

Fate of organic matter in Arctic intertidal sediments: Is utilisation by meiofauna important?

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Received 31 October 2005; accepted 15 May 2006

Available online 17 June 2006

Abstract

This paper presents (1) a study of the fate of high-quality detritus in Arctic sandy beaches, in particular its use by the sandy beach meiobenthos, and (2) a comparison of organic matter mineralisation rates with those in other climatic regions. We performed a tracer experiment in which lyophilised ¹³C-labelled cyanobacteria were added to sediments of two intertidal beaches (Tyskehytte and Breoyane) at Kongsfjorden (Spitsbergen) with contrasting sediment properties, benthic metabolic rates and meiobenthic communities. Tyskehytte was characterised by coarse sands on an exposed beach and Breoyane by medium sands on a relatively sheltered beach. Organic matter addition stimulated benthic metabolism in the coarser sediment but not in the finer one. Correspondingly, the added carbon was metabolised faster in the coarser sediment, respiration being its major short-term fate. Faster mineralisation of organic matter in coarser sediments was probably linked to a better availability to microbes and fauna in deeper sediment strata, resulting from a higher sediment porosity and a faster penetration of (labelled) organic matter to deeper sediment layers. Overall, organic matter mineralisation rates at both beaches compared favourably with those in temperate sediments. All major meiofauna taxa incorporated the added carbon source on both beaches, but specific uptake was substantially higher in the coarser sediment than in the finer one. Oligochaetes accounted for the largest share of meiobenthic carbon uptake. Despite a very high specific uptake, meiofaunal consumption accounted for but a small portion (<5% at both beaches) of the total ¹³C-mineralisation. Thus our results do not support the hypothesis that meiofauna have a comparatively larger role in Arctic sandy beaches impoverished in macrofauna. However, more research including analyses on different spatial and temporal scales is needed before generalisations can be made.

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Keywords: Arctic zone; Beaches; Organic matter processing; Meiobenthos; Stable carbon isotopes; Sediment respiration

1. Introduction

Sandy and gravel intertidal beaches are permeable sediments, i.e. their texture and structure allow measurable porewater flows under natural pressure gradients.

One major feature of such sediments is effective transport (Huettel et al., 1996; Huettel and Rusch, 2000). Despite generally low organic matter concentrations and low standing stocks of reactants, these sediments are biogeochemically active and may play an important role in marine carbon cycles (Shum and Sundby, 1996).

Gravel and sandy beaches are common along the Arctic coasts of Spitsbergen (Węśławski et al., 1993),

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but little is known on their biotic communities and functioning. Macrofauna appear to be scant in comparison with beaches from other climatic regions (Węślawski et al., 1993, 1997). As a consequence, it has been suggested that meiofauna may have a comparatively larger role in benthic intertidal carbon fluxes in the Arctic (Szymelfenig et al., 1995). Meiofauna can affect the breakdown of organic matter in sediments both directly, through grazing on bacteria, and indirectly, through bioturbation, mucus production and perhaps other mechanisms that can affect the activity and/or species composition of microbial communities (Tietjen, 1980; Findlay and Tenore, 1982; Alkemade et al., 1992; De Mesel et al., 2004; Moens et al., 2005). Meiofauna thus can potentially contribute significantly to organic matter turnover in sediments (Kuipers et al., 1981; Coull, 1999). Their densities and biomass in Arctic intertidal sediments, while both being highly variable, are generally similar to those in non-Arctic beaches (Radziejewska and Stańkowska-Radziun, 1979; Mokievsky, 1992; Szymelfenig et al., 1995); however, studies on their activity and functioning are lacking.

A principal source of organic matter in glacial fjords is detritus derived from degraded macrophytes as well as from phyto- and zooplankton. Steep environmental gradients in sedimentation and salinity in glacial fjords result in high phytoplankton and zooplankton mortality (Węślawski and Legeżyńska, 1998; Zajäckowski and Legeżyńska, 2001). Organic matter produced in fjord waters partly settles through the water column and partly swashes out into the intertidal (Hop et al., 2002). Studies on organic matter mineralisation in Arctic marine sediments suggest that rates are similar to those in temperate and tropical environments because they are governed primarily by organic matter quality and availability rather than by temperature (Arnosti et al., 1998; Glud et al., 1998; Rysgaard et al., 1998, 2000; Kostka et al., 1999). Again, however, studies on Arctic intertidal habitats are lacking.

A major question, therefore, pertains to the fate of organic matter in Arctic intertidal sediments and to the importance of meiofauna in organic matter processing. In this study, we report on a tracer experiment in which ^{13}C -labelled detritus was added to sediments of two intertidal beaches with contrasting sediment properties in Kongsfjorden (Spitsbergen). Our aims were two-fold: (1) to study the fate of freshly deposited phytodetritus in Arctic sandy beaches and compare mineralisation rates with those in other climatic areas, and (2) to assess the contribution, if any, of meiofauna to organic carbon mineralisation in these beach sediments. In addition, we

measured rates of benthic oxygen consumption on both beaches and compared our results with published rates for non-Arctic beaches.

2. Materials and methods

2.1. Study site

This study was carried out in Kongsfjorden — a glacial, open Arctic fjord located on the west coast of Spitsbergen at 79°N, 12°E (Fig. 1). Kongsfjorden is 20 km long and its width varies from 4 to 10 km. The hydrology of this fjord is strongly influenced by freshwater inputs as meltwater from large tidal glaciers (Kronebreen and Kongsvegen at the head of the fjord, Conwaybreen and Blomstrandbreen on its northern coast) (Svendsen et al., 2002). Kongsfjorden is frozen during winter but open and influenced by the ocean during summer.

Phytoplankton in fjord waters is dominated by diatoms and daily primary production during summer ranges between 0.024 and 0.80 g C m⁻² (Hop et al., 2002). The most abundant zooplankton are copepods (*Oithona similis*, *Calanus* spp., *Pseudocalanus* spp.), euphausiids (*Thysanoessa* spp.), amphipods (*Themisto* spp.), pteropods and ctenophores. Concentrations of particulate organic carbon (POC) in suspended matter in the fjord waters range between 0.70 and 1.46 g C m⁻³ in spring and summer, respectively (Hop et al., 2002).

Two intertidal sites differing substantially in sediment texture (Table 1) were selected for the experiment: (1) a beach in Tyskehytte dominated by coarse sand and gravels, and (2) a more sheltered beach characterised by finer sand, located on Breoyane Island, opposite the glacier Blomstrandbreen (Fig. 1). Water depth at high tide averaged 55 and 71 cm at the Breoyane and Tyskehytte sites, respectively. Details on the meio-benthos of both beaches have been reported elsewhere (Urban-Malinga et al., 2005); samples for the present experiment were taken in between the low- and mid-water levels reported in that study.

Sediment granulometry at both sites was determined in each of six samples taken to a depth of 10 cm. Analysis was done by standard sieving. The sediment fractions were defined according to the Wentworth scale as recommended by Buchanan (1984). Sediment organic carbon and nitrogen content were determined in each of six sediment samples taken to a depth of 10 cm by thermal combustion using a CHN-analyzer (Perkin Elmer 2400). Samples for C_{org} were pre-treated with dilute HCl to remove carbonates. Concentrations of suspended organic/inorganic matter in the water were

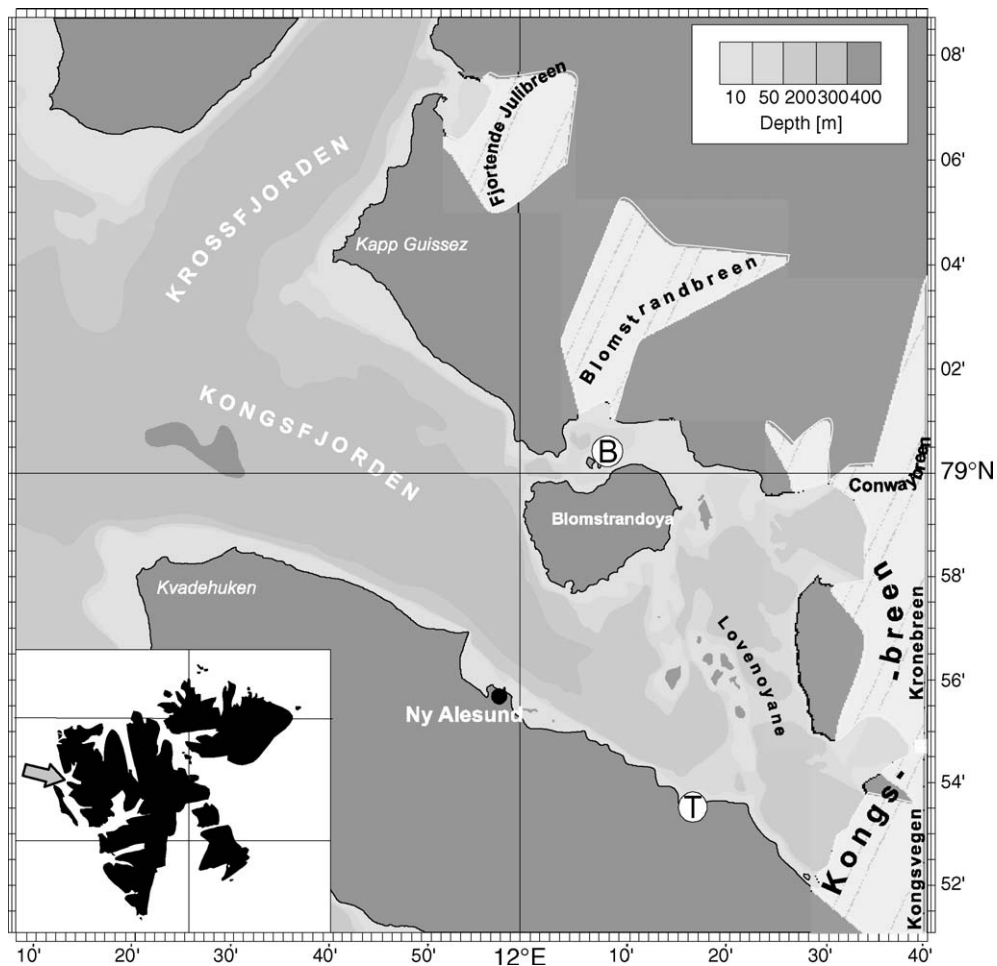


Fig. 1. Location of the study sites. T: Tyskehytte, B: Breoyane.

estimated by filtration of 5 l fjord water on Whatman GF/C glass-fibre filters. The amount of total suspended matter in the water was determined after drying of the filters at 60 °C for 24 h.

2.2. Enrichment experiment

Three undisturbed perspex cores (14 cm inner diameter, sediment column of ca. 15 cm) were taken from each site (between low and medium water mark) during low tide on 3 August 2001 and transported to the research station at Ny Alesund. The cores were closed and the sediment was allowed to stabilise for 24 h at in situ temperature. Water and air temperatures during the experiment ranged between 2.7–4.1 and 3.2–4.3 °C, respectively. After stabilisation, one subcore (10 cm² surface area) was taken from each core to study the initial carbon content and vertical distribution of meiofauna before enrichment (time-zero samples, T₀).

These subcores were sectioned into four depth layers: 0–2, 2–4, 4–6 and 6–10 cm. Samples were stored frozen until analysis. Immediately upon withdrawal of these subcores, empty cores of identical diameter were inserted in these pits to avoid the collapse of surrounding sediment.

Habitat water filtered on Whatman GF/C glass-fibre filters was subsequently added gently to all cores until a water cover of approximately 15 cm was obtained. Lyophilised ¹³C-labelled cyanobacteria (>98% ¹³C, Cambridge Isotope Laboratories) were suspended in small aliquots of habitat water, frozen, and added as small ice-cubes to the overlying water in the cores. This procedure yielded an acceptably homogeneous distribution of the organic matter, variability between different subsamples of a core typically being much lower than when the lyophilised algae were suspended in the overlying water (Moens, unpubl. data). Final concentration of added organic matter was 0.6 g C m⁻² (i.e.

Table 1

Some characteristics of the investigated beaches and sediments (mean \pm SD of 6 replicates)

	Tyskehytte	Breoyane
Beach width (m)	15.5	15
Beach slope (°)	3°30′	3°
Salinity PSU	25	30
Phi (mean diameter)	−0.2	1.3
Sorting	1.0	0.8
Silt %	0.0	0.0
v. fire sand %	0.5	0.4
Fine sand %	1.9	19.6
Medium sand %	5.6	59.3
Coarse sand %	41.7	14.0
v. coarse sand %	28.0	2.7
Gravel %	22.4	4.0
C _{org} %	0.1	0.12
N _{org} %	0.02	0.02
C/N	5.2	7.3

50 mmol C m^{−2}). Although cyanobacteria are not an important natural carbon source on intertidal beaches, these lyophilised cyanobacteria were readily utilised by nematodes and other meiofauna from several other — albeit temperate — intertidal sediments (Moens et al., 2002; unpubl. data).

After 6 d of incubation (T₆), one subcore (10 cm² surface area) was withdrawn from each of the experimental cores for the study of ¹³C-incorporation into meiofauna and other metazoans. These were sectioned into the same depth strata as at T₀. Subsamples (1 cm² surface area) were taken from these sediment sections for the analysis of ¹³C-penetration into the sediment; this analysis essentially inventories all organic ¹³C, i.e. ‘unmetabolised’ cyanobacterial carbon, dissolved organic carbon and ¹³C in consumer biomass (bacteria and meiofauna). All samples were frozen immediately after collection.

Meiofauna was collected from thawed samples via density centrifugation with the colloidal silicagel Ludox HS 40 (Heip et al., 1985) and rinsed with tap water. Animals retained on a 38 µm sieve were counted, handpicked with a fine needle and separated at the higher taxon level. They were rinsed in sterile artificial seawater (ASW, Dietrich and Kalle, 1957) and transferred to a drop of distilled water in 2.5×6 mm aluminium cups (Elemental Microanalysis Limited). Aluminium cups were pretreated for 4 h at 550 °C in order to remove all exogenous organic carbon. Cups with meiofauna were oven-dried, closed and stored in glass tubes until analysis. Small sediment samples were oven-dried, weighed into 12.5×5 mm silver cups (Elemental Microanalysis Limited) and acidified ‘in

situ’ with dilute HCl to remove carbonates (Nieuwenhuize et al., 1994).

Carbon isotopic analyses of sediment organic matter and meiofauna used a Carlo-Erba CN-analyser coupled online via a conflo-2 interface to a Finnigan Delta S mass spectrometer. Results are reported in the δ notation with Vienna PDB as reference standard, and expressed in units of ‰, according to the standard formula: $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3\text{‰}$, where R is the ratio of ¹³C/¹²C. Analytical precision was typically better than 0.2‰.

The inventory (I) of ¹³C (in mg) in the sediment or in meiofauna was calculated from the excess (above background) ¹³C.

$$I = E \cdot B \quad (1)$$

where E is the excess ¹³C and B is sediment organic matter content or animal biomass (Middelburg et al., 2000). Excess ¹³C is the difference between the fraction ¹³C (F) of control (T₀) and sample (T₆), i.e.

$$E = F_{\text{sample}} - F_{\text{control}} \quad (2)$$

with: $F = {}^{13}\text{C}/({}^{13}\text{C} + {}^{12}\text{C}) = R/(R + 1)$, and

$$R = (\delta^{13}\text{C}/1000 + 1) \cdot R_{\text{VPDB}}$$

where R_{VPDB} = 0.0112372 = the carbon isotope ratio of the reference material (Vienna PDB).

Sediment organic matter was derived from the sediment dry weight and % organic carbon. Meiofaunal biomass was estimated from the product of their density and mean individual biomass. Mean individual biomass was estimated by means of a volumetric method. The body length (mm) and maximum width (mm) of an animal were measured and body volume (nl) was calculated by assuming conversion factors specific for each taxon (Feller and Warwick, 1988). Body volume was translated to wet weight (µg wwt) by assuming a specific gravity of 1.13 (Wieser, 1960) and converted into dry weight (µg dwt) using a dry/wet weight ratio of 0.25 (Feller and Warwick, 1988). Carbon was estimated at 40% of animal dry weight (Feller and Warwick, 1988).

2.3. Sediment respiration

Sediment community metabolism was measured in terms of sediment oxygen consumption on three separate undisturbed sediment cores from each site. These cores were taken intact by hand with perspex

cores (14 cm inner diameter, sediment column of ca. 15 cm) between the medium and low water mark at low tide. They were closed at the bottom with rubber stoppers and transported to the research station within 1 h of collection. At the station, the cores were submerged in an incubation tank with running ambient sea water at in situ temperature. The sediment was allowed to stabilise for 24 h. For measurements, the cores — with an overlying water column of about 10–15 cm — were tightly closed with perspex lids sealed with rubber rings. Before and during oxygen measurements, the overlying water was gently stirred with a mechanical stirrer protruded through the lid. Care was taken to adjust the position and rotation speed of the stirrer such that the sediment surface was not disturbed. Oxygen concentration in the overlying water was monitored with a WTW CellOx 325 electrode. Cores were incubated for 4 h. Sediment oxygen consumption was determined as the difference between the initial and final oxygen concentration. Parallel measurements of oxygen uptake in seawater not overlying sediment served as controls. Unfortunately, technical problems prohibited oxygen consumption measurements at T₆.

3. Results

At the start of the experiment (T₀), mean total meiofaunal densities were significantly higher (Mann-Whitney U-test, $p < 0.05$) in the finer sediment at Breoyane than in the coarser one at Tyskehytte: 741 ± 400 ind 10 cm^{-2} (mean \pm 1SD) vs 50 ± 41 ind 10 cm^{-2} .

These densities corresponded to a biomass of 1741 ± 940 and 576 ± 472 $\mu\text{g dwt } 10\text{ cm}^{-2}$, respectively (Fig. 2). A total of four meiofaunal higher taxa were recorded (Oligochaeta, Turbellaria, Nematoda, Harpacticoida). Oligochaetes were the most abundant taxon, with a peak density of 1180 ind 10 cm^{-2} noted in one replicate at Breoyane Island. Other taxa were numerically less important: Nematoda (a maximum of 8 and 13 ind 10 cm^{-2} in coarse and fine sand, respectively), Turbellaria (a maximum of 5 ind 10 cm^{-2} in both coarse and fine sand), and Harpacticoida (a maximum of 12 and 2 ind 10 cm^{-2} , in coarse and fine sand, respectively). A decrease (albeit statistically not significant, Mann-Whitney U-test, $p > 0.05$) of the total meiofaunal abundance was observed at the end of the experiment (T₆) in finer sand (a mean total density of 499 ± 349 ind 10 cm^{-2}) but not in coarse sediment. No clear vertical pattern of meiofaunal distribution was observed during the experiment (data not shown).

Mean oxygen consumption was significantly lower (Mann-Whitney U-test, $p < 0.05$) at Tyskehytte: 6.48 ± 3.12 mmol $\text{O}_2\text{ m}^{-2}\text{ d}^{-1}$ (mean \pm 1SD) than at Breoyane: 15.12 ± 1.2 mmol $\text{O}_2\text{ m}^{-2}\text{ d}^{-1}$, these values being equivalent to, respectively, 70 and 145 mg of organic carbon metabolised $\text{m}^{-2}\text{ d}^{-1}$.

At the end of the labelling period, the ^{13}C inventories in the sediment (i.e. ‘unmetabolised’ cyanobacterial carbon, dissolved organic carbon and ^{13}C in consumer biomass for the upper 10 cm sediment layer) were significantly lower ($p < 0.05$, Mann-Whitney U-test) at Tyskehytte than at Breoyane: 96.3 ± 43.2 mg C m^{-2} vs.

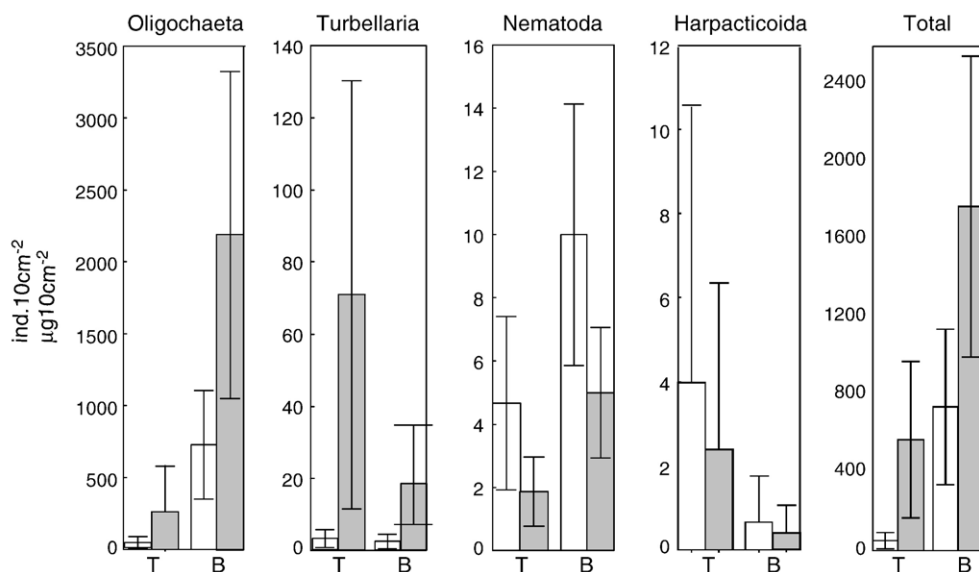


Fig. 2. Densities (white bars) and biomass (dry weight) (shaded bars) of meiofaunal taxa in both beaches studied. Means \pm SD.

$378.0 \pm 176.8 \text{ mg C m}^{-2}$. These values represent on average 16 and 63%, respectively, of the total amount of carbon added at T_0 . In Breoyane, 80–92% of the label recovered in the bulk organic fraction of the sediment at the end of the experiment was present in the upper 2 cm and a gradual decrease of the label concentration with depth was observed. By contrast, in the coarser sediments of Tyskehytte, labelled carbon penetrated deeper and only 49–68% was found in the upper 2 cm of the sediment (Fig. 3). Only a very small portion of the label recovered from deeper layers can be attributed to meiofaunal (mainly oligochaete) uptake (see further), the majority of this ^{13}C then potentially consisting of particulate and/or dissolved organic carbon and bacteria. The relative importance of these compartments can, however, not be assessed from our data.

Specific uptake ($\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{control}}$) by all major meiofauna taxa was substantial. For all meiofaunal taxa (except harpacticoid copepods, which were only obtained in sufficient quantity from the coarser sediment), specific uptake was higher in coarse sediment than in finer sediment (Table 2) (this

Table 2

Specific uptake ($\delta^{13}\text{C}$, ‰), carbon uptake of different meiofaunal taxa, sediment respiration before enrichment and calculated amount of carbon respired during the enrichment experiment (means \pm SD of 3 replicates)

Variable	Tyskehytte	Breoyane
Respiration ($\text{mg C m}^{-2} \text{ d}^{-1}$)	70 ± 33	144 ± 11
^{13}C respired ($\text{mg } ^{13}\text{C m}^{-2} \text{ d}^{-1}$)	84 ± 7	37 ± 29

Specific uptake ($\Delta\delta^{13}\text{C}$) over the entire 6-day incubation

Sediment	228 ± 78	954 ± 450
Oligochaetes	2202 ± 1152	1470 ± 834
Turbellaria	534	18
Nematoda	378	198
Harpacticoida	492	nd

Carbon uptake ($\text{mg } ^{13}\text{C m}^{-2} \text{ d}^{-1}$)

Sediment	16.05 ± 5.5	63 ± 29.7
Oligochaetes	0.3 ± 0.16	0.42 ± 0.24
Turbellaria	0.080	0.001
Nematoda	0.001	0.002
Harpacticoida	0.003	nd
Total meiofauna	0.384	0.423

nd – not determined

^{13}C -uptake is expressed per day for comparison with respiration data under the assumption that it remained constant over the entire 6-day experiment. In case of lack of replicates (limited number of animals) no standard deviation is given.

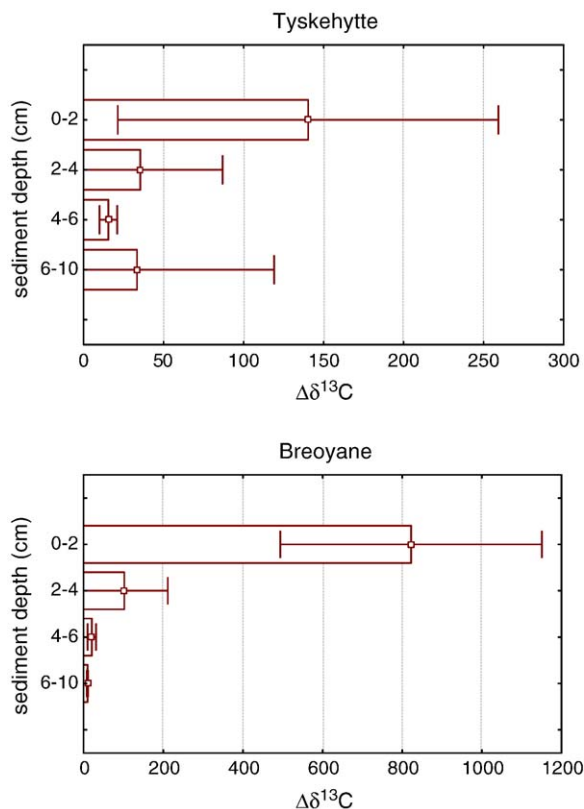


Fig. 3. Inventory (expressed as $\Delta\delta^{13}\text{C}$) of added ^{13}C -labelled organic matter at different sediment depths in both stations studied. Means \pm SD.

difference was statistically significant for oligochaetes, Mann-Whitney U-test, $p < 0.05$; note that in all taxa except oligochaetes, individuals from different depth strata and replicates were pooled into a single sample in order to obtain sufficient biomass for analysis). In the coarser sediments of Tyskehytte 90% of the label recovered in oligochaete biomass was in animals from below 4 cm. Similarly, in Breoyane, 77% of the label recovered in oligochaetes was present in deeper sediment layers (4–8 cm).

In spite of significant labelling of meiofauna, these values represent a small portion of the total ^{13}C -inventory (Table 2): in the coarse sandy sediment of Tyskehytte, 0.2–7.1%, 0.17% and 0.003% of the ^{13}C -inventory at the end of the experiment was recovered in, respectively, oligochaete, turbellarian and nematode biomass. In Breoyane, 0.15–0.63%, 0.0007% and 0.0002% of the total ^{13}C added, and 0.06–1.18%, 0.001% and 0.0004% of the ^{13}C recovered at the end of the experiment, was recovered in oligochaete, nematode and turbellarian biomass, respectively. The total amounts of ^{13}C incorporated in meiofaunal biomass were nearly identical for both stations: $2.299 \text{ mg } ^{13}\text{C m}^{-2}$ at Tyskehytte and $2.517 \text{ mg } ^{13}\text{C m}^{-2}$ at Breoyane (Mann-Whitney U-test, $p > 0.05$).

4. Discussion

The respiration rates obtained here generally compare well with rates reported for sandy beaches in South Africa that differ with respect to tidal level and exposure (4.80 to 18.96 mmol O₂ m⁻² d⁻¹; Dye, 1980, 1981) and sandy subtidal sediments from other areas (11.52 to 19.92 mmol O₂ m⁻² d⁻¹; Malan and McLachlan, 1991; see Table 3 for a full overview). Comparisons between studies are sometimes difficult due to differences in methods used and their inherent limitations. However, the wide range of oxygen consumption rates at different tidal levels and different beach types, and the comparatively higher respiration rates in the finer-grained, labile-carbon-rich sediment of Breoyane (this study), do not suggest a major impact of temperature on beach metabolic rates. Our own data rather support the contention that benthic metabolic rates depend more on organic matter quality and availability (Arnosti et al., 1998; Glud et al., 1998; Rysgaard et al., 1998, 2000; Kostka et al., 1999). Furthermore, respiration rates in sandy-gravel beaches on the oceanic Arctic Bear Island averaged 2.40 and 7.92 mmol O₂ m⁻² d⁻¹ in an exposed and sheltered beach, respectively (Urban-Malinga et al., 2004), and thus were generally lower than in the present study. Although sediment organic matter loads were similar in beaches on Bear Island and in Kongsfjorden, lower C/N-ratios in the latter suggest that organic matter quality was higher on Kongsfjorden beaches. Meiofaunal densities at Breoyane were also nearly twice as high as densities in the sheltered beach at Bear Island (Urban-Malinga et al., 2004, 2005). Finally, the respiration rates at the Kongsfjorden beaches exceeded rates in deeper Arctic sediments (1.92–12.00 mmol O₂ m⁻² d⁻¹, Hulth et al., 1994; 1.92–4.32 mmol O₂ m⁻² d⁻¹, Piepenbug et al., 1995).

While the respiration rate at Breoyane can account for the metabolism of four-fold the amount of ¹³C that disappeared from Breoyane sediment in our labelling experiment, the respiration rate at Tyskehytte (70 mg C m⁻² d⁻¹) is lower than the metabolic rate for Tyskehytte sediment in the ¹³C-experiment (84.1±7.2 mg C m⁻² d⁻¹ under the assumption that metabolism remained constant over the entire 6-d incubation). This suggests that our organic matter addition stimulated benthic metabolism at Tyskehytte, while not contributing importantly to the benthic metabolism at Breoyane, where the four-fold higher chl-a concentrations in the sediment (Urban-Malinga et al., 2005) indicate a generally higher-quality organic matter supply. This is in accordance with the fast disappearance of ¹³C from Tyskehytte sediment, and strongly indicates that respiration was the major fate of the labile organic matter in this coarse sandy beach sediment. Similarly, CO₂ was a major sink of organic carbon in shallow marine sediments in more temperate environments (Olafsson et al., 1999; Moodley et al., 2000). Our data also illustrate that the respiration rates measured at Tyskehytte were limited by organic matter availability, while this was probably less the case for the finer-grained sediment at Breoyane. It is well-known that in spite of generally lower microbial and faunal densities and biomass, coarse sediments can be biogeochemically very active, for instance because of their high filtration rates (Huettel et al., 2003). As such, higher transport rates in coarser sediments can outweigh the effect of a higher surface area in finer-grained sediments (Rasheed et al., 2003). However, under the enclosed conditions of our experiment, the natural pressure gradients and advective water flows that cause such high transport rates were excluded. Hence, the faster mineralisation of labile organic matter in Tyskehytte sediments is probably linked to the better availability to microbes and fauna in deeper sediment strata, which results from a higher sediment porosity and a faster penetration of (labelled) organic matter to deeper sediment layers.

Cyanobacteria used here were utilised as a carbon source by all major meiobenthic taxa found, viz. oligochaetes, nematodes, turbellarians and harpacticoid copepods. Enchytraeid oligochaetes are typical opportunistic detritus- and (associated) microbial feeders (Giere and Pfannkuche, 1982) and their distribution pattern is directly related to the distribution of beach casts (Koop and Griffiths, 1982; Giere and Pfannkuche, 1982; Colombini and Chelazzi, 2003). Indeed their density, and that of other meiobenthic taxa, was markedly higher a few metres higher up on the beaches of Tyskehytte and Breoyane, where wrack and carrion

Table 3
Overview of published data on oxygen consumption rates on sandy intertidal beaches

Geographical location	Oxygen consumption mmol O ₂ m ⁻² d ⁻¹	References
South Africa	4.7–14.3	Dye (1979)
South Africa	8.5–11.5	Dye (1980)
South Africa	14.5–18.9	Dye (1981)
South Africa	11.5–19.8	Malan and MacLachlan (1991)
Baltic Sea	2.1–40.1	Yap (1991)
Bear Island (Arctic)	2.5–7.8	Urban-Malinga et al. (2004)
Kongsfjorden (Arctic)	6.5–15.1	this study

were more prominently present (Urban-Malinga et al., 2005). We measured the carbon isotope ratios of macroalgal wrack (*Fucus* sp.) and carrion (*Themisto* sp.) collected on the Kongsfjorden beaches at the time of our experiment. Both were rather similar, with $\delta^{13}\text{C}$ values for macroalgal wrack ($-17.59 \pm 0.36\text{‰}$, $N=3$) being slightly heavier than those for carrion ($-19.48 \pm 0.09\text{‰}$, $N=3$). The natural $\delta^{13}\text{C}$ of oligochaetes, then, effectively mirrored these potential carbon sources: at Breoyane, their carbon isotopic values ($-16.57 \pm 0.37\text{‰}$, $N=3$, upper 4 cm) suggest macroalgal wrack as their principal food source, while at Tyskehytte (-19.45‰ , single value, upper 4 cm) carrion may have predominated in their diet. Other meiobenthic taxa had more depleted $\delta^{13}\text{C}$ values, but in the absence of sample replication we prefer not to speculate on possible causes.

Specific uptake by meiofauna was significantly higher in Tyskehytte sediment than in Breoyane sediment. This supports our contention that the beach benthos at the former location was probably food-limited at the time of our experiment and hence shifted to feeding on the added cyanobacteria, whereas this was less the case at Breoyane. Specific uptake in oligochaetes at Tyskehytte was also higher than in any meiofauna in similar experiments (same organic matter source, same concentration) performed in temperate beach and tidal flat locations with comparatively high loads of organic matter (Moens and Urban-Malinga, unpubl.).

However, in spite of high specific uptake, only a small portion of the total ^{13}C -inventory at the end of the experiment was present in meiofauna. Meiobenthos at Tyskehytte and Breoyane incorporated, respectively, 0.38 and 0.42 $\text{mg C m}^{-2} \text{d}^{-1}$, corresponding to 0.48 and 0.81% of average daily ^{13}C -losses. The following considerations are important when trying to estimate from these figures the contribution of meiobenthos to the mineralisation of the added cyanobacterial carbon. First, we can assume that the measured ‘incorporation’ reflects assimilation *sensu stricto*, i.e. carbon incorporated into animal tissue (Penry, 1998). Data on assimilation efficiencies (AE, this is assimilation/consumption) in meiobenthos are scant, but for nematodes, e.g., it is generally assumed that AE is low, typically in the order of 20%. Reviews of meiobenthic assimilation efficiencies generally propose a slightly higher average of 25% (Heip et al., 1985; Somerfield et al., 2005), but define assimilation as the sum of production (\approx assimilation *sensu stricto*) and respiration. The same reviews propose an average production efficiency (PE, i.e. production/(production+respiration)) of 80%, hence our AE estimate of 20%. Second, freezing and

subsequent thawing of animals typically results in label leakage yielding loss of more than half of the label absorbed in short-term incubations (up to 24 h) (Moens et al., 1999). However, because this mostly concerns low-molecular weight metabolites rather than ‘structural’ compounds (Rivkin and DeLaca, 1990; Moens et al., 1999), we assume that such losses were less important in the present study. Based on our first consideration, we estimate that the meiobenthos consumed five times more carbon than was measured in meiobenthic biomass, i.e. 2.4 and 4.05% of the carbon metabolised in our experiment at Tyskehytte and Breoyane, respectively. In view of our second consideration, this estimate should be considered conservative. Oligochaetes are by far the largest meiofaunal consumers of organic matter in our beaches, with nematodes contributing only 0.5% of the total meiobenthic uptake at both stations. Turbellarians accounted for 27% of meiobenthic carbon uptake at Tyskehytte but contributed negligibly ($<0.1\%$) at Breoyane. In the absence of macrofauna, this implies that bacteria accounted for by far the largest share of the benthic metabolism at these Arctic beaches.

The relatively low contribution of meiobenthos to total sediment metabolism and carbon mineralisation in this study is at variance with the proposed larger role for meiobenthos in Arctic beach sediments, which are often characterised by low macrofauna biomass (Szymelfenig et al., 1995). It is, however, in accordance with recent estimates on the (low) quantitative importance of meiobenthos (mainly nematodes) as consumers of microphytobenthic and bacterial production in estuarine tidal flat sediments (Middelburg et al., 2000; Moens et al., 2002; Van Oevelen et al., in press). It should be stressed, however, that the densities of oligochaetes and nematodes in the sediments used in the present experiment are considerably lower (four-fold at Tyskehytte and 25-fold at Breoyane) than higher up and lower down on the same beaches. Hence, their organic matter consumption and contribution to sediment metabolism may well differ even over small spatial scales. More research including different spatial and temporal scales is therefore needed before generalisations can be made.

Acknowledgements

This study was realised thanks to a ‘Large Scale Facility for Arctic environmental research’ grant in Ny Alesund (Svalbard, 2001), provided by the Norwegian Polar Institute (NP-29/2001-‘Organic enrichment effects on an Arctic sandy beach’). T.M. is a postdoctoral fellow with the Flemish Fund for Scientific Research (FWO).

Jozwa Wiktor is gratefully acknowledged for his invaluable help with the field work and Steven Bouillon (Laboratory of Analytical Chemistry, Free University Brussels) for assistance with the isotopic analyses.

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