Respiration partitioning in contrasting subtidal sediments: seasonality and response to a spring phytoplankton deposition

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Keywords
Bacteria; macrobenthos; meiobenthos; North Sea; respiration; sediment community oxygen consumption (SCOC).

Abstract
Biomass and respiration rates of bacteria, nematodes and macrobenthos were estimated in relation to the deposition of the spring phytoplankton bloom at two contrasting sites in the Southern North Sea: one with fine-grained sediment close to the coastline and another with highly permeable sediments. Sediment community oxygen consumption (SCOC) was also measured. Bacterial biomass was relatively similar at both stations, whereas nematode and macrobenthic biomass were higher in fine-grained sediment. In fine sediments, bacterial biomass increased quickly after deposition of the phytoplankton bloom, whereas the response of nematodes and macrobenthos was delayed. In coarser sediments, nematodes and macrobenthos also showed a fast response in terms of density and biomass. Respiration in permeable sediments was mainly dominated by bacteria at all periods of the year. Hence, nematode and macrobenthic respiration did not contribute strongly to SCOC. This is in contrast to the patterns observed in finer sediments, where both macrofauna and nematodes were important oxygen consumers as well. Macrobenthos contributed more to total SCOC than did nematodes in winter. However, shortly after the arrival of phytodetritus at the sea floor, nematodes and macrobenthos contributed equally to the total SCOC, indicating that all benthic size classes should be taken into account when investigating marine benthic respiration rates.

Problem
All but a few (e.g. hot vents and cold seeps) marine benthic communities are directly or indirectly dependent on primary production from the euphotic zone. In coastal subtidal sediments, the deposition of high-quality phytodetritus from phytoplankton blooms represents a major source of organic matter (OM) to the benthos, and sediment characteristics such as texture importantly affect the fate of this organic material (Graf 1992).

In fine-grained sediments, accumulation of phytodetritus, e.g. after spring bloom sedimentation, can cause steep vertical profiles of labile OM (Steyaert 2003). Remineralisation of newly settled OM can induce hypoxic/anoxic conditions (Graf 1992) and the decomposition of this OM is often delayed (Boon & Duineveld 1998; Provoost et al. unpublished data). In coarser, permeable sediments, such vertical gradients are often absent and subsurface peaks of chlorophyll a are common (Jenness & Duineveld 1985; Ehrenhauss & Huettel 2004; Ehrenhauss et al. 2004a; Vanaverbeke et al. 2004b). These sediments are typically characterised by a rapid degradation of OM (Ehrenhauss et al. 2004b; Vanaverbeke et al. 2004b; Janssen et al. 2005; Bühring et al. 2006).

The different biogeochemical processes in such contrasting sediments can affect the response of the resident
benthos. Hubas et al. (2007a), for instance, observed different relative contributions of bacteria, meiobenthos and macrobenthos to total heterotrophic production in intertidal stations with contrasting sediment characteristics.

Nematode communities from different environments can have different roles in the benthic carbon cycle, depending on differences in OM quality and quantity as well as in the biogeochemistry of the sediment (Hubas et al. 2007a). In general, however, the nematode contribution to benthic metabolic activity is poorly known. For instance, estimates of the contribution of nematodes to total carbon turnover range from <1% in an estuarine tidal flat (Van Oevelen et al. 2006a) to maximum values of 13% at a 206-m-deep station at the continental slope of the Goban Spur (NE Atlantic Ocean) (Soetaert et al. 1997) and 10.7–36.6% at a depth of ±830 m at the Hydrate Ridge, off Oregon, USA (Somerfield et al. 2005).

The above estimates are typically based on allometric relationships between body mass and respiration because of methodological limitations at measuring nematode respiration rates under (close to) in situ conditions (Somerfield et al. 2005). The present study similarly uses allometric relationships between biomass and respiration for nematodes and macrobenthos, as well as estimates of bacterial respiration based on production measurements. It aims at comparing the response of total sediment community oxygen consumption (SCOC) and of the major benthic size groups, bacteria, nematodes (the predominant meiobenthic taxon) and macrobenthos, to a spring phytoplankton bloom deposition at two contrasting continental shelf sediments in the North Sea. By comparing the response in biomass and metabolic activity of these three major heterotrophic benthic compartments to the OM input, we aim at clarifying their relative importance in the mineralisation of the OM that reaches the sediment. Chlorophyll a concentration in both water and sediment was used as an indicator of OM availability.

Possible sediments. The other is a depositional station with finer sediment and rich in labile OM. Earlier research on these contrasting stations (Steyaert 2003; Vanaverbeke et al. 2004b; Franco et al. 2007, 2008a,b; Van Oevelen et al. 2009) showed that this has important consequences on the diversity and densities of the bacterial, meiobenthic and macrobenthic communities on one hand and on the food web dynamics of the meiobenthos on the other. In the fine sediments, nematodes become numerically important shortly after the phytoplankton bloom, suggesting that their importance in carbon mineralisation processes may also increase in spring. In contrast, the harsh conditions for metazoan organisms in permeable sediments lead to the hypothesis that their benthic metabolism may be strongly dominated by bacteria.

By comparing patterns in biomass and metabolic activity of bacteria, nematodes and macrobenthos in two contrasting continental shelf sediments in the North Sea, prior to, during and after the spring phytoplankton bloom deposition, we aim at clarifying their relative importance in the mineralisation of the OM that reaches the sediment.

Study area

Samples were taken from the Belgian Continental Shelf (BCS) stations 115bis_{fine}, located close to the coast (51°09.2′N; 02°37.2′E; 13 m depth), and 330_{coarse}, located further offshore (51°26.0′N; 02°48.5′E; 20 m depth) (Fig. 1). Station 115bis_{fine} is a deposition station, characterised by the presence of fine sediments (median grain size: 185 μm) with a small fraction of mud (4%) (Steyaert 2003). Station 330_{coarse} consists of medium sand (median grain size: 329–361 μm) without mud (Vanaverbeke et al. 2004a,b).

Details about biological (bacteria, meio- and macrobenthos) and biogeochemical patterns at both study sites can be found in Steyaert (2003), Vanaverbeke et al. (2004b), Franco et al. (2007, 2008a,b) and Van Oevelen et al. (2009).

Material and Methods

Sampling

Sampling at both stations was conducted in February, April and October 2003 from the RV Belgica. The following sampling procedures were conducted at both stations (115bis_{fine} and 330_{coarse}) at all three sampling dates.
The water column was sampled 3 m below the air–sea interface and 1 m above the sea floor using 10-l Niskin bottles. Pigment samples were collected by filtering 500 ml of water from each depth onto GF/F glass microfibre filters (i.d. 4.7 cm) using a vacuum pump. This procedure was repeated three times. The samples were kept in the dark, preserved at −20 °C on board and stored at −80 °C at the laboratory.

The sediment was sampled for sediment community oxygen consumption (SCOC), chlorophyll a, meio- and macrobenthic activity, and bacterial production (BP) using a box corer, deployed three times to obtain three independent replicates. Only box cores with clear overlying water and undisturbed sediment surface (visual inspection) were retained. From each of the three replicated box corers, one perspex core (i.d. 9.5 cm, with O-ring fitted Teflon lids to prevent pore water leakage) was taken for SCOC measurement; one perspex core (i.d. 3.6 cm) for chlorophyll a concentration; one perspex core (i.d. 3.6 cm) for nematode density and biomass analysis; one perspex core (i.d. 3.6 cm) for bacterial density and biomass analysis and one perspex core (i.d. 14 cm) for BP measurements.

The SCOC and bacterial production cores were filled with water collected 1 m above the sea floor using 10-l Niskin bottles, closed and transported to the laboratory. From the cores for chlorophyll a concentration, the top layer (0–1 cm) was removed and preserved at −20 °C on board and stored at −80 °C at the laboratory. The cores for bacterial and nematode counts and biomass determinations were sliced in 1-cm slices down to a maximum depth of 5 cm, and the samples preserved with a neutral hot 4% formaldehyde-tap water solution. Samples for bacterial abundance and biomass analyses were thoroughly shaken and stored in the refrigerator. Bacterial abundance and biomass were determined using only the three independent replicates. Only box cores with clear overlying water and undisturbed sediment surface. The oxygen concentration in the water was monitored every 2 min for a period of 18 h. SCOC, expressed as mmol O2·m−2·day−1, was calculated by means of linear regression of the decrease in oxygen concentration over time (1–10 h after start incubation) (Moodley et al. 1998). During this time O2 concentration never decreased >30% such that oxygenated conditions were maintained. Blank incubations showed no detectable O2 consumption. Due to methodological problems, only one replicate was available at station 330_coarse in February.

Bacterial biomass

Samples for bacterial counts were prepared following Starink et al. (1994). Ultrapure water (prepared by a Milli-Q system) was added to the sample until a volume of 9.5 ml and 0.5 ml Na2P2O7 (0.2 m) was added. This mixture was sonicated five times for 30 s using a Soni-prep 150 (10 W). In between sonication pulses, the sample rested on ice for 30 s. Before staining samples were diluted 10–1000 times using tris(hydroxymethyl)aminomethane (TRIS). A subsample was filtered onto a 0.2-μm polycarbonate filter and stained with Sybrgold (Molecular Probes). Filters were then mounted on slides. Counting of bacterial cells was performed using a Leica confocal microscope connected to QWIN software. From every image, 16 scans were made 0.2 μm vertically apart from each other. In such a way, a 3.2-μm thick image was analysed. From each scan, all particles >0.2 μm were counted and allocated to a size class. Per slide, 50–100 images were analysed. Bacteria were assumed to be spherical and their volume was calculated as $4 \times \pi \times r^3/3$ ($r$ = radius), with a radius estimation of half the average of the largest (L) and smallest (S) diameter. Bacterial volume ($\mu m^3$) was converted to biomass (fg C) using a conversion factor of 310 fg C/μm3 (Fry 1990). Biomass was therefore calculated according to:

$$(4 \times 3.141593 \times ((L + S)/4)^3/3) \times 310$$

At both stations bacterial biomass and densities did not differ between the two sediment layers (0–1 and 4–5 cm)
(Franco et al. 2007), and therefore bacterial biomass and densities in the 0–5 cm layer were calculated as the value for the 0–1 cm layer multiplied by five.

**Bacterial production**

BP was measured using the $^3$H-leucine incorporation method as modified from Van Duyl & Kop (1994) and Hamels et al. (2001). After transport to the laboratory, the sediment cores were incubated in the dark at in situ temperature and allowed to stabilise for 24 h. Overlying water was then gently siphoned off; the sediment was removed from the cores by allowing it to slide down gently. The 0–1 cm and 4–5 cm horizons were sliced off and retained for BP measurements.

Aliquots of 200 μl of sediment were pipetted into 2-ml Eppendorf tubes using an automatic pipette with cut-off tips, and 100 μl of a leucine solution was added. The tubes were again incubated in the dark at in situ temperature for 40–60 min, after which the incubation was stopped through the addition of 1.5 ml ice-cold 5% trichloroacetic acid (TCA). Isotope dilution was determined using three different leucine concentrations, containing 0.2, 0.4 and 0.6 nmol leucine (0.1%) for 24–48 h at room temperature. Sediment particles were removed by centrifugation (5 min at 1000 g), and the supernatant was transferred to glass scintillation vials where it was mixed with 10 ml of a scintillation cocktail (Lumasave Plus, Lumac). Radioactivity was measured as disintegrations per minute (dpm) on a Beckman LS-6000 liquid scintillation counter. Quenching was corrected for by automatic external standardisation. After subtraction of blanks, BP was calculated as:

$$\text{Production (mgC \cdot m}^{-1} \cdot \text{h}^{-1}) = \text{dmp} \times \frac{60}{t} \times \frac{1}{\left(2.2 \times 10^{12}\right)} \times M \times \frac{1}{\% \text{Leu}} \times \frac{C/\text{Prot}}{\text{volume (ml)}} \times \frac{1}{\text{total Leu added (nmol) + isotope dilution (nmol)}} \times \frac{\text{SA} \times [^3\text{H}] \text{Leu added (nmol)}}{$$

where $t$ = incubation time (min); 1 Ci = $2.2 \times 10^{12}$ dpm; $M =$ the molecular weight of leucine; $% \text{Leu} = 0.073$, i.e. the fraction of leucine in protein; $C/\text{Prot} = 0.86$, i.e. the carbon to protein ratio (Simon & Azam 1989); SA = specific activity of the added leucine in Ci:mmol$^{-1}$, and then converted to units of mg C m$^{-2}$ day$^{-1}$.

**Nematodes**

Meiobenthos (the animals passing through a 1-mm sieve and retained on a 38-μm sieve) was extracted from the sediment by centrifugation with LUDOX HS-40 at a specific density of 1.18. Centrifugation was repeated three times (Heip et al. 1985). After staining with Rose Bengal, nematodes were counted under a binocular microscope. From each 1-cm sediment slice (up to 5 cm deep) 120 nematodes were randomly picked (following Vincx 1996) and mounted on Cobb slides for measurement of length and maximal width. When <120 individuals were present, all nematodes were picked out. Measurements were performed using an image-analyser (Quantimet 500+).

Nematode individual biomass was calculated from Andrassy’s (1956) formula:

$$\text{PP} = \frac{w^2 \times l}{1.6 \times 10^6}$$

where WW is the individual wet weight (μg) and $w$ and $l$ the maximum width (μm) and nematode length (μm), respectively. We assumed a dry-to-wet-weight ratio of 0.25 (Wieser 1960) and a carbon content of 51% of dry weight (de Boveé 1987).

For the biomass estimates two replicate cores per station and sampling occasion were processed, each core comprising five depth strata.

**Macrobenthos**

Macrobenthos samples were sorted, counted and the organisms picked up separately according to taxa. The organisms were washed with distilled water and paper dried and then weighed to determine wet weight (WW). They were dried at 60 °C in an oven for 4 days to determine the dry weight (DW) and dried once again at 500 °C in a muffle furnace for 2 h to determine the ash free dry weight (AFDW).

**Respiration estimates**

**Bacterial respiration**

Bacterial respiration (BR, expressed in mg C m$^{-2}$ day$^{-1}$) was estimated from BP using a fixed bacterial growth efficiency (BGE) of 20% (Osinga et al. 1997). Potential implications of the use of a fixed BGE for the interpretation of our results are treated in the pertinent Discussion section. BR was converted to oxygen units assuming a respiratory quotient (RQ) of 1 (del Giorgio & Cole 1998). As, at station 115bisVINE, oxygen is only present in the
0–1 cm layer (Steyaert 2003), all oxic BR at this station was assumed to be limited to the 0–1 cm layer. At station 330 COARSE oxygen is present throughout the whole sediment depth studied (Vanaverbeke et al. 2004b). BP did not differ between the 0–1 cm and 4–5 cm sediment layers (data not shown). Therefore BR for the 0–5 cm depth stratum at station 330 COARSE was obtained by multiplying the respiration of the 0–1 cm layer by 5.

Nematode respiration
Total nematode respiration was estimated based on the summed individual DW following de Bovée & Labat (1993), assuming a Q10 expression for temperature dependence, and extrapolated to the total number of nematodes present in a sample:

\[ R(T) = 0.0449 \times DW^{0.8544} \times \exp^{[\ln(2)](T-20)} \]

where R is respiration (µg C day\(^{-1}\)), DW is individual dry weight (µg C), T is temperature (°C) and Q10 = 2.

Macrobenthos respiration
For macrobenthos, an organic carbon content of 50% of AFDW was assumed (Wijsman et al. 1999). Respiration was estimated based on the AFDW using the Mahaut et al. (1995) formula for shallow-water macrobenthos:

\[ R = 0.0174 \times W^{0.844} \]

where R is respiration (mg C day\(^{-1}\)) and W is the mean individual AFDW (mg C), valid for the temperature range of 15–20 °C. Respiration was then corrected for temperature, assuming a Q10 of 2.

Respiration rates of nematodes and macrobenthos were converted to oxygen consumption assuming an RQ of 0.85 (Hargrave 1973).

Data analysis
One-way and two-way analyses of variance (ANOVA) were performed on biomass and densities for bacteria, nematodes and macrobenthos to test for differences between sampling stations and dates. One-way ANOVA was used to test for differences in SCOC and contributions of bacteria, nematodes and macrobenthos to SCOC between sampling dates for each station. Whenever significant differences were found, post hoc Tukey HSD tests were performed. Homogeneity of variances was tested using Bartlett’s Chi-squared test and data were fourth root, inverse or arcsine (in the case of relative data) transformed whenever necessary. Whenever homogeneity of variances was not achieved, even upon transformation, Kruskal–Wallis (one-way ANOVA by ranks) tests were conducted. Whenever significant differences were found, Mann–Whitney U-tests were conducted on each pair of groups and the P-value adjusted with the Bonferroni method (Salkind 2007). The STATISTICA 6 software package was used. It should be noted that maximum robustness of ANOVA is not obtained in our analysis due to the low number of replicates available.

Results
Chlorophyll \(a\) concentrations
Chlorophyll \(a\) concentrations in the water column did not change with water depth and showed comparable values at both stations, ranging from 3 to 52 mg m\(^{-3}\) (Fig. 2). Chlorophyll \(a\) concentrations in the water peaked in April when the spring phytoplankton bloom occurred. In the sediment, on the other hand, chlorophyll \(a\) concentrations differed greatly between both stations, being around 10 times lower at station 330 COARSE than at station 115bis FINEx (Fig. 2). At station 115bis FINEx chlorophyll \(a\) concentrations in the sediment followed those in the water column, with the highest values in April (106 mg m\(^{-2}\) ± 21 SE). At station 330 COARSE chlorophyll \(a\) concentrations in the sediment also increased in April (12 mg m\(^{-2}\) ± 1 SE) after the spring phytoplankton bloom, but showed equally high values in October (11 mg m\(^{-2}\) ± 3 SE) in spite of the low chlorophyll \(a\) concentrations in the water column.

Biomass and densities
Bacterial biomass did not differ significantly between stations (two-way ANOVA, F = 0.29; df = 1; P > 0.05; Fig. 3), ranging from 1.6 g C m\(^{-2}\) ± 0.6 SE to 5.9 g C m\(^{-2}\) ± 1.2 SE at station 115bis FINEx and from 1.2 g C m\(^{-2}\) ± 0.7 SE to 3.6 g C m\(^{-2}\) ± 0.3 SE at station 330 COARSE. However, differences between sampling dates (F = 11.9; df = 2; P < 0.01) and in the interaction term station × date (F = 4.27; df = 2; P < 0.05) were significant. Differences between sampling dates were most pronounced at station 115bis FINEx where bacterial biomass in April was significantly higher than in February and October. Temporal differences in station 330 COARSE were not statistically significant, although values observed in October were markedly lower. Bacterial densities varied in the same way as biomass at both stations, ranging from 12.4 cells \(\cdot\) m\(^{-2}\) (±5.9 SE) to 28.0 cells \(\cdot\) m\(^{-2}\) (±3.2 SE) at station 330 COARSE.

Total nematode biomass was much higher at station 115bis FINEx than at station 330 COARSE (Fig. 3). At station 115bis FINEx biomass was lowest in February (0.42 g
Fig. 2. Chlorophyll a concentration in the water column (mg m\(^{-2}\)) and sediment surface 0–1 cm deep (mg m\(^{-2}\)) at stations 115\(_{\text{fine}}\) and 330\(_{\text{coarse}}\) during the sampling campaigns of February, April and October 2003. Vertical bars represent the standard error. Note the different scales of both right y-axes.

Fig. 3. Biomass (g C m\(^{-2}\)) and densities of bacteria (cells × 10\(^{12}\) m\(^{-2}\)), nematodes (ind × 10\(^{6}\) m\(^{-2}\)) and macrobenthos (ind × 10\(^{9}\) m\(^{-2}\)) from stations 115\(_{\text{fine}}\) and 330\(_{\text{coarse}}\) during the sampling campaigns of February, April and October 2003. Vertical bars represent the standard error. Note the different scales of the graphs.

C m\(^{-2}\) ± 0.02 SE), highest in April (1.46 g C m\(^{-2}\) ± 0.99 SE) and again lower in October (0.62 g C m\(^{-2}\) ± 0.38 SE).

At station 330\(_{\text{coarse}}\), nematode biomass was lowest in February (0.018 g C m\(^{-2}\) ± 0.003 SE) and increased with time up to 0.079 g C m\(^{-2}\) ± 0.043 SE in October. Nematode densities varied in the same way as biomass at both stations, ranging from 3.32 individuals (ind) × 10\(^{6}\) m\(^{-2}\) (±0.11 SE) to 5.01 ind × 10\(^{6}\) m\(^{-2}\) (±1.12 SE) at station
Macrobenthos biomass (Fig. 3) was higher at station 115bisfine than at station 330coarse (two-way ANOVA, F = 134.9; df = 1; P < 0.001). At station 115bisfine macrobenthos biomass was 23.2 g C m\(^{-2}\) (±3.70 SE) in February, reaching lowest values in April (5.8 g C m\(^{-2}\) ± 3.4 SE) and increasing up to a maximum of 61.3 g C m\(^{-2}\) (±16.1 SE) in October, with temporal differences being significant between April and October. At station 330coarse the lowest values were observed in February (0.44 g C m\(^{-2}\) ± 0.13 SE) and the highest in October (1.8 g C m\(^{-2}\) ± 0.34 SE), with intermediate values in April (1.10 g C m\(^{-2}\) ± 0.69 SE); however, these differences were not significant. Macrobenthos densities followed a relatively similar pattern as biomass except at station 330coarse in April and October, when biomasses were similar but densities were considerably higher in April (Fig. 3). Macrobenthic densities varied between 723 ind. m\(^{-2}\) (±11 SE) and 268 ind. m\(^{-2}\) (±27 SE) at station 330coarse. In terms of biomass bivalves dominated the macrobenthic community at station 115bisfine, decreasing from values of 91.1% (±1.8 SE) in February to 60.2% (±9.0 SE) in October (Table 1). Polychaetes represented 18.6% (±3.0 SE) of the macrobenthic biomass in April, with lower values (c. 5%) in February and October. Cnidarians increasingly contributed to macrobenthic biomass, from a complete absence in February to 31.1% (±9.1 SE) in October. In terms of densities, bivalves and polychaetes were dominant, together accounting for 90–97% of macrobenthic individuals. Bivalves were proportionately more abundant in February and October, whereas polychaete dominance was higher in April.

At station 330coarse the macrobenthic community was dominated by polychaetes in terms of biomass and densities (Table 1). This dominance decreased with time, particularly in terms of biomass. In February, polychaetes represented 74.8% (±15.6 SE) of macrobenthic biomass, decreasing to 38.6% (±12.9 SE) in October, while in terms of densities they decreased from 68.7% (±2.8 SE) in February to 51.9% (±3.5 SE) in October. At station 330coarse other macrobenthic taxa (Bivalvia, Crustacea and Echinodermata) were also abundant; bivalves and echinoderms contributed more to biomass than to densities, whereas the opposite was true for crustaceans.

### Sediment community oxygen consumption

Water temperature was 6.0 and 6.4 °C in February at station 115bisfine and 330coarse, respectively, 9.3°C in April at both stations and 15.1 and 15.0 °C in October at station 115bisfine and 330coarse respectively. SCOC at station 115bisfine varied between 5.5 (±0.3 SE; February) and 18.8 mmol O\(_2\) m\(^{-2}\) day\(^{-1}\) (±0.8 SE; October), with April showing SCOC values very close to the October ones (Fig. 4). At station 330coarse SCOC ranged between 1.2 (February) and 8.7 mmol O\(_2\) m\(^{-2}\) day\(^{-1}\) (±3.9; April), with October showing intermediate values. Due to absence of replication at station 330coarse in February it was not possible to conduct a one-way ANOVA to compare values obtained at all sampling dates. At station 115bisfine, SCOC showed significant differences between sampling dates (one-way ANOVA, F = 17.7; df = 2; P < 0.05). Post hoc tests revealed that values recorded in

### Table 1. Relative dominance (%) of the different macrobenthic taxa in terms of biomass and densities at stations 115bisfine and 330coarse in February, April and October 2003 (mean % ± SE).

<table>
<thead>
<tr>
<th>station</th>
<th>date</th>
<th>Bivalvia</th>
<th>Cnidaria</th>
<th>Crustacea</th>
<th>Echinodermata</th>
<th>Polychaeta</th>
<th>Nemertea</th>
<th>Osteichthyes</th>
</tr>
</thead>
<tbody>
<tr>
<td>relative dominance in terms of biomass</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>115bisfine Feb-03</td>
<td>91.1 ± 1.8</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>2.3 ± 1.2</td>
<td>5.3 ± 1.4</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
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<tr>
<td>115bisfine Apr-03</td>
<td>73.2 ± 5.5</td>
<td>3.8 ± 3.8</td>
<td>0.4 ± 0.2</td>
<td>0.8 ± 0.7</td>
<td>18.6 ± 3.0</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
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<tr>
<td>115bisfine Oct-03</td>
<td>60.2 ± 9.0</td>
<td>31.1 ± 9.1</td>
<td>0.3 ± 0.3</td>
<td>3.2 ± 1.7</td>
<td>5.2 ± 0.7</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td></td>
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<tr>
<td>330coarse Feb-03</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>6.5 ± 3.1</td>
<td>17.1 ± 16.5</td>
<td>74.8 ± 15.6</td>
<td>0.1 ± 0.1</td>
<td>0.0 ± 0.0</td>
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<tr>
<td>330coarse Apr-03</td>
<td>6.7 ± 6.7</td>
<td>0.0 ± 0.0</td>
<td>15.3 ± 10.5</td>
<td>20.3 ± 12.4</td>
<td>57.6 ± 18.1</td>
<td>0.0 ± 0.0</td>
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<tr>
<td>330coarse Oct-03</td>
<td>15.1 ± 15.1</td>
<td>0.0 ± 0.0</td>
<td>17.0 ± 13.1</td>
<td>18.7 ± 16.8</td>
<td>38.6 ± 12.9</td>
<td>1.9 ± 1.9</td>
<td>3.6 ± 2.4</td>
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<tr>
<td>relative dominance in terms of densities</td>
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<tr>
<td>115bisfine Feb-03</td>
<td>51.6 ± 6.7</td>
<td>0.0 ± 0.0</td>
<td>1.7 ± 0.7</td>
<td>1.3 ± 0.7</td>
<td>45.2 ± 7.0</td>
<td>0.2 ± 0.2</td>
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<tr>
<td>115bisfine Apr-03</td>
<td>34.9 ± 4.5</td>
<td>0.2 ± 0.2</td>
<td>8.8 ± 1.8</td>
<td>0.4 ± 0.3</td>
<td>55.2 ± 6.0</td>
<td>0.4 ± 0.4</td>
<td>0.0 ± 0.0</td>
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<tr>
<td>115bisfine Oct-03</td>
<td>53.6 ± 4.2</td>
<td>5.1 ± 1.8</td>
<td>0.4 ± 0.4</td>
<td>4.2 ± 1.6</td>
<td>36.4 ± 6.8</td>
<td>0.2 ± 0.2</td>
<td>0.2 ± 0.2</td>
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</tr>
<tr>
<td>330coarse Feb-03</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>21.9 ± 4.8</td>
<td>1.3 ± 1.3</td>
<td>68.7 ± 2.8</td>
<td>8.2 ± 2.7</td>
<td>0.0 ± 0.0</td>
<td></td>
</tr>
<tr>
<td>330coarse Apr-03</td>
<td>0.6 ± 0.6</td>
<td>0.0 ± 0.0</td>
<td>21.4 ± 6.2</td>
<td>7.1 ± 4.3</td>
<td>65.0 ± 7.6</td>
<td>6.0 ± 2.6</td>
<td>0.0 ± 0.0</td>
<td></td>
</tr>
<tr>
<td>330coarse Oct-03</td>
<td>1.2 ± 1.2</td>
<td>0.0 ± 0.0</td>
<td>24.1 ± 9.1</td>
<td>9.5 ± 7.1</td>
<td>51.9 ± 3.5</td>
<td>9.6 ± 6.2</td>
<td>3.7 ± 2.8</td>
<td></td>
</tr>
</tbody>
</table>
February were significantly lower than in April and October (Fig. 4). SCOC did not differ significantly between April and October at either station (station 330coarse, one-way ANOVA, $F = 0.57$; $df = 1$; $P > 0.05$; station 115bisfine, Tukey HSD test, $P > 0.05$).

Respiration of different benthic size groups
BP and BR were higher at station 115bisfine than at station 330coarse at the 0–1 cm layer (Table 2). However, depth-integrated BR (0–5 cm depth at station 330coarse) was higher at station 330coarse (BR ranging from 8.3 to 22.9 mmol O$_2$·m$^{-2}$·day$^{-1}$) than at station 115bisfine (BR ranging from 7.7 to 10.0 mmol O$_2$·m$^{-2}$·day$^{-1}$) (Kruskal–Wallis; $P < 0.001$) (Fig. 4). Macrofaunal respiration is defined as respiration by organisms retained on a 1-mm sieve, while nematode respiration is the oxygen consumed by nematodes passing through a 1-mm sieve and retained on a 38-μm sieve.

On an annual basis, respiration values of nematodes at station 115bisfine were lower than those of bacteria and macrobenthos (Kruskal–Wallis; $P < 0.01$), while the latter two groups did not differ from each other. At station 330coarse bacteria showed clearly higher respiration values than nematodes and macrobenthos (one-way ANOVA, $F = 144$; $df = 2$; $P < 0.001$) (Fig. 4). Macrobenthos respiration was also significantly higher than nematode respiration.

A one-way ANOVA performed on BR at each station revealed significant differences between sampling dates for both stations (station 115bisfine: $F = 6.41$; $df = 2$; $P < 0.001$; station 330coarse: $F = 61.79$; $df = 2$; $P < 0.001$).

Table 2. Bacterial production (mg C·m$^{-2}$·day$^{-1}$) and respiration (mg C·m$^{-2}$·day$^{-1}$) for the sediment layer 0-1 cm and bacterial respiration (mmol O$_2$·m$^{-2}$·day$^{-1}$) for a sediment depth of 5 cm, at stations 115bisfine and 330coarse in February, April and October 2003. Bacterial respiration estimated using a fixed BGE of 20% (mean ± SE).

<table>
<thead>
<tr>
<th>station</th>
<th>date</th>
<th>production (0–1 cm) mg C·m$^{-2}$·day$^{-1}$</th>
<th>respiration (0–1 cm) mg C·m$^{-2}$·day$^{-1}$</th>
<th>respiration (0–5 cm) mmol O$_2$·m$^{-2}$·day$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>115bisfine</td>
<td>Feb 03</td>
<td>23.4 ±0.9</td>
<td>93.8 ±3.7</td>
<td>7.8 ±0.3</td>
</tr>
<tr>
<td>115bisfine</td>
<td>Apr 03</td>
<td>30.0 ±1.9</td>
<td>120.2 ±7.4</td>
<td>10.0 ±0.6</td>
</tr>
<tr>
<td>115bisfine</td>
<td>Oct 03</td>
<td>23.1 ±1.5</td>
<td>92.2 ±6.2</td>
<td>7.7 ±0.5</td>
</tr>
<tr>
<td>330coarse</td>
<td>Feb 03</td>
<td>5.0 ±0.7</td>
<td>19.8 ±2.9</td>
<td>8.3 ±1.2</td>
</tr>
<tr>
<td>330coarse</td>
<td>Apr 03</td>
<td>9.2 ±0.5</td>
<td>36.7 ±2.2</td>
<td>15.3 ±0.9</td>
</tr>
<tr>
<td>330coarse</td>
<td>Oct 03</td>
<td>13.7 ±0.3</td>
<td>54.9 ±1.3</td>
<td>22.9 ±0.6</td>
</tr>
</tbody>
</table>

Fig. 4. Sediment community oxygen consumption (SCOC, mmol O$_2$·m$^{-2}$·day$^{-1}$), respiration rates (mmol O$_2$·m$^{-2}$·day$^{-1}$) and respiration shares (%) from SCOC of bacteria, nematodes and macrobenthos from stations 115bisfine and 330coarse during the sampling campaigns of February, April and October 2003. Vertical bars represent the standard error.
At station 115bis, BR in February was significantly lower than in April, while at station 330, all sampling dates were significantly different from each other.

Total nematode respiration was significantly higher at station 115bis than at station 330 (two-way ANOVA: F = 40.1; df = 1; P < 0.001) (Fig. 4). At station 115bis, nematode respiration was lowest in February (0.94 mmol O₂ m⁻² day⁻¹ ± 0.03 SE), highest in April (3.56 mmol O₂ m⁻² day⁻¹ ± 2.23 SE) and lower again in October (2.50 mmol O₂ m⁻² day⁻¹ ± 1.50 SE), but these differences were not statistically significant. At station 330, nematode respiration was lowest in February (0.041 mmol O₂ m⁻² day⁻¹ ± 0.004 SE) and increased up to October (0.34 mmol O₂ m⁻² day⁻¹ ± 0.17 SE), differences again not being statistically significant.

Total macrobenthos respiration was higher at station 115bis than at station 330 (Kruskal–Wallis; P < 0.001) (Fig. 4). At station 115bis, macrobenthic respiration decreased from February to April (when it reached a minimum of 3.57 mmol O₂ m⁻² day⁻¹ ± 0.76 SE), increasing afterwards with highest values in October (53.6 mmol O₂ m⁻² day⁻¹ ± 12.8 SE) (F = 28.5; df = 1; P < 0.001). All sampling dates were significantly different from each other. At station 330, macrobenthic respiration was lowest in February (0.08 mmol O₂ m⁻² day⁻¹ ± 0.05 SE), and highest in October (0.70 mmol O₂ m⁻² day⁻¹ ± 0.38 SE) (F = 4.65; df = 1; P < 0.05), with significant differences only between these two sampling dates.

Summed contributions of bacterial, nematode and macrobenthic respiration always exceeded measured SCOC at both stations, except at station 115bis in April, when the sum of estimated heterotrophic respiration reached 93% of SCOC. The relative shares of each group in the SCOC differed between the two stations (Fig. 4). At station 115bis, bacteria and macrobenthos had a similar relative importance in February (c. 140% and 200% of SCOC, respectively) with nematodes showing a much lower contribution (c. 17%). In April, nematode and macrobenthos community respiration became very similar (c. 20% and 18%, respectively), but were both greatly exceeded by BR (c. 55%). In October, macrobenthos represented c. 260% of measured SCOC, with much lower contributions for bacteria and nematodes (c. 40% and 13%, respectively). At station 330, SCOC was dominated by BR throughout the year. Assuming a fixed BGE of 20%, BR clearly exceeded measured SCOC in February, April and October with c. 680%, 175% and 400%, respectively, of measured SCOC values. Nematodes contributed very little to SCOC at station 330, with a maximum of about 6% in October. Macrobenthos also showed only a small contribution to measured SCOC, ranging from 7% (April) to 23% (February and October).

**Discussion**

**Methodological considerations**

Summed estimates of heterotrophic respiration rates (e.g. Schwinghamer et al. 1986), and estimates of bacterial respiration rates (Van Duyl & Kop 1990; Cammen 1991; Alongi 1995), exceeding measured SCOC values have been reported before and are likely the result of methodological or computational shortcomings. When measuring SCOC in different kinds of sediments and comparing respiration rates of different benthic size groups, problems encountered include the accurate measuring of SCOC in permeable sediments, assessing bacterial production, conversion of basic measurements to respiration and the use of Q₁₀ values. As such, absolute values reported here should be treated with care but we are confident that the patterns observed in both sediment types reflect the in situ patterns for reasons explained below.

In permeable sediment, such as in station 330, advective pore water transport can increase sediment oxygen uptake by a factor of 1.38–3 (Ehrenhauss & Huettel 2004; Janssen et al. 2005). This advective pore water transport was absent in our cores, and therefore the SCOC values reported for station 330 should be considered a minimum and difficult to compare with the values observed at St 115bis.

BP rates, for instance, may have been overestimated if leucine addition, and/or exposure of otherwise anoxic sediments to oxygen during experimental incubations, stimulated bacterial metabolism. The latter explanation can be ruled out in the case of the well-oxygenated sediments of station 330, and the former explanation is not supported by the results of the measured isotope dilution series (data not shown). On the other hand, BP estimates for the coarse sediment are probably influenced by the absence of advective pore water transport. Further potential methodological biases associated with BP measurements have been discussed by Kemp (1990). However, our BP measurements are well within the range, and even at the lower end, of values reported from 15 other North Sea stations by Hondeveld et al. (1995).

Another difficulty is in the conversion of BP to respiration. When using the model I regression proposed by del Giorgio & Cole (1998) (BR = 3.7 × BP⁰·⁴¹) instead of a fixed BGE, only the BR at station 330 in February exceeded measured SCOC values. However, application of this regression consistently yielded bacterial growth efficiencies between 45 and 67%, which is far above the range of values proposed for bacteria growing on detritus (Osinga et al. 1997; del Giorgio & Cole 1998). Hubas et al. (2007b) recently reported highly variable BGE in intertidal sediments, with peak values up to 74%. Organic matter (OM) availability was the single most important
determinant of BGE in their study, low OM concentrations typically yielding high BGE (Hubas et al. 2007a). Applying a fixed BGE to our contrasting stations may therefore bias direct comparisons of absolute BR rates between stations. If BGE at station 330 coarse exceeded 20%, our estimates of BR would be lower and less in excess of SCOC. This would not, however, alter the conclusion that BR largely dominated SCOC at this station. Similarly, if BGE at station 115bis coarse decreased in response to the spring deposition of *Phaeocystis* (see Hubas et al. 2007b), our BR results may effectively be underestimates, and the contribution of bacteria to SCOC in April may in reality have been even higher. This equally implies that our conclusion that the relative importance of BR in total sediment oxygen consumption at station 115bis fine was by far the highest during/shortly after the *Phaeocystis* deposition, is unlikely to be overstated.

There are also uncertainties in our respiration estimates of both meio- and macrobenthos. Allometric relationships between biomass and respiration are mostly based on a range of species representing different functional groups and will therefore only give an estimate of respiration rather than ‘absolute’ values. However, comparison of meio- and macrofaunal contribution to SCOC is acceptable, as the exponents of the allometric respiration (0.854 and 0.844, respectively) are nearly identical. Moreover, both within (Moens et al. 1999) and across (Moodley et al. 2008) trophic and taxonomic groups of meiofauna, measured respiration rates indeed exhibit a strong proportionality to biomass. Comparison of the respiration rates in the present study (e.g. determined by allometric scaling with biomass) with C-specific respiration rates, following Moodley et al. (2008), show a striking resemblance (Table 3).

Use of a *Q*10 value different from 2 could affect the magnitude of seasonal differences in macrobenthic and nematode respiration, but not the overall pattern. For instance, assuming a *Q*10 of 1 would double the macrobenthic respiration in February and April, but the April value would still be eight times lower than that in October. By contrast, assuming a *Q*10 higher than 2 would further accentuate the seasonal patterns reported here. Similarly, for nematodes, a *Q*10 of 1 would emphasise the comparatively high nematode respiration in April more than a *Q*10 of 2. *Q*10 values in excess of 2 would have the opposite effect. However, in aquatic nematodes, such high *Q*10 values have only been found for fast-growing, opportunistic nematode species typical of detritus-enriched littoral habitats, and/or near the temperature extremes tolerated by specific nematodes (Moens & Vincx 2000, and references therein).

Response to phytoplankton sedimentation: biomass and densities

The sediment type has important consequences for the responses of densities and biomasses of the inhabiting fauna to the sedimentation of the same phytoplankton bloom. Sedimentation of the phytoplankton bloom at station 115bis fine leads to accumulation of phytodetritus at the sediment surface which is buried gradually (Provoost et al. unpublished data). Phytodetritus is more slowly degraded compared to permeable sediment encountered at station 330 coarse, which are characterised by a rapid mineralisation of OM (Ehrenhauss et al. 2004b; Vanaverbeke et al. 2004b; Janssen et al. 2005; Bühring et al. 2006).

Bacterial biomass was within the range of values reported for other subtidal North Sea stations (Van Duyl et al. 1993; Van Duyl & Kop 1994). Bacterial densities and biomass were fairly similar for stations 115bis fine and 330 coarse, in contrast to the general expectation that bacterial densities and biomass increase from coarser to finer sediments (Köster & Meyer-Reil 2001; Hubas et al. 2006). In April, however, bacterial densities and biomass at station 115bis fine were substantially higher than at station 330 coarse. This is probably linked to the high chlorophyll *a* concentration (as an indicator of labile OM), which is known to stimulate bacterial growth (Goedkoop et al. 1997; Ding & Sun 2005). At the sediment surface at that time and site, chlorophyll *a* concentration was twice as high as on the other sampling dates at station 115bis fine and c. 10 times higher than the corresponding values at station 330 coarse. The temporal fluctuations in bacterial densities and biomass at our stations, and their links to sedimentary chlorophyll *a* concentrations, are mirrored by shifts in bacterial community composition, which differed for all three sampling events at station 115bis fine, but only between October and February + April at station 330 coarse (Franco et al. 2007).

### Table 3. Nematode respiration estimates (mmol O2 m−2 d−1) from the present study and applying nematode respiration rates of 1.6 µl O2 h−1 mg C−1 (Min) and 2.5 µl O2 h−1 mg C−1 (Max) (Moodley et al. 2008) to the nematode’s biomass and density data from the present study (mean ± SE).

<table>
<thead>
<tr>
<th>Station</th>
<th>Date</th>
<th>Present Study</th>
<th>Min a</th>
<th>Max a</th>
</tr>
</thead>
<tbody>
<tr>
<td>115bis fine</td>
<td>Feb-03</td>
<td>0.861 ± 0.031</td>
<td>0.941 ± 0.220</td>
<td>1.470 ± 0.343</td>
</tr>
<tr>
<td>115bis fine</td>
<td>Apr-03</td>
<td>3.267 ± 0.204</td>
<td>2.504 ± 1.803</td>
<td>3.912 ± 2.818</td>
</tr>
<tr>
<td>115bis fine</td>
<td>Oct-03</td>
<td>2.280 ± 1.362</td>
<td>1.026 ± 0.583</td>
<td>1.603 ± 0.911</td>
</tr>
<tr>
<td>330 coarse</td>
<td>Feb-03</td>
<td>0.043 ± 0.007</td>
<td>0.032 ± 0.006</td>
<td>0.050 ± 0.010</td>
</tr>
<tr>
<td>330 coarse</td>
<td>Apr-03</td>
<td>0.110 ± 0.026</td>
<td>0.076 ± 0.024</td>
<td>0.119 ± 0.037</td>
</tr>
<tr>
<td>330 coarse</td>
<td>Oct-03</td>
<td>0.305 ± 0.148</td>
<td>0.174 ± 0.112</td>
<td>0.272 ± 0.174</td>
</tr>
</tbody>
</table>

* aConversion from volumetric to molar units obtained using the Ideal Gas Law at standard temperature and pressure (STP) conditions.
Densities and biomasses of both meio- and macrofauna were always higher in station 115bis_FINE compared to station 330_COARSE, which is again related to the higher availability of OM at the finer-grained sediment. However, both size groups responded faster to phytoplankton sedimentation at station 330_COARSE. The nematode community at this station responds rapidly to inputs of OM (Vanaverbeke et al. 2004a,b, Franco et al. 2008b), as illustrated by the increase in nematode biomass and densities from February to April and again in October, when a second deposition event occurred at this station (Franco et al. 2008b). The temporal differences in nematode density and biomass at station 115bis_FINE have to be interpreted carefully, as c. 80% of the nematode community was found in the upper 5 cm of the sediment in April (the depth stratum considered in the present study), compared to only 60% in October. Total depth-integrated nematode densities were even higher in October than in April, indicating a time-lagged response (Franco et al. 2008b). At station 115bis_FINE higher macrobenthic biomass in October indicates that macrobenthos had a delayed response to the deposition of the phytoplankton bloom as well. At station 330_COARSE macrobenthos already showed an increase in biomass in April, maintaining similar values in October. Even though macrobenthic densities in the fine sediment were slightly lower in April than in February, biomass was considerably lower, indicating that smaller organisms were present in April. This was mainly due to a decrease in bivalve and echinoderm densities to about half and a third, respectively, from February to April. Individual biomass decreased to about a third in both groups (data not shown). This was also observed in a long-term analysis (1995–2003) of the diversity and densities of the macrobenthos from the same study area (Van Hoey et al. 2007). Low winter and early spring densities are explained as due to mortality and emigration (Van Hoey et al. 2007 and references therein). In spring and summer, recruitment of polychaete larvae occurs in the area, whereas the main bivalve recruitment only occurs in full summer (Van Hoey et al. 2007). Our sampling period (April) therefore reflects the onset of the macrobenthic recruitment period, resulting in low densities of small individuals.

In October the increase in biomass was much higher than the increase in densities, representing larger organisms, which is again in accordance with the data presented by Van Hoey et al. (2007). For all macrobenthic taxa the highest individual biomass was registered in October, supporting the delayed response macrobenthos showed to the phytodetritus deposition.

Sediment community oxygen consumption

SCOC showed a similar seasonal pattern to other stations in the North Sea with comparable sediment types and water temperatures (Boon & Duineveld 1998; Boon et al. 1998). However, the SCOC values at both our study sites only resembled those previously published for coarse sediments and were much lower than values for fine-grained sediments (up to 30 and 50 mmol O₂·m⁻²·day⁻¹ in April and October, respectively) (Boon & Duineveld 1998; Boon et al. 1998).

In sediments with a thin oxic surface layer, a substantial part of sediment oxygen uptake is not caused by aerobic respiration, but rather by the reoxidation of reduced inorganic metabolites close to the oxic/anoxic interface (Kristensen 2000) and by the oxidation of reduced metals (Canfield et al. 1993). This is likely the case at station 115bis_FINE, particularly after the phytoplankton bloom deposition in April (Steyaert 2003), and may explain why at this time and site, not all SCOC could be attributed to the heterotrophic compartments considered here. On the other hand, SCOC at station 330_COARSE is largely underestimated due to the absence of advection of pore water through the sediment (Ehrenhauss & Huettel 2004; Janssen et al. 2005).

Respiration rates of different benthic size groups

Before comparing respiration rates of different benthic size groups in contrasting sediment types, it should be pointed out that our results are based on one station per sediment type. Although our data show clear differences between respiration shares for the different sediment types, we first compare our results with the few available data in the literature.

BP values were among (station 115bis_FINE) or below (station 330_COARSE) production values reported for several other subtidal stations in the North Sea (Van Duyl et al. 1993; Van Duyl & Kop 1994). BP and BR were higher on a volume basis at station 115bis_FINE; however, when considering depth-integrated values, bacterial aerobic respiration was higher at station 330_COARSE (Fig. 4). In coastal sediments there is a large fraction of dead or inactive bacteria (Luna et al. 2002) and the percentage of active bacteria may change rapidly (Créach et al. 2003). Therefore, production is a better measure of bacterial activity than cell densities or biomass.

Hubas et al. (2007a) estimated BP for two contrasting intertidal sites. Applying a fixed BGE of 20% to their BP data, and extrapolating in the same way to a 0-5 cm sediment depth stratum, BR for fine intertidal sediments in the Hubas et al. (2007a) study would range from 8 to 32 mmol O₂·m⁻²·day⁻¹ and from 0 to 120 mmol O₂·m⁻²·day⁻¹ in coarse sediments. Our subtidal BR rates were slightly lower and the difference between the coarse and fine site less spectacular, but the emerging picture is that differences in BR rates between fine and coarse sediments may be quite consistent in subtidal and intertidal systems.
Nematode respiration rates at station 115bis were high when compared to deeper subtidal stations with comparable nematode densities (de Bovée et al. 1996). Comparisons of respiration rates of nematodes from station 115bis with those of muddy estuarine sediments give variable results: Kennedy (1994) reported three times lower respiration rates for a nematode community with half the density found at station 115bis. Tita et al. (1999) estimated individual nematode respiration, which, extrapolated to the densities at station 115bis would account for values even higher than the measured SCOC for station 115bis and Warwick & Price (1979), studying a nematode community about three times more abundant than at station 115bis observed nearly five times higher respiration rates.

At station 330, respiration rates of nematodes were similar to values reported at deeper subtidal stations (0.05–0.39 mmol O₂·m⁻²·day⁻¹, de Bovée et al. 1996) and in estuarine intertidal sandy sediments (Kennedy 1994). Unfortunately, we know of no published data from other subtidal stations with comparable depths.

Our results generally show a high contribution of bacterial respiration to total SCOC in permeable sediments, and a higher share of meio- and macrobenthic respiration in fine-grained sediments. The increasing importance of BP to total benthic community production with increasing grain size seems to be a consistent feature as it has been shown in subtidal (this study) and intertidal (Hubas et al. 2007a) sediments. Assuming a fixed BGE, this implies higher BR in coarser sediments where total meio-benthic and macrobenthic respiration is lower compared to fine-grained sediments, again leading to a high contribution of BR in the benthic metabolism. Bacterial communities inhabiting sands are often regarded as highly active (Rusch et al. 2003, Ehrenhauss et al. 2004a) but, as mentioned before, if BGE is inversely proportional to OM availability, this conclusion may need to be reconsidered.

The higher relative importance of macrobenthic (Boon & Duineveld 1998) and meio-benthic respiration (Tita et al. 1999) in fine sediments than in coarser sediments was reported before. Direct information on respiration partitioning between meio- and macrobenthos is scarce and a general picture is lacking so far. Macrobenthos often has a higher share in benthic respiration (e.g. Moodley et al. 1998; Heip et al. 2001; Van Oevelen et al. 2006b), whereas the opposite has been observed as well (Schwinghamer et al. 1986; Hubas et al. 2007a). Our results indicate that macrofauna is more important for SCOC during most of the year, but we also show that nematodes contribute equally to SCOC in April. At that time, macrobenthic recruitment is still in its early phase, resulting in low abundances and individual biomasses, whereas nematode densities have increased already as a response to phytoplankton deposition and higher individual nematode biomasses occur (M. A. Franco, personal observation) leading to a higher meiobenthic contribution to SCOC.

Conclusions

Our results indicate that sediment respiration is partitioned differently among different benthic size groups in contrasting sediments. In coarse, permeable sediments, bacteria are responsible for the bulk of the respiration throughout the year. In contrast, next to bacteria, metazoan organisms are important oxygen consumers in winter and early spring. In winter, the macrobenthos is more important than the nematode communities. In spring, shortly after the arrival of phytodetritus to the sea floor when macrobenthic densities and biomass is low, the importance of nematode respiration (20%) is striking. This indicates that seasonal sampling and incorporation of all benthic size classes is needed in further research aiming at unraveling benthic responses to phytoplankton deposition.

Acknowledgements

We would like to thank the master and crew of the RV Belgica for their skilful help during sampling. This research was funded by the Belgian Science Policy (TROPHOS – Contract no. EV/02/25A) and UGENT-BOF project 01GZ0705 Biodiversity and Biogeography of the Sea (BBSea) (2005–2010). M.A.F. was financially supported by a PhD grant from the Foundation for Science and Technology (FCT - SFRH/BD/10386/2002). Leon Moodley provided a lot of advice. We are grateful to two anonymous referees and the editor for improving the quality of this paper. The authors acknowledge the support by the MarBEF Network of Excellence ‘Marine Biodiversity and Ecosystem Functioning’, which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community’s Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This is publication 4578 of the Netherlands Institute of Ecology (NIOO-KNAW), Yerseke.

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