**Sampling and analytical procedures**

The four sampling sites in this study were visited with the R.V. Pelagia at 14 to 24 February, 24 to 31 May and 15 to 31 August 1994. Sediment samples were taken with a cylindrical boxcorer (\(\varnothing\) 31 cm), which encloses a 30 to 50 cm long sediment column together with 15 to 25 l of overlying bottom water. Disturbance of the sediment-water interface and intrusion of overlying water is prevented by a tightly sealing top valve. For the phytopigment and fatty acid analyses, multiple sediment cores (from different box cores) with a length of 10 cm were taken with cut-off 50 ml syringes. For the nucleic acid analyses sediment cores were taken with cut-off syringes of 10 ml (8 cm length). Samples were frozen in liquid nitrogen after which they were stored at -80\°C until processing in the laboratory. There the frozen samples were sliced, in sections of 0 to 1, 1 to 2, 2 to 3, 3 to 5, 5 to 7 and 7 to 10 cm for phytopigment and fatty acid analyses, and in sections of 0 to 0.5, 0.5 to 1, 1 to 2, 2 to 3, 3 to 4 and 4 to 6 cm for the nucleic acid analyses.

<table>
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<th>Station</th>
<th>Latitude (N)</th>
<th>Longitude (E)</th>
<th>Depth (m)</th>
<th>Mixing</th>
<th>Sediment type</th>
<th>Org. Carbon (% in sed.)</th>
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<td>Broad Fourteens</td>
<td>53°00</td>
<td>3°52</td>
<td>28</td>
<td>mixed</td>
<td>medium coarse sand</td>
<td>0.05 - 0.1</td>
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<td>Frisian Front</td>
<td>53°42</td>
<td>4°30</td>
<td>39</td>
<td>transitional</td>
<td>fine sand and silt</td>
<td>0.5 - 1</td>
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<tr>
<td>German Bight</td>
<td>54°05</td>
<td>8°09</td>
<td>20</td>
<td>mixed</td>
<td>silt with fine sand</td>
<td>1 - 2</td>
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<td>Skagerrak</td>
<td>58°12</td>
<td>10°15</td>
<td>270</td>
<td>stratified</td>
<td>clayey silt</td>
<td>1.5 - 2</td>
</tr>
</tbody>
</table>

Prior to analyses, the sediment samples were lyophilised. To reduce the amount of fatty acid analyses, only the sediment sections of 0 to 1, 2 to 3 and 5 to 7 cm depth were processed. Phytopigment analyses on the samples were performed by reverse-phase high performance liquid chromatography (RP-HPLC), using the methodology described in Boon et al. (1998). Fatty acids were extracted according to Boon et al. (1975), with minor modifications. Analyses were performed with gas chromatography (GC) and identification took place with gas chromatography mass spectrometry (GC-MS). More information on the analytical procedure concerning fatty acid analyses is given in Boon & Duineveld (1996).

Nucleic acids in the sediment were extracted in a Tris-HCl buffer with 2\% SDS and 10\% EDTA at room temperature. The mixture was sonicated and subsequently centrifuged (3000 rpm). The supernatant was filtered over a 0.45 \(\mu\)m cellulose acetate filter to remove particulate material and injected into a HPLC system equipped with a Nucleogen 4000-7 DEAE anion exchanger column (Machery-Nagel) In accordance with Coppella et al. (1987) we used an urea buffer with a KCl gradient as eluent. Nucleic acids were detected by their absorption at 260 nm.
The identity of the peaks in the chromatogram was verified through co-injection of standards (calf-thymus DNA and Baker’s yeast RNA, Merck) and digestion with RNase and DNase (Merck). Peak areas were converted into concentrations using calibration curves obtained from solutions of standard DNA and RNA (+ SDS, EDTA) which like the samples had been sonicated. Recovery of RNA and DNA standards added to sediment varied between 90 and 95%. Data were normalised to sediment dry weight after freeze-drying. Preliminary results from a comparison of methods for RNA and DNA extraction and quantification including the above one, showed comparable results (Dell’Ano et al. unpubl. res.).

Sediment Oxygen Demand (SOD), which covers the aerobic respiration of the sediment community and partly the oxidation of reduced substances as well (Canfield et al. 1993), was measured in shipboard incubated sediment cores (2 to 4 replicate). Detachable polyester cores (Ø 30 cm) were inserted in the cylindrical box corer described above. On-deck, the core tubes were placed into a water bath with an opaque lid to prevent light from entering. The water was cooled to in-situ temperature. A height-adjustable lid was fit into each core tube by means of an inflatable ring in the outer rim, allowing adjustment of the water volume in the core. The lid held a stirring device and an oxygen electrode (Yellow Spring Instruments 620) to monitor the oxygen concentration in the head space. The electrode was calibrated in aerated, oxygen-saturated water (100% O₂), and in oxygen-depleted (sodium sulphite) water (0% O₂). SOD was estimated from the linear part of the first 2 to 3 hours of the concentration-time series. The sediment oxygen demand was corrected for the oxygen use by the electrode.

Anova with Tukey’s HSD tests were used to check on significant differences between stations and months. Relations between marker compounds or compound groups were calculated with Pearson correlations. All statistics were done using Systat for Windows™.

6.3 Results

Water column characteristics

Table 6.2 summarises the near-bottom water (nbw) temperature, chlorophyll a equivalents, transmission and the oxygen concentration in the nbw as measured with CTD-casts at the stations during sampling (see Boon & Duineveld 1996). The nbw temperature at the stations BF, FF and GB was lowest in February, between 3.9 and 5 °C, and highest in August with a maximum between 17.5 and 18.9 °C. At stn SK, the bottom water temperature increased from 3.4 °C in February to 6.4 °C in August.

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<td>2.0</td>
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<td>309</td>
<td>11.8</td>
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<td>1.2</td>
<td>60</td>
<td>258</td>
<td>17.5</td>
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<td>248</td>
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<tr>
<td>GB</td>
<td>3.9</td>
<td>1.5</td>
<td>4</td>
<td>337</td>
<td>10.2</td>
<td>1.7</td>
<td>20</td>
<td>293</td>
<td>18.8</td>
<td>3.0</td>
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<tr>
<td>SK</td>
<td>3.4</td>
<td>0.2</td>
<td>77</td>
<td>253</td>
<td>5.8</td>
<td>0.2</td>
<td>74</td>
<td>256</td>
<td>6.4</td>
<td>0.2</td>
<td>78</td>
<td>265</td>
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</table>

The water column showed multiple thermoclines and haloclines during each cruise (data not shown). Station FF exhibited a (weak) thermocline only in May, while the
Chapter 6

water column at the stations BF and GB was mixed on every cruise. At all stations and during each cruise, the nbw was well oxygenated.

**Sediment oxygen demand**

In Fig. 6.2, the average sediment oxygen demand (SOD) is given. On all three occasions, highest SOD was measured at the stations FF and GB (p<0.01) and the lowest values at stn BF. The measurements in May at this station did not successful, due to technical problems. Earlier May SOD measurements at this station (Van Duyl & Kop 1994, Boon & Duineveld 1998) varied around 370 µmol O₂.m⁻².h⁻¹. Maximum SOD values at the stns FF and SK were found in May, and at stn GB in August (p<0.05).

**Pigment concentration and composition**

Fig. 6.3 shows the inventories of chlorophyll a per cm² sediment in the top 10 cm of the sediment. For the calculation of these inventories, we converted the concentrations per gram into concentrations per cm³, using a specific density of 2.6 g.cm⁻³, and an average porosity of 0.4, 0.53, 0.66 and 0.84 (Lohse et al. 1995, De Haas et al. 1997) at stations BF, FF, GB and SK, respectively. Although spatial and temporal trends are obvious, ANOVA with Tukey HSD test yielded only few significant differences as a result of heterogeneity in sedimentary chlorophyll a concentrations. Overall, highest concentrations were found in May, when months were compared, and at stn SK, when stations were compared (p<0.05). Further, an increasing trend in concentrations of sedimentary chlorophyll a can be seen from stn BF to stn FF to stn GB. The chlorophyll a concentrations were significantly lowest in February at stn BF compared to all other stations (p<0.05) and significantly highest at stn SK in May compared to stns BF and FF (p<0.05). In the majority of the cores, we found a decrease of chlorophyll a with depth. A substantial number of cores showed a subsurface maximum, while in some cores the concentration of chlorophyll a was erratic or showed an increasing trend with depth. The latter profiles were mostly found in May. Fig. 6.4 shows some characteristic down-core distributions of chlorophyll a and phaeopigment concentrations (phaeohorbid a and phaeophyhtins a). We could not distinguish a trend among the stations regarding the down-core distribution of chlorophyll a. When the chlorophyll a concentrations decreased with depth, this was also the case for the phaeopigments. Subsurface maximums in chlorophyll a concentration coincided with subsurface maximums in the phaeopigment concentration. However, in most cores the proportion of phaeopigments to the sum of phaeopigments and chlorophyll a increased with depth, resulting in negative correlations between the two in many cores (at stns BF, GB and SK; p<0.05).

**Fatty acid concentration and composition**

In Table 6.3, the inventory percentages of individual fatty acids in the total fatty acid concentrations per station and month are given. A total of 46 different fatty acids was found when all samples are considered. A total of 46 different fatty acids was found when all samples are considered. Although spatial and temporal trends are obvious, ANOVA with Tukey HSD test yielded only few significant differences as a result of heterogeneity in sedimentary chlorophyll a concentrations. Overall, highest concentrations were found in May, when months were compared, and at stn SK, when stations were compared (p<0.05). Further, an increasing trend in concentrations of sedimentary chlorophyll a can be seen from stn BF to stn FF to stn GB. The chlorophyll a concentrations were significantly lowest in February at stn BF compared to all other stations (p<0.05) and significantly highest at stn SK in May compared to stns BF and FF (p<0.05). In the majority of the cores, we found a decrease of chlorophyll a with depth. A substantial number of cores showed a subsurface maximum, while in some cores the concentration of chlorophyll a was erratic or showed an increasing trend with depth. The latter profiles were mostly found in May. Fig. 6.4 shows some characteristic down-core distributions of chlorophyll a and phaeopigment concentrations (phaeohorbid a and phaeophyhtins a). We could not distinguish a trend among the stations regarding the down-core distribution of chlorophyll a. When the chlorophyll a concentrations decreased with depth, this was also the case for the phaeopigments. Subsurface maximums in chlorophyll a concentration coincided with subsurface maximums in the phaeopigment concentration. However, in most cores the proportion of phaeopigments to the sum of phaeopigments and chlorophyll a increased with depth, resulting in negative correlations between the two in many cores (at stns BF, GB and SK; p<0.05).
Table 6.3: Fatty acid percentages of total fatty acid concentrations per station per month.

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<th>FF Feb</th>
<th>FF May</th>
<th>FF Aug</th>
<th>GB Feb</th>
<th>GB May</th>
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**a** Nomenclature: total number of C atoms : number of double bonds sex, with x being the position of the ultimate double bond from the terminal methyl group. Prefix 'i', 'a', 'ip' refers to methyl-branching, in respectively iso, ante-iso or isoprenoid positions.

**b** Location of double bond derived tentatively from retention time and literature.
in the sediment gives a relative indication of the bacterial biomass in the sediment (e.g. Reemtsma et al. 1990). The PUFA (polyunsaturated fatty acids) group consists of all fatty acids with 2 or more unsaturated bonds. The TERR group consists of saturated straight-chain fatty acids with chain lengths of 24 carbon atoms and longer. Cuticular waxes on terrestrial plant leaves are known to possess such long-chain fatty acids and alkanes (Kolattukudy 1976). As a result, the presence of long-chain fatty acids in sediments can indicate a terrestrial source of the sedimentary organic matter. However, certain algae are known to possess relatively low amounts of the same compounds (Volkman et al. 1986). Due to their lower decay rate in comparison to their shorter counter-parts (De Baar et al. 1983), an increased proportion of TERR could also result from preferential decay of short-chain fatty acids in marine organic matter (Reemtsma et al. 1990).

The inventories of TFA are depicted in Fig. 6.3, next to the inventories of chlorophyll a. In Fig. 6.5, the PUFA are given as a percentage of the TFA inventory per core. Important PUFA in this study were C20:5 and C22:6, but in many cases also C16:4, C16:3, C18:4, C18:3, C18:2, C20:4, C20:3 a and C22:5 were found. The PUFA are uniquely synthesised by algae (DeMort et al. 1972, Viso & Marty 1993, Dunstan et al. 1994), and are therefore markers for the (fresh) algal input. Because the variation in PUFA concentrations accounted for the largest part of TFA concentrations (stations pooled: \( r=0.85 \)), both groups show corresponding trends. Figs 6.3 and 6.5 clearly illustrate the strong similarity between the temporal and spatial variations of PUFA and chlorophyll a (\( r \geq 0.72, \ p < 0.001 \)). There is a similar difference between stations with respect to TFA and PUFA inventories as to those of chlorophyll a: highest at stn SK, lowest at stn BF, and intermediate values at stns FF and GB, with a seasonal maximum in May.

The inventories of the BACT group did not show explicit temporal cycles (Fig. 6.5). However, there are noticeable differences between stations with respect to BACT, comparable to those of chlorophyll a and TFA: increasing concentrations in the order of stns BF, FF, GB and SK (\( p \leq 0.06 \)). When stations are pooled, we find a positive correlation with PUFA (\( r=0.53, \ p < 0.01 \)). If we express BACT as a percentage of TFA (Fig. 6.6), differences between months and stations diminished. When each core is considered separately, there is a lack of correlation between the down-core concentration of BACT on the one hand and that of PUFA or TFA on the other hand. While PUFA shows a decrease with depth in most cores, this is not the case with BACT. Expressed as concentrations, BACT does not show any consistent pattern, while expressed as a proportion of TFA, BACT shows a negative correlation with the PUFA concentration (stations pooled: \( p < 0.001 \)). This underlines the lack of relation between PUFA and BACT.

The inventories of the long-chain fatty acids (TERR) were relatively low at stn BF and slightly higher at stn FF (Fig. 6.5). The other two stations, GB and SK, distinguished themselves with significantly higher concentrations of TERR (\( p < 0.05 \); months pooled). When TERR are expressed as percentages of TFA (Fig. 6.6), the differences between stations are still visible, although they are less pronounced. Also TERR shows a positive correlation with TFA and PUFA when all stations are considered, but not when calculated per station.

### Nucleic acids

The inventories of both RNA and DNA displayed a comparable trend at all stations (Fig. 6.7), with low values in February, highest concentrations in May and intermediate concentrations in August. In May and August, there were distinct differences between stations. Like wise the chlorophyll a and the fatty acids, station BF had the lowest RNA and DNA values, stn FF showed intermediate concentrations, and the highest
values were measured at the stns GB and SK. The inventories of RNA in the sediment were always lower than those of DNA, resulting in RNA:DNA (R/D) ratios below 1. No consistent temporal trend in the R/D ratios could be discerned. At stns FF and SK it appeared to be highest in May, but this is not the case at the other two stations. The R/D ratios seem to be higher at stns GB and SK than at stns BF and FF. In general, the concentrations of RNA and DNA decreased with depth, though in some cores, a subsurface maximum in RNA and DNA was found. In Fig. 6.8, the down-core R/D ratios in February, May and August at stn SK are depicted. In most cores, the down core decrease in RNA is stronger than that of DNA, resulting in a decline in the R/D ratio with depth. In the May and August cores from stations GB and SK, the R/D ratio was around 1 in the top 2 cm, below this the R/D ratio declined rapidly.

6.4. Discussion
Phytodetrital supply

The temporal trends in the inventories of chlorophyll a, total fatty acids and polyunsaturated fatty acids were comparable at all stations, with a maximum in May. Also the proportions of PUFA in the total fatty acid concentrations peaked in May, with percentages over 20 % compared to <10% in February. Such a pattern is fully in line with the occurrence of a prominent algal spring bloom characteristic for coastal seas at temperate latitudes, like the North Sea. Here, the spring bloom usually takes place late April or early May (Joint & Pomroy 1993), and has a pronounced effect on the inventory of chlorophyll a in the sediments (Cramer 1990, Boon et al. 1998).

Differences between the stations in sedimentary chlorophyll a concentrations could only be proven significant in the case of stns BF and SK. Because the spatial trends in chlorophyll are paralleled by those in PUFA and TFA concentrations, there is enough support to rank the station regarding supply of fresh phytodetritus as BF<FF<GB<SK, with stn BF having the lowest concentrations. Similarly low inventories of chlorophyll a at stn BF were found in 1993 (Boon et al. 1998). These consistently low values are most likely the result of the relatively high near-bottom water (nbw) current velocities (max. 45 cm.s⁻¹) resulting in high turbulence of the water column, which keeps particles in suspension or even resuspends the top layer (Jago et al. 1993, Boon unpubl. res.). However, periodic input of fresh phytodetritus still is considerable due to sedimentation and burial around slack tide (Jenness & Duineveld 1985, Boon unpubl. res.).

The differences we found between the chlorophyll a inventories at stn BF and at stn FF conforms with previous studies. These attributed the relative detrital enrichment of sediments at stn FF to an enhanced and prolonged primary production caused by the presence of a tidal front in the area of stn FF in combination with lower nbw-current velocities (Creutzberg 1985, Boon & Duineveld 1998). Our data on TFA concentrations and especially on PUFA support the contention that the sediment at stn FF receives a greater supply of labile algal detritus than at stn BF (Creutzberg et al. 1984, Duineveld et al. 1990, Cramer 1990, Boon et al. 1998).

The chlorophyll a and PUFA inventories at stn GB equal or surpass those at stn FF in spite of the higher nbw current velocities at stn GB (max. ~40 cm.s⁻¹; Boon & Duineveld 1996). The explanation for this is 2-fold. Firstly, the algal biomass in the German Bight is highest in the range found in the southern North Sea (Joint & Pomroy 1993). There are strong indications that this elevated algal stock in the German Bight is the result of eutrophication through fluvial (Elbe, Weser) supply of nutrients (Radach et al. 1990, Bauerfeind et al. 1990). Secondly,
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sedimentation of particulate matter in the German Bight is promoted by the local hydrographic conditions, i.e. a higher supply of particulate material during flood than is removed during ebb and a counter-clockwise eddy, which retain suspended material (Eisma & Kalf 1987b, Otto et al. 1990). Puls et al. (1997) calculated a net-deposition of particulate matter in the German Bight of $3 \times 10^6$ ton.yr$^{-1}$.

An unexpected result of this study is our finding that sediment inventories of algal markers in May and August at stn SK were equal to or higher than those at stn GB. Because the depth of station Skagerrak (270 m) is about an order of magnitude greater than of GB, we expected the flux of organic matter reaching the seabed to be accordingly lower (De Baar et al. 1983, Reemtsma et al. 1990). This even more so as (model) estimates for the primary production in the area of stn SK present a moderate figure of 100-150 g C.m$^{-2}$.y$^{-1}$ (Skogen et al. 1995) and CZCS satellite images do not reveal high concentrations of pigments in the surface water. Karlson et al. (1996), however, found that the subsurface chlorophyll maximum can contribute considerably to water column-integrated primary production and the CZCS images may therefore not be representative. Nevertheless, earlier measurements on ammonium fluxes and sedimentary chlorophyll a at stn SK neither gave indications for a high input of fresh organic matter (Lohse et al. 1995, Van Duyl & Kop 1994) and the same holds for the sulphate-reduction rates measured during the same expedition of the present study (C. van der Zee, pers. comm.).

Hence, our data suggest an input of fresh algal detritus at stn SK comparable to that at stn GB. This contrasts to what we expected taking the depth and the relatively low primary production into account. If the overlying photic zone forms the source of the algal markers at stn SK, their relative fresh signature (relatively low ratio phaeopigments to chlorophyll a and a high proportion of pufa) implies a rapid downward transport. Usually this is possible through pellet formation due to macro-zooplankton grazing (Azam et al. 1993), or increased aggregation during the senescence of diatoms (Alldredge & Gotschalk 1989). Diatoms form at least an important component of the algal community in spring in the Skagerrak while dinoflagellates or diatoms dominate in August (Karlson et al. 1996), which supports the possibility of diatom aggregation and sedimentation as a rapid transport mechanism in the Skagerrak. However, Kjærboe et al. (1990) found that an efficient microbial loop developed at the end of May in the central Skagerrak, dominated by small zooplankton and bacteria. The combination of small fecal pellets produced by the small zooplankters and the subsequent colonisation and breakdown by bacteria results in low detrital sedimentation rates. Alternative to local production and sedimentation, the phytodetritus could be produced elsewhere, e.g. along the northern Danish coast or at the Kattegat-Skagerrak front, after which it is rapidly transported to the southern slope of the Skagerrak. Coastal Danish waters exhibit a higher production of larger phytoplankton species than central Skagerrak waters (Karlson et al. 1996), which sink faster and are less easily grazed upon. Furthermore, temporarily high nww current velocities can develop along the southern Skagerrak slope which are capable of rapid advective transport of detrital material (Eisma & Kalf 1987a). If such a mechanism is important here, it is rather efficient given the undegraded state of the sedimentary phytodetritus.

**Bacterial and terrestrial nature of sedimentary OM**

Bacterial (BACT) and algal (PUFA) fatty acids were positively correlated when all stations were pooled. This result agrees with that of Conte et al. (1995) who also found a significant positive correlation between these two fatty acid groups in North Atlantic sediments when the stations were collectively considered. However, in our study, no significant relationships emerged.
when trying to correlate bacterial and algal fatty acid concentrations at each individual station, indicating no relationship between sedimentary algal and bacterial biomass. In other studies a similar lack of correlation between bacterial biomass and phytodetritus in sediments was found (Jørgensen & Revsbech 1989, Van Duyl & Kop 1994). In our case, we attribute the overall positive correlation between bacterial and algal markers to the coincidence of high phytodetrital inventories in fine-grained sediments in combination with the well-documented positive relation between specific surface area and bacterial biomass of sediments (Dale 1974, DeFlaun & Mayer 1983). Hence, a causal relationship between concentrations of BACT and PUFA is doubtful.

A comparable situation is encountered concerning terrestrial and algal fatty acids: overall, a positive correlation, but no relation when stations are considered separately. Again, stns GB and SK showed elevated concentrations of these compounds in their sediments, in contrast to stns BF and FF. In the case of the German Bight, the nearby rivers Elbe and Weser are an obvious source for the terrestrial fatty acids. Terrigenous organic matter transported by rivers contains a higher concentration of long-chain fatty acids than marine organic matter (Kolattukudy 1976, Saliot et al. 1988). Increased concentrations of terrestrial fatty acids were also found in near-bottom samples from the German Bight, likely as a result of sediment resuspension (Boon & Duineveld 1996). To some extent, this contrasts the findings of Puls et al. (1997). They state that the net-deposited matter in the German Bight area has a marine origin, and that fluvial particles mainly settle in the river mouth and estuary.

In several studies on Skagerrak sediments a high input of terrestrial (organic) matter has been postulated (Anton et al. 1993, De Haas 1997, Liebezeit 1987). We too found elevated concentrations of long-chain fatty acids in the sediments of stn SK. By contrast, the material collected in the near-bottom sediment trap in February and August 1994 at stn SK contained relatively low concentrations of such fatty acids, comparable to the trap samples from stn FF (Boon & Duineveld 1996). These long-chain fatty acids in the Skagerrak sediments can have several sources. Supply of water and particles from the Norwegian and Swedish fjords and the Kattegat is only minor (Svansson 1975), and due to the eastward flow of water along the southern slope of the Skagerrak, matter from these areas is not likely to end up at our study site. The most probable source is suspended matter from the North Sea. The supply of particles to the Skagerrak is supposed to occur pulse-like (De Haas & Van Weering 1997), and a 12 hr deployment of a sediment trap might easily miss such an input.

Whether the long-chain fatty acids in the Skagerrak sediments indeed have a terrestrial origin is disputable. Increased concentrations of these compounds may also come from the preferential decay of short-chain fatty acids. Haddad et al. (1991) found a strong down-core increase of long-chain fatty acids in sediments from Cape Lookout Bight, USA, not related to the input from rivers. Also sedimenting (decaying) algal matter showed increased concentrations of long-chain fatty acids (De Baar et al. 1983). The sediment fatty acid composition at stn SK indicates that long-chain fatty acids are important in these sediments, but it is likely that at least part of the elevated concentrations of these fatty acids in the Skagerrak sediments originate from the relatively high supply of refractory marine-organic matter from the North Sea. (De Haas & Van Weering 1997).

**Benthic detritus vs. metabolism: a special case for the Skagerrak?**

We estimated the activity of the whole benthic community by means of the sediment oxygen demand (SOD). The RNA and DNA concentrations in the sediment exclude large benthos and was expected to be a proxy for the metabolic reaction of relatively small
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benthic organisms, mainly bacteria.

Sediment oxygen demand is closely related to the presence of labile (phytodetrital) organic matter in combination with near-bottom water (nbw) temperature (Cramer 1990, Van Duyl & Kop 1994, Boon et al. 1998). Hence, we expected the SOD to vary accordingly at our stations. As expected, the SOD increased in May, concurrent with an increased phytodetritus content of the sediment. However, while the temperature at stn FF increased with about 6°C from May to August and the chlorophyll $a$ and fatty acid inventories were comparable in August, the SOD showed a significant drop of almost 50% in the latter month. Earlier studies by Cramer (1990) and Boon et al. (1998) did show a conjointly maximum SOD and nbw temperature in August at this station. As yet, we don’t have an explanation for our unexpected decrease in SOD in August.

The SOD values at stn GB, with a minimum in February and a maximum in August, were as expected with rising temperatures and an abundance of food. This station is known to demonstrate the highest nutrient and oxygen fluxes measured in the North Sea (Lohse et al. 1995), as well as the only area in the North Sea with a predominance of sulphate-reduction in total carbon mineralisation (Upton et al. 1993).

An unexpected situation was observed at stn SK. The Skagerrak sediments show a SOD maximum in May, with a decrease in August, co-varying with the concentration of labile organic matter. The temperature increase from May to August was only 0.6°C. Interestingly, when comparing inventories of labile organic matter and SOD at stns GB and SK, we found consistently much lower SOD values at the latter station, while concentrations of labile organic matter were comparable. Our depressed SOD values agree with earlier studies (Van Duyl & Kop 1994, Lohse et al. 1995), as well as with measurements on nutrient fluxes and sulphate-reduction rates performed during the cruises of this study (C. van der Zee pers. comm.), which all indicated a relatively low bacterial metabolism in these sediments.

Using a $Q_{10}$ of 3.5 for bacterial respiration (Roden & Tuttle 1996) and a nbw temperature difference of 12°C in August with stn GB, the difference in SOD between the stations is expected to be factor 4.2. However, the actual difference in SOD is c. 10-fold. Hence, the temperature difference explains roughly 40% of the SOD differences and since neither the absolute amount of labile organic matter nor the oxygen concentration is limiting, another factor should be responsible for the major part of the depressed metabolic rates at stn SK. Keil et al. (1994) illustrated that sorption of labile organic matter plays a role in the preservation of organic matter in recent sediments with a high mineral surface area. They showed a slowing down of mineralisation rates up to 5 orders of magnitude due to this process. In an electron microscopy study on suspended material and sediment, Ransom et al. (1997) showed that labile organic matter in fine-grained sediment exists as blebs, mainly associated with clay minerals. This interaction, together with textural evidence, suggests that low permeability (decreased capillary diameters) are responsible for depressed degradation rates and enhanced organic matter preservation in fine-grained sediments. Hence, our study presents an important new result indicating the potential conservation of degradable carbon in the Skagerrak sediments.

The Skagerrak sediments contain about 20% clay and 50% fine silt (De Haas & Van Weering 1997) and thus some sorptive process might be an explanation for the remaining part of the depressed benthic metabolism at this site. The actual organic matter degradation rate in these sediments can be estimated. According to Sun et al. (1994) and Boon & Duineveld (1998), the carbon flux to the sediment can be assessed by multiplying the chlorophyll $a$ inventory with the first-order decay-rate $\lambda$, presupposing steady-state conditions. Further, assuming a decay rate $\lambda$ of 0.02 d$^{-1}$ at relatively low temperatures (Sun et al. 1994) and a carbon to chlorophyll $a$ ratio of
Benthic organic matter supply and metabolism at depositional and non-depositional sites

50 (Boon & Duineveld 1998), we find an annual average flux of 320 mg C.m\(^{-2}\).d\(^{-1}\). The SOD amounts to an average of the carbon mineralisation rate of 87 mg C.m\(^{-2}\).d\(^{-1}\), assuming 77% conversion of carbon to carbon-dioxide (Canfield et al. 1993). To achieve a match between supply and metabolism, a chlorophyll \(a\) decay rate of about 0.005 d\(^{-1}\) is needed, which is lower than rates actually calculated from field data or laboratories experiments (Bianchi et al. 1988, Sun et al. 1993, 1994). Moreover, if we use the chlorophyll \(a\) related carbon flux to calculate the annual supply of carbon to the sediments, it amounts to c. 110 g C.m\(^{-2}\).y\(^{-1}\), equal to estimates of local primary production (Skogen et al. 1995). This is not a likely figure, and together with the low decay-rate of chlorophyll \(a\) this underlines the possibility of a depressed metabolism as the result of limited availability of labile organic matter to decay processes.

Another measure by which we tried to assess the metabolic reaction of the benthic organisms on the detrital input was the RNA and DNA concentration in the sediment. This approach has previously been applied on bacterial cultures (Kerkhof & Ward 1993, Kemp et al. 1993), bivalves (Mayrand et al. 1994) and fish larvae (Westerman & Holt 1994, Clemmesen 1994). Especially in bacteria, the RNA content per cell and the ratio of RNA to DNA has shown to be positively related to the growth rate (Kerkhof & Ward 1993, Kemp et al. 1993). Hence, assuming the sedimentary nucleic acids to originate mostly from bacteria, applying this analysis on down-core slices would enable us to follow benthic metabolic reactions in time as well as in depth.

RNA as well as DNA inventories showed temporal and spatial patterns close to those of chlorophyll \(a\) and fatty acids: highest concentrations were found in May, and at stns GB and SK. According to the above mentioned studies using the RNA to DNA (R/D) ratios as a metabolic measure, we expected an R/D pattern congruent to that of the SOD. However, such a pattern was only visible at stns FF and SK. At the other stations hardly any trend in R/D ratios could be discerned. Regarding the nucleic acid concentrations and ratios in sediments and their use as metabolic markers, we need to address the following questions. Firstly, do the concentrations of RNA and DNA reflect active, living matter, and secondly, do the nucleic acids originate from bacteria alone or do they also come from detritus and small metazoans, and if so to what extent?

It is commonly assumed that RNA is very labile and will be degraded upon release from the cell, or even within a senescent cell by lysosomes. We therefor presume that RNA is derived from living cells and this excludes (phyto)detritus as a source of RNA. About the stability of DNA, there still is some discussion. The correlation between DNA and chlorophyll \(a\), and the lack of correlation between bacterial fatty acids and DNA indicates that a part of the sedimentary DNA originates from detritus. Hence, we do not consider DNA to be a good marker for bacterial biomass.

If we assume the RNA to originate mostly from bacteria, its concentration gives an impression of the activity of the bacterial community. The pattern of RNA is largely comparable to that of the SOD, except for the August measurements at stn GB and all values at stn SK. When compared to other stations, bacterial activity (RNA) at stn SK is much higher than the metabolic response (SOD) here suggests. When the RNA inventory is divided by the SOD (Fig. 6.9), this is clearly visible. To remove the effect of bacterial biomass, and because DNA is unreliable as a bacterial biomass measure, we calculated the RNA to BACT ratio (Fig. 6.10). Such a ratio can be interpreted as a specific bacterial activity, comparable to the specific bacterial growth rates. We expected to find a depressed ratio at stn SK, since the bacterial biomass is relatively high (our BACT, or Van Duyl & Kop 1994), but not very active (SOD). Here, the RNA/BACT ratio suggests a higher bacterial activity than the SOD does. It is unclear why again at stn SK such deviant values are found.
Actually, the temporal variations of these ratios at our stations compare reasonably to those of the specific growth rates measured by Van Duyl & Kop (1994), except for stn SK. Our study indicates that extended research on metabolic processes in Skagerrak sediments in relation to labile organic matter supply should yield some interesting data. Benthic ecological studies in the Skagerrak are few, especially compared to what is known about the southern North Sea.