Seasonal benthic microbial activity in the southern North Sea; oxygen uptake and sulphate reduction

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ABSTRACT: From an initial cruise, 6 sites were selected from the 41 sampled to be representative of the major types of sediment in the southern North Sea. The 6 sites in the mixed, frontal and stratified areas of the southern half of the North Sea exhibited a wide range of environmental conditions, particularly sediment type, water depth and organic matter content. Benthic microbial activity, and its seasonal variability, were determined at bimonthly intervals from September 1988 to September 1989. The significance of aerobic and anaerobic respiration in the degradation of organic carbon was investigated by measuring the rate of oxygen uptake and sulphate reduction for each sediment. All sites showed significant rates of oxygen uptake (range 5.3 to 27.8 mmol O2 m⁻² d⁻¹) and sulphate reduction (range 0.05 to 11.8 mmol SO₄²⁻ m⁻² d⁻¹), and hence of organic matter mineralization. Aerobic respiration accounted for between 47 and 89% of annual organic matter degradation depending on the site, the balance being due to anaerobic sulphate reduction. Benthic mineralisation rates were greatest at a station near the Dogger Bank and one near the Dutch/Belgian coast. However, benthic mineralisation as a proportion of the net annual primary production in the water column was higher at stratified stations in the central North Sea (average 47%) than in the more southerly stations with mixed water columns (average 26%). Estimates of benthic organic mineralisation were used to calculate the magnitude of total benthic mineralisation in the southern half of the North Sea and compared to estimates of net primary production for the same area. On the average, for the whole of the southern North Sea, benthic mineralisation was equivalent to 17–45% of the total net primary production. These results demonstrate that the bottom sediments are important sites of organic degradation in the North Sea system.

INTRODUCTION

In aquatic systems degradation of primary and secondary biomass can occur in the water column, or on and in the bottom sediments when organic detritus settles from the water column (Nedwell 1984). The relative importance of the bottom sediments in organic mineralisation will depend in part upon the depth of the water column as, other things being equal, the shallower the water column the more organic material will survive settlement through the water column and impact the bottom sediments. However, in shallow waters increased turbulence may diminish settlement rates, thus modifying the downward flux of material. In shallow coastal waters up to 50% of the organic matter production may be degraded in the bottom sediments (Jørgensen 1982, 1983).

Degradation of organic detritus in the sediment will result from the cumulative action of the benthic heterotrophic biota, both aerobic and anaerobic. Aerobic mineralisation is limited to the surficial layer of sediment into which oxygen penetrates; usually to only a few mm depth in most shallow water sediments (e.g. Revsbech et al. 1980). Below the aerobic layer organic...

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matter will be mineralised by anaerobic microbial activity. In marine sediments sulphate reducing bacteria tend to be by far the most important group of anaerobes because of the abundant sulphate in seawater (Jørgensen 1980). Bioturbation increases the transport of organic matter from the sediment surface to deeper, anaerobic layers, and therefore tends to enhance the relative importance of sulphate reduction to total degradation of organic material (Berner & Westrich 1985). In inshore marine sediments where organic input is relatively high, and where bioturbation may be significant, sulphate reduction can account for up to half of the total organic matter degradation (Jørgensen 1980, 1982, Parkes & Buckingham 1986, Christensen 1989).

The present work was undertaken as part of the North Sea Community Research Programme of the Natural Environment Research Council (UK). The intention of the research programme was to develop understanding of the southern half of the North Sea where the water is shallow, generally <50 m. Therefore the bottom sediments potentially are very important in the budgets of organic degradation and nutrient cycling. Although measurements of benthic processes have been made in the North Sea (e.g. Jørgensen & Revsbech 1989, Jørgensen et al. 1990, van Raaphorst et al. 1990, 1992), these have tended to be either for a restricted period or at only 1 or 2 stations. The present work was intended to measure benthic processes at a number of stations covering the range of sedimentary types present in the southern bight of the North Sea, and to continue measurements at regular intervals so that the seasonal ranges of activities could be evaluated.

**MATERIALS AND METHODS**

**Sample sites.** During April–May 1988, an initial survey cruise was made in RRS 'Challenger' along the standard cruise track of the NERC North Sea Programme. Forty-one benthic sites, evenly spaced along the cruise track, were sampled with a multicorer and samples of the 0 to 10 cm horizons taken for measurement of particle size distributions, organic content and sulphate reduction rates. On the basis of these initial data 6 sites were selected as representative of the sediments sampled during the initial cruise: Stn 1, 51° 45.36' N, 02° 59.96' E; Stn 2, 53° 37.10' N, 04° 35.70' E; Stn 3, 55° 30.00' N, 06° 06.10' E; Stn 4, 55° 29.90' N, 00° 54.50' E; Stn 5, 54° 39.16' N, 00° 31.06' E; Stn 6, 53° 30.78' N, 02° 59.33' E (Fig. 1). Stns 1, 2 & 6 were characteristic of the sandier sediments in the southernmost region of well-mixed water columns near the English Channel. Stns 2 & 6 also were near the position where a front develops in the water column during the summer. Stns 3, 4 & 5 were characteristic of the more northerly muddy stations in the central region of the North Sea which stratify during summer. Water depths varied from 25 to 81 m, with the deeper sites in the northern stratified part of the southern bight (Fig. 1, Table 1). The sites were sampled at approximately bimonthly intervals from September 1988 to September 1989, returning to the position of each station as accurately as possible within the operating characteristics of the DECCA navigation system.

**Sampling method.** Undisturbed sediment cores, between 15 and 25 cm in length, were collected from the sites using a Multiple Core (Barnett et al. 1984). Special core tubes (internal diameter 5.78 cm) were developed to incorporate 2 sections that were joined with an outer perspex sleeve and sealed with 'O' rings. The lower section of each core tube (length 39.6 cm), in which the sediment core was collected, was removed from the corer only when excess water in the upper section had been siphoned off. The upper portion of the lower section was accurately machined to enable insertion of, and effective sealing by, stirring heads for oxygen uptake measurements. Modification of the longer core tubes used by Barnett et al. (1984) was essential as these made extraction and accurate sectioning of the sediment difficult and were too long to enable effective mixing at the sediment water interface during flux measurements. The volume of water overlying the sediment was between 100 to 400 ml in these modified cores. On average 20 cores were collected from each site per cruise, with 2 deployments of the corer.

**Measurement and analyses of biological activity and sediment characteristics.** Immediately after collection sediment cores were sealed top and bottom...
with rubber bungs and placed in a cold room at the
temperature of the water immediately overlying the
sediment (i.e. the in situ temperature). At each site sea-
water (approximately 100 l) was collected from as close
to the sea bed as possible with water sampling bottles
on the CTD. This water was placed in a darkened
PVC tank and aerated, circulated and cooled using a
thermocirculator (Churchill Instruments Ltd, Ux-
bridge, UK), at the in situ temperature of that site. Nine
sediment cores with their tops removed were carefully
placed vertically in the tank, without disturbing the
sediment, and incubated completely immersed for
between 4 and 18 h. This allowed the sediment to re-
equilibrate after coring before rates of oxygen uptake
and sulphate reduction were measured. The length of
the equilibration period depended on the time interval
available between sampling stations. Measurements of
the vertical profiles of the physical and chemical char-
acteristics of the sediment were taken from the
remaining cores as soon as possible. This was normally
< 2 h after sampling.

Oxygen uptake rates. Six of the intact equilibrated
cores were used to measure the oxygen uptake at each
site. The measurements were made according to the
method and equipment of Parkes & Buckingham
(1986) with the cores incubated at the in situ temperature
and in the dark. The tops of the core tubes were
sealed with an electronic magnetic stirrer (Rank Broth-
ers Ltd, Scientific Division, Cambridge, UK) which
could be moved further into the core to compensate for
sample removal. Enclosed water was sampled with a
10 ml glass syringe for analysis of dissolved oxygen
concentrations using an automated Winkler ampero-
metric back-titration (Talling 1973; Mettler DL20 titra-
tor, MSE, Crawley, UK). Water current velocity above
the sediment surface without resuspending the sedi-
ment itself. The data from both treatments was aver-
aged and thus the oxygen uptake data includes a mea-
sure of the effects of different near-sediment current
velocities.

Three dissolved oxygen determinations were made
from each core. The first was just prior to each core
being sealed (time zero), the second at a midpoint time
interval, and the third at the end of the incubation
period. Oxygen uptake rate was calculated from the
mean time zero value and the 12 measured dissolved
oxygen concentrations. The length of each incubation
period depended on the time available between
sampling stations and the requirement not to allow
oxygen depletion from the overlying seawater to
exceed approximately 15% of air saturation. The incu-
bation periods therefore varied from between 2 and
10 h depending on the site and the time of year.

As soon as the cores had been removed from the corer
the overlying water from 1 core was siphoned into Win-
kler bottles (4 ⩾ 125 ml volume). Two were fixed imme-
diately and 2 were incubated in the dark at the in
situ temperature these subcores were
injected with 2 yCi (74 MBq) of 35S0, (between 2 and
10 μl was injected, depending on the specific activity)
throughout the length of each sub-core. The samples
were incubated under OFN at their in situ temperature
for 24 h. The samples were then frozen at -20°C and
stored for later analysis in anaerobic jars under OFN to prevent any sulphide reoxidation. Zero time blanks were precooled in a freezer (approximately 30 min) prior to injection and immediately frozen under OFN at -20 °C after injection.

After return to the laboratory the samples were analysed for 35S in acid volatile sulphide (AVS) and pyrite plus elemental sulphur [S0] (PVS) (Parkes & Buckingham 1986). Sulphate reduction rates were calculated according to the method of Jørgensen (1978) after subtraction of any activity in the blanks.

Water and organic matter content. One core from each site was divided into 5 cm depth sections and 10 ml from each stored frozen. The percentage water content was calculated by weight loss on freeze drying (Edwards High Vacuum, Crawley, UK). The percentage organic matter content was calculated as weight loss on heating aliquots of dried samples at 450 °C overnight in a muffle furnace (Gallenkamp, Loughborough, UK).

RESULTS

Sediment characteristics

The mean organic matter content and particle size distributions of each sediment are shown in Figs. 2 & 3. Particle size fractions were determined according to the Wentworth scale, but are summarized in 2 fractions; sand and fine silt/clay. The surface sediment (0 to 5 cm) at Stn 1 was coarse sand with a low organic matter content (<1%). Each of the other sites had fine sand with higher organic matter, usually 1 to 2%. Stn 3 had the highest organic content (mean 2.9%) and highest percentage silt/clay. The sites in decreasing order of organic matter content were Stns 3, 4, 6, 5, 2 and 1.

Temperature and dissolved oxygen

The temperature of the water immediately overlying the sediment at each site is shown in Fig. 4. Stns 1 & 2 in the continental coastal region and Stn 6 in the southern British coastal region had well-mixed water columns throughout the year showing a seasonal temperature variation between 7 and 18 °C. The more northerly Stns 4 & 5 near the British coast exhibited stratified water columns during the summer and temperatures in the water immediately overlying the sediment remained between 6 and 10 °C throughout the year. Stn 3, at a similar latitude to Stns 4 & 5 but in the eastern area of the central North Sea, exhibited a well-mixed water column in September 1988 but stratification was present in September 1989, indicating that the front developed in a different position in the 2 summers.

The dissolved oxygen concentration in the water immediately overlying the sediment is shown for each site in Fig. 4. The concentration at stratified Stn 3 was found to be depleted to 2.7 mg L⁻¹ in September 1989, equivalent to a depletion to 27% of the concentration...
measured in winter (February 1989). When the salinity (34.4 to 34.8%) and seasonal changes in water temperature were taken into account, this represented a summer decrease of dissolved oxygen to 42% of air saturation, compared to 147% saturation of oxygen with respect to air during the winter (February 1989). All the other sites had summer oxygen concentrations in the water of approximately 7 to 9 mg l⁻¹, and were often supersaturated with respect to air. In contrast, during July 1984, Kremling et al. (1987) failed to detect any depletion of oxygen below the thermocline in a north-south transect of the North Sea which encompassed the stratified area.

**Benthic activity**

Seasonal changes in benthic microbial activity, as reflected by the rates of oxygen uptake at the sediment surface and sulphate reduction within the sediment, are shown in Figs. 5 & 6. There were no significant differences (p > 0.05) between the triplicate cores measured at the 2 different stirring rates. All 6 replicates for a station were therefore pooled, and the rates of O₂ uptake which are shown (Fig. 5), and the associated standard errors, include any differences due to the stirring regimes used. Oxygen uptake in the incubated bottom water samples was on average <5% of the measured sediment oxygen uptake. This was considered to be part of the benthic boundary layer metabolism and hence not subtracted from the sediment oxygen uptake rates. Oxygen uptake rates in winter (December 1988 to February 1989) were between 5 and 10 mmol O₂ m⁻² d⁻¹ at all sites. In contrast, during the summer the uptake rates were found to be more variable and site dependent. Stns 2 & 3 had marked increases in rates during the summer to between 15 and 28 mmol O₂ m⁻² d⁻¹, compared to Stns 1 & 6 which only reached 7 to 15 mmol O₂ m⁻² d⁻¹. At Stns 4 & 5 there was little seasonal change in the rates of O₂ uptake because of stratification of the water column during summer. The measured daily O₂ uptake rates were integrated with respect to time to give annual O₂ uptake for each of the 6 sites (Table 1). The range of annual O₂ uptake rates was relatively narrow, with the highest at Stn 2 being only a factor of 1.6 higher than the lowest rate at Stn 5.

Depth profiles of sulphate reduction showed that on average >80% of the depth-integrated sulphate reduction over 0 to 25 cm occurred within the top 0 to 15 cm horizon (e.g. see Fig. 7). Therefore, although depth-integrated rates of sulphate reduction were only available down to 20 cm (Fig. 6), as this was the normal depth of sediment recovered by the corer, deeper sediments would not have made a substantial contribution to the measured rates. Rates of sulphate reduction were generally <1 mmol SO₄ m⁻² d⁻¹ in the winter with a small increase in the summer period. Stn 6 was rather different with winter rates of approximately 3 mmol SO₄ m⁻² d⁻¹ which doubled during the summer. Overall, O₂ uptake increased to a greater extent in the summer (x2) than sulphate reduction (x1.6).
highest sulphate reduction rates measured were at Stn 2 in September 1988 (11.8 mmol SO4 m-2 d-1), where rates were elevated at all depths but particularly at 5 to 10 cm (124.2 mmol SO4 ml-1 d-1). Sulphate reduction rates decreased sharply during winter at this site and began to increase again during late summer. Unfortunately, no measurement is available for September 1989. At Stns 4 & 5 seasonal variation was limited compared to the other sites. Over 80% of sulphate reduction was to acid volatile sulphides (AVS) rather than to elemental sulphur and pyrite (PVS).

The depth-integrated values for sulphate reduction (Fig. 6) were also integrated with respect to time to yield an estimate of the annual total of sulphate reduction for each station (Table 1). These annual rates of sulphate reduction were much more variable than annual rates of O2 uptake: the highest rate at Stn 6 was a factor of 9 greater than the lowest value at Stn 1.

**DISCUSSION**

Our data demonstrate that the North Sea bottom sediments studied were important sites of organic matter accumulation and degradation. Stns 3 & 4 in the stratified region exhibited the highest organic matter contents, with greatest concentrations in the surface layers, decreasing with increased depth. This suggests that these were accumulative sites, corroborated by their higher percentage of fine silt/clay particles. Profiles of 210Pb and 137Cs (Nedwell et al. 1993) confirmed that net accumulation of sediment occurred at Stns 3 & 4 but at other sites net accumulation of sediment could not be demonstrated. The other 4 sites, with a lower content of fine particles, had lower organic contents which tended to increase with sediment depth. The reason for this increase is unclear but it might reflect depositional changes, mixing of sedimented material by physical processes or bioturbation, changes in rates of organic matter decomposition or...
The sedimentary organic content did not appear to be related to the rates of organic matter degradation, there being no significant correlations (p > 0.5) between sedimentary organic content and either sulphate reduction or oxygen uptake. This probably reflected differences in the relative rates of turnover of the organic inputs at each site and differences in the refractility of the organic matter remaining at each site.

In all cases appreciable rates of both aerobic and anaerobic degradation of organic matter were measured (Table 2). Van Raaphorst et al. (1990) reported O$_2$ uptake rates during July and August 1988 averaging 12 (± 6) mmol O$_2$ m$^{-2}$ d$^{-1}$ for 6 stratified stations in the Dogger Bank area nearest to our Stns 3, 4 & 5. Their measurements compare well with the 10 to 15 mmol O$_2$ m$^{-2}$ d$^{-1}$ determined by us for the northernmost 3 stations at the same time of the year (Fig. 5). Again, at their Stn FF, van Raaphorst et al. (1992) reported benthic O$_2$ uptake during July and August 1989 as 32 to 40 mmol O$_2$ m$^{-2}$ d$^{-1}$, which is similar to our rate at the nearby Stn 2 of 28 mmol O$_2$ m$^{-2}$ d$^{-1}$ at the same time of the year. Cramer (1990) reported a winter rate at Stn FF of 5 mmol O$_2$ m$^{-2}$ d$^{-1}$ which is similar to our measured rate at Stn 2 during winter.

There are no data available for sulphate reduction rates in the North Sea proper although Jørgensen & Revsbech (1989) reported sulphate reduction rates varying between 0.08 and 6.9 mmol SO$_4$ m$^{-2}$ d$^{-1}$ during July and August for sediments ranging in depth from 14 to 200 m water depth across the Baltic-North Sea transition zone and rates of oxygen uptake of 8.1 to 22.7 mmol O$_2$ m$^{-2}$ d$^{-1}$. For the same transition zone, Jørgensen et al. (1990) reported sulphate reduction rates during July 1979 of 2.4 to 7.9 mmol SO$_4$ m$^{-2}$ d$^{-1}$, although in both of these studies only sulphate reduced to AVS was measured and they did not also measure PVS as we did in our study. The range of sulphate reduction for our sites at the same time of year was 0.054 to 2.5 mmol SO$_4$ m$^{-2}$ d$^{-1}$, and less than 20% was due to PVS. Taking into account only AVS (range 0.043 to 1.97 mmol SO$_4$ m$^{-2}$ d$^{-1}$) suggests that while the rates of oxygen uptake (range 9.9 to 27.9 mmol O$_2$ m$^{-2}$ d$^{-1}$) in the southern half of the North Sea that we studied were similar to those of the Baltic-North Sea transition zone, the rates of sulphate reduction were significantly lower. The Baltic-North Sea transition zone is atypical of the rest of the North Sea, however, being an area of strong deposition and silty, organic sediments where anoxic organic degradation might be expected to be more significant.

Seasonal changes in the rates of benthic oxygen uptake were particularly apparent at Stns 1, 2 & 6, with little seasonal change at Stns 4 & 5 (Fig. 5). This was probably correlated with the differences in water column depth and stratification, with strong seasonal changes of temperature occurring at the first 3 stations where the water column was usually homogeneous in a mean water depth of 35 m. At the stratified Stns 4 & 5 (mean water depth 72 m) there was little seasonal change of bottom water temperature (Fig. 4) and the sediments and bottom water were therefore likely to be partially isolated from seasonal changes in the epilimnion. Stn 3 was shallower than Stns 4 & 5 and was only stratified during the 1989 summer, but as there was still a strong seasonal increase in O$_2$ uptake during this period, the sediments must have been closely coupled with changes in the surface water. Although for data from all sites there was a significant correlation between temperature and O$_2$ uptake (p < 0.02), and temperature and sulphate reduction (p < 0.05), there was considerable variability in these relationships between different sites. There were significant (p < 0.05) relationships between temperature and both O$_2$ uptake and sulphate reduction rates at Stn 6; between temperature and O$_2$ uptake only for Stns 1, 2 & 5; between temperature and sulphate reduction only at Stn 3; and no significant relationships between temperature and either O$_2$ uptake or sulphate reduction for Stn 4. Presumably the significant relationship with temperature is both direct and indirect, e.g. via seasonal changes in water column productivity. A positive relationship with both O$_2$ uptake and sulphate reduction at Stn 6 may reflect a strong coupling between water column and benthic processes, which is also consistent with the dominant role of sulphate reduction in organic matter degradation at this site (Table 2). The lack of significant relationship with temperature for the stratified Stn 4 may reflect some uncoupling between the water column and benthic processes. The remaining sites represent a situation between these 2 extremes.

Increased benthic oxygen uptake during the summer was reflected in decreases in the dissolved oxygen concentration of bottom water at all sites (Fig. 4), but most significantly at stratified Stn 3 where the dissolved oxygen concentration fell to 0.5 mmol O$_2$ m$^{-1}$.
solved oxygen concentration decreased to only 42% of air saturation. Although, except for Stn 6, this O2 depletion of bottom water seemed to be associated with only a limited increase in sulphate reduction rates (Fig. 6), when expressed relative to the low rates measured previously at each site the increases were similar \((\times 1.9)\) to the increase of O2 uptake during the same period \((\times 1.3)\).

Total organic carbon mineralisation was calculated stoichiometrically from the measured O2 uptake, assuming that sulphide was reoxidised within the surface oxic layer of sediment and therefore contributed to O2 uptake rate, and that there was a 1:1 ratio between O2 uptake and organic matter oxidation to CO2 (Jørgensen 1983). The contribution of anaerobic sulphate reduction to organic matter degradation was calculated from the 1:2 stoichiometry between sulphate reduction and organic carbon, and the estimate of the total organic carbon mineralization (Jørgensen 1983). On an annual basis benthic organic matter mineralisation was dominated by aerobic metabolism (Table 2), sulphate reduction accounting for between 11 and 53% of the total. The smallest proportion of sulphate reduction was at Stn 1, where the large amount of coarse sand (44%) and low organic content presumably facilitated oxygen penetration into the sediment and maximised the aerobic layer. Conversely, the largest proportion of detrital degradation driven by sulphate reduction (53%) was at Stn 6 which was predominantly fine sand (88%) with a higher organic content. Concurrently with our study, Joint and coworkers (I. Joint pers. comm.) measured primary production at or near 5 of our 6 stations. Table 3 shows their estimates of annual net primary production (NPP), together with our estimates of benthic mineralisation of organic carbon. If we ignore any effects of lateral transport to or from adjacent areas, at the 5 stations benthic mineralisation accounted for between 16.2 and 55.2% of the NPP. The smallest proportion was at Stn 1 in the turbulent, well-mixed southerly area near the English Channel mouth where concentration of organic carbon was equivalent to 35.5% of the NPP in the water column, showing that the bottom sediments were important sites for organic matter degradation, and hence recycling of elements from settled biomass back to the water column.

Aletsee & Rick (1988, cited in Kempe & Pegler 1991) have estimated the NPP in the whole 517 000 km² of the North Sea as \(150 \times 10^6\) t C yr\(^{-1}\). The area of the southern half of the North Sea is approximately \(2.4 \times 10^{11}\) m\(^2\) between 55° 30' N and the entrance of the Dover Straits, and proportionate NPP would be equivalent to \(69.6 \times 10^6\) t C yr\(^{-1}\). Reid et al. (1990) indicated that NPP in the southern North Sea was about 200 g C m\(^{-2}\) yr\(^{-1}\) or ca \(40 \times 10^6\) t C yr\(^{-1}\) in the southern half. In a study of primary production in the southern North Sea, which was also a component of the North Sea Programme, Joint & Pomroy (1992) measured the net annual primary production in the 6 southerly ICES boxes. When allowance was made for the proportion of the areas of the ICES boxes which corresponded to the study area of the North Sea Programme, their estimate of the total annual NPP was ca \(26 \times 10^6\) t C yr\(^{-1}\). Thus estimates of NPP for the southern half of the North Sea range between 26 and \(69.6 \times 10^6\) t C yr\(^{-1}\).

Estimates of total organic matter degradation in the bottom sediments of the southern half of the North Sea (south of 55° 30' N) can be obtained in a number of ways. If an average value for annual mineralisation at the 6 sites \(4.06 \pm 0.8\) mol C m\(^{-2}\) yr\(^{-1}\) is used the total mineralisation of detrital organic carbon on an annual basis in the southern part of the North Sea is approximately \(9.74 \times 10^{11}\) mol C yr\(^{-1}\) \((1.17 \times 10^6\) t C yr\(^{-1}\)). Alternatively, data on the types of bottom deposits in the southern bight of the North Sea are available (Anon. 1965, Veenstra 1971) and have been characterised into 6 types: mud 0.4%; sand 23.0%; mud/sand 21.3%; sand/gravel 38.2%; mud/sand/gravel 10.2%; rock/sand/gravel 6.9% (D. Hydes & S. Thomson pers. comm.). Considering only the 5 significant areas of sediment types, Stns 2, 5 & 6 occurred on sand; Stn 3 was on mud/sand; Stn 4 was on sand/gravel; and Stn 1 was taken as characteristic of both mud/sand/gravel and rock/sand/gravel bottoms. The annual organic matter mineralisation on each sediment bottom type was calculated from the rates at the representative stations and the area of each type of bottom in the southern bight. This gave a total annual mineralisation of \(1.11 \times 10^7\) t C yr\(^{-1}\) which is very similar to the figure derived from an annual rate averaged from all stations. Considering the range of the various estimates of NPP, our estimation of benthic mineralisation of organic

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**Table 3. Benthic mineralisation of organic matter as a percentage of the net primary production at each station**

<table>
<thead>
<tr>
<th>Stn</th>
<th>Primary production* (mol C m(^{-2}) yr(^{-1}))</th>
<th>Benthic mineralisation (mol C m(^{-2}) yr(^{-1}))</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>20.0</td>
<td>3.2</td>
<td>16.2</td>
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<tr>
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<td>11.6</td>
<td>4.6</td>
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<td>6</td>
<td>20.0</td>
<td>4.5</td>
<td>22.2</td>
</tr>
</tbody>
</table>

*Primary production data from I. Joint (pers. comm.)
matter in the southern North Sea is equivalent to 17 to 45% of the total net primary production in this area, emphasising the importance of the bottom sediments in organic matter degradation and nutrient recycling.

Acknowledgements. This paper is a contribution from the Natural Environment Research Council's North Sea Community Research Programme, and the work was funded by a research grant (CST/02/328) to D.B.N. and R.J.P. The authors thank Mr. J. Watson for his invaluable assistance on the cruises, and the NERC Dunstaffnage Marine Laboratory, Oban, for the use of the Multiple Corer and other facilities. The authors also acknowledge the technical support on the cruises and laboratory analyses by Miss S. Vaughan, Mr M. Rutter and Dr M. James. Our thanks also go to the officers, crew and support staff of the RRS 'Challenger'.

LITERATURE CITED


