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Processing of ^{13}C-labelled diatoms by a bathyal community at sub-zero temperatures

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ABSTRACT: The carbon (C) budget in bathyal permanently cold sediments was assessed by means of a pulse-chase experiment in the deep Faroe-Shetland Channel (FSC). The food pulse was simulated by adding 500 mg C m^{-2} of the ^{13}C-labelled marine diatom *Chaetoceros radicans* to sediment cores retrieved from 1080 m in the FSC. The fate of the tracer was followed over 6 d into the dissolved inorganic C pool (DI^{13}C) as well as the bacterial and faunal (metazoan macrofauna and meiofaunal-sized nematode) biomass. After 3 d of incubation, 14.9 and 0.81 mg C m^{-2} of the algal C was recovered from bacterial and faunal biomass, respectively, while only 3.8 mg C m^{-2} was respired. Respiration was the dominant tracer pathway after 6 d of incubation (44 mg C m^{-2}). Bacterial tracer uptake did not increase significantly between Days 3 and 6. The tracer recovered from metazoan fauna at the end of the experiment constituted 3.2% (2 mg C m^{-2}) of the total processed C, with meiofauna contributing only ~1% to the total metazoan uptake. The bacterial response was characterised by varying bacterial growth efficiency (BGE). During the first half of the experiment, low respiration and high bacterial uptake of the ^{13}C-labelled substrate resulted in particularly high BGE, while the opposite was observed in the second half of the incubation. We postulate that the high BGE at the start of the experiment represents the absorption and metabolism of the readily available labile components of the added organic matter (OM). The decrease in BGE possibly corresponds to the initiation of the energetically costly hydrolytic processes necessary for the consumption of more recalcitrant OM.

KEY WORDS: Stable isotope labelling · Benthos · Bacterial growth efficiency · Bathyal sediments · Faroe-Shetland Channel · δ^{13}C · PLFA

INTRODUCTION

Production in the deep-sea is almost entirely fuelled by the import of particulate organic matter (OM) from the upper mixed layer (Gage & Tyler 1991). Seasonal and interannual variations in the vertical particle flux to the deep sea are linked to variability in surface ocean productivity and pelagic community structure in overlying waters (Turley et al. 1995, Jickells et al. 1996, Wassmann 1998, De La Rocha & Passow 2007). In the temperate and boreal regions of the world's oceans, a large fraction of the vertical flux arrives on the deep-sea floor in episodic pulses related to phytoplankton blooms in surface waters (Billett et al. 1983, Lampitt 1985, Smith et al. 1994). Benthic processes are closely linked to the sedimentation of particulate organic carbon (POC), such that interannual variability in surface water production is 'mirrored' in deep-sea processes (Pfannkuche et al. 1999). The benthic response to these seasonal phenomena is an active field of research due to its importance for understanding ecosystem functioning in the deep ocean, as well as the biogeochemical cycling of organic carbon (OC) in deep-sea sediments (Gooday 2002).

Bacteria are considered to be the most important biological component involved in the transformation and mineralization of OC in the biosphere (Falkowski et al. 2008). They contribute to the cycles of carbon (C) and

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nutrients in 2 ways: by producing new biomass (bacterial secondary production, BP) and by remineralizing OC and nutrients (bacterial respiration, BR) (del Giorgio & Cole 1998). The relative magnitudes of BR and BP are expressed by the bacterial growth efficiency (BGE), which represents the amount of new bacterial biomass produced per unit of substrate assimilated and hence the efficiency with which C is made available to higher trophic levels (del Giorgio & Cole 1998). The factors that influence BGE are currently not well understood, and as a result the real magnitude of OC flow through bacteria in the world's oceans remains largely unknown (del Giorgio & Cole 2000).

The bacterial response to naturally occurring, seasonal inputs of POC has been documented in various studies (Lochte 1992, Pfannkuche 1993, Pfannkuche et al. 1999). It is first detectable as an intensification of metabolic activity, reflected in adenosine triphosphate concentration (Graf 1989) and extracellular enzyme production (Boetius & Lochte 1994). The extracellular hydrolysis of OM is a prerequisite for bacterial cells to gain access to macromolecules, since only low molecular weight compounds can be transported across bacterial membranes (Benz 1985). Bacterial growth may follow enzyme production provided that the exploitable energy of the substrate is sufficiently high (Boetius & Lochte 1994, 1996). Other small-sized organisms, such as protozoa and foraminifera, are also highly responsive to food pulses and may undergo changes in density (Gooday & Rathburn 1999) and species composition (Lambshead & Gooday 1990) or show episodic recruitment of opportunistic species (Ohga & Kitazato 1997). The response of benthic metazoans in terms of population dynamics has been more difficult to establish, perhaps because of their slower turnover rates (Gooday 2002). On the timescale of several months, however, metazoan communities show shifts in their structure in relation to upper-ocean conditions and food supply (Ruhl & Smith 2004, Sellanes et al. 2007, Ruhl et al. 2008).

In recent years, stable isotope techniques have enabled the direct observation of POC utilization by benthic communities. The role of each benthic component in the short-term C processing can be assessed quantitatively using labelled substrates as food sources. Previous labelling studies demonstrated that benthic C processing can be rapid in deep-sea sediments (Blair et al. 1996, Moodley et al. 2002, 2005, Witte et al. 2003a,b). Tracer uptake by faunal groups varies with environmental setting and community structure (Moodley et al. 2000, Witte et al. 2003b, Woulds et al. 2007). Despite the attempts to categorise previous observations in order to predict benthic response patterns in unexplored regions (Woulds et al. 2009), the factors that control the speed, magnitude, and relative importance of the different food web components in contrasting oceanic environments remain unclear. Nonetheless, it is apparent that bacteria typically dominate C mineralization in deep-sea sediments and that temperature plays a key role in limiting the overall benthic response (Moodley et al. 2005). The quantity and quality of available substrates have also been suggested to affect C processing patterns in bathyal and abyssal sediments (Bühring et al. 2006, Aspetsberger et al. 2007). These findings are not entirely surprising considering the wealth of studies that document interacting effects between temperature and substrate supply in limiting the growth of heterotrophic bacterial communities in other marine environments (reviewed by Pomeroy & Wiebe 2001, Apple et al. 2006).

The present study examined the response of a bathyal benthic community to an influx of OM under mesotrophic conditions (Kaariainen 2006) and subzero temperatures. A food pulse was simulated by adding ^{13}C-labelled diatoms to undisturbed sediment cores retrieved from the deep Faroe-Shetland Channel (FSC). The mineralization of the added C by the benthic community was followed for 6 d while the uptake of tracer by the different food web components was measured on 2 sampling intervals (Days 3 and 6). The progress of the benthic response and the changes in BGE during the incubation were evaluated by the release of dissolved inorganic ^{13}C ($DI^{13}C$) in the overlying water and by the incorporation of ^{13}C-uptake into the biomass of bacteria, metazoan macrofauna, and meiofaunal-sized nematodes.

MATERIALS AND METHODS

Study site. The experiment was carried out in May 2007 on FRV 'Scotia' (Marine Scotland). The FSC is a deep-water channel separating the Faroe Plateau from the Scottish shelf and is a major pathway through which Arctic bottom water escapes to the south (Fig. 1) (Turrell et al. 1999). The sampling station was located at 1080 m in the FSC (61° 13′ 88″ N, 2° 40′ 62″ W) (Fig. 1). The sediment type was muddy sand with some gravel, and the grain size ranged from very fine to medium (Bett 1997). OC content in the top centimetre was 0.2%. Bottom water oxygen content averaged 306 ± 6.5 µmol l^{-1} (± SD, n = 9). Bottom water temperature and salinity at the time of sampling were −0.7°C and 34.9, respectively.

Algal culture. The cosmopolitan chain-forming diatom *Chaetoceros radicans* (CCMP, Bigelow Marine Laboratories; cell size: 6 µm diam.) was cultured at 15°C (16 h light:8 h dark cycle) in artificial seawater (Grasshoff et al. 1999) amended with f/2 medium

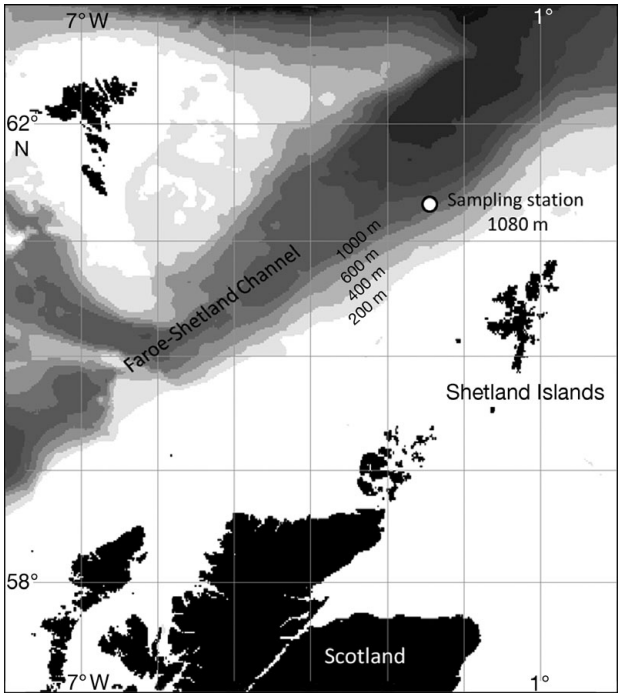

Fig. 1. Study area and location of sampling station (produced on the GEBCO Digital Atlas software; www.gebco.net)

(CCMP) and ^{13}C-bicarbonate (99 atom % ^{13}C-enriched $NaHCO_3$; Cambridge Isotope Laboratories). The algal material was harvested after 3 wk by centrifugation (1400 × *g*, 15 min) and washed 3 times with sterile-filtered (0.2 µm) seawater to remove excess $NaH^{13}CO_3$ and any dissolved organic ^{13}C exuded by the diatoms. The harvest was frozen in liquid nitrogen to avoid cell rupture and stored at −80°C until freeze-drying. The dried algae contained 46 atom % ^{13}C (measured on a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} Advantage isotope ratio mass spectrometer; Thermo Finnigan). Before use in the pulse-chase experiment, the algae were suspended in 0.2 µm filtered seawater. Despite thorough rinsing of the algal material during harvesting, the possibility of simultaneous introduction of ^{13}C-dissolved organic carbon (DOC) into the cores cannot be excluded. The amount of ^{13}C-DOC added to our experimental cores was not quantified. Nonetheless, a similar ^{13}C study has previously demonstrated that this artefact contributes <5% of the total added ^{13}C (Andersson et al. 2008).

Sampling and experimental design. A Bowers & Connelly maxicorer equipped with 8 coring mechanisms was used for sediment core retrieval. The sediment cores (10 cm internal diameter, i.d.) used in the incubation experiment (n = 15) were collected from 3 maxicorer deployments. In order to simulate the sedimentation of POC, 60 mg of freeze-dried *Chaetoceros radicans*, equivalent to 0.5 g OC m^{-2}, were carefully added to 12 experimental cores with a long pipette (separate for each core) in order to achieve even distribution of algae on the sediment surface. Bottom water temperature was maintained by incubating the cores in a chilling unit. Three control cores (without labelled algae addition) were also incubated together with the experimental cores and served for recording the background sediment community oxygen consumption (SCOC) as well as the determination of the background δ^{13}C of bacterial phospholipid fatty acids (PLFA). All cores were sealed with lids to prevent gas exchange with air and incubated at ambient temperature (range: −1 to 0°C) in the dark for 6 d. The overlying water was sampled for oxygen and DI^{13}C measurements at regular intervals (Time 0 and then after 1, 2, 3, 4, and 6 d). Oxygen concentration was measured onboard using Winkler titration and did not decrease more than 20% of the initial value (Hulth et al. 1994). The DI^{13}C samples were filtered through a 0.2 µm syringe filter into 12 ml gas-tight glass vials sealed with rubber septa and poisoned with 100 µl of saturated $HgCl_2$ solution to stop bacterial activity. The samples were kept at 4°C until analysis. Six replicate cores were sectioned after 3 and 6 d of incubation. For each experimental time, 3 cores were sampled for faunal analysis, and the remaining 3 were used for bacterial PLFA analysis. Control cores were sectioned on Day 6 and samples were used for the determination of background bacterial PLFA isotopic signatures.

Faunal samples were taken from 0 to 2, 2 to 5, and 5 to 10 cm. Part of the slice was kept for meiofaunal (defined here as animals passing through 250 µm and retained on a 32 µm mesh sieve) stable isotope analysis with the aid of a subcore (2.5 cm i.d.), and the rest was sieved through a 250 µm mesh sieve to retain macrofauna specimens. Meio- and macrofauna samples were stored in 10% formalin until picking and identification (in the case of macrofauna) under a binocular microscope. Detailed methodology of the macrofaunal analysis and results on the macrofaunal community structure, biomass, and ^{13}C uptake at the family or genus level are presented elsewhere (Gontikaki et al. in press). In the case of meiofauna (nematodes), only the 0 to 2 cm depth layer was analysed based on the macrofaunal vertical distribution pattern in the FSC, which suggested a particularly shallow dwelling community (90% of macrofaunal animals recovered from the 0 to 2 cm layer) (Gontikaki et al. in press). A minimum of 100 nematodes per sample were picked to ensure sufficient biomass for a reliable isotope analysis. The nematode biomass (OC content) was measured directly from the area counts given in the standard output of the isotope ratio mass spectrometer.

Sediment samples used for bacterial PLFA analysis were taken from 0 to 0.5, 0.5 to 1, 1 to 2, 2 to 3, 3 to 5, and >5 cm horizons. The samples were placed in glass vials and stored at –20°C until analysis.

DI^{13}C analysis. The C isotope ratio of dissolved inorganic carbon (DIC) was determined following its quantitative conversion to carbon dioxide (CO_2) by acidification. Of the samples, 2 ml were added to 12 ml Exetainers® (Labco). The Exetainers® were capped and then flush filled with He at a flow rate of 100 ml min^{-1} for 5 min. 100 µl of 1.3 M phosphoric acid was injected into each sample through the rubber septum in the cap. The head space of the Exetainer® containing the released CO_2 was then transferred to a second Exetainer® as described by Midwood et al. (2006). The C isotope ratio of the CO_2 in this second Exetainer® was then analysed using a Gas-bench II connected to a Delta^{Plus} Advantage isotope ratio mass spectrometer (both Thermo Finnigan). The C isotope ratios, all expressed relative to Vienna PeeDee Belemnite (VPDB), were calculated with respect to CO_2 reference gasses injected with every sample and traceable to International Atomic Energy Agency (IAEA) reference material NBS 19 TS-Limestone. Through use of the Valco valve and a sample loop within the gas bench and the instrument software, each Exetainer® was sampled 9 times, of which the last 5 values were averaged to give a single sample value. Repeated analysis of a quality control standard gas indicated that the precision of the gas bench for analyzing $\delta^{13}C$ of CO_2 at a concentration of 450 ppm in exetainers was –35.03 ± 0.24‰ (mean ± SD, n = 65). The amount of DIC in the sample was determined from the mean amplitude of the last 5 replicate sample peaks compared against a standard curve constructed from a range of similarly treated solutions.

Lipid extraction and separation. Total lipids were extracted following the Bligh & Dyer (1959) extraction procedure as modified by White et al. (1979). Approximately 9 g of freeze-dried sediment was weighed out in glass centrifuge tubes with a PTFE lined cap. The lipids were extracted using a single phase extractant consisting of chloroform, methanol, and citrate buffer (1:2:0.8 v/v/v) for 2 h. The total lipid extract was fractionated into polarity classes on silicic acid columns (6 ml ISOLUTE SIS PE columns; International Sorbent Technology) by sequential elution with chloroform (neutral lipids), acetone (glycolipids), and methanol (phospholipids). The phospholipids were transmethylated under alkaline methanolysis to yield fatty acid methyl esters (FAME).

FAME quantification and identification. Individual FAME were identified and quantified on a Shimadzu GC-2014 gas chromatograph flame ionization detector equipped with a Zebron ZB-WAX fused silica capillary column (30 m × 0.25 mm i.d.) with helium as the carrier gas. The oven temperature was programmed to rise from 50 to 160°C at 25°C min^{-1}, then 160 to 240°C at 4°C min^{-1} and then hold for 10 min. Quantification was performed by comparing peak areas to an internal standard (19:0). Individual components were identified by reference to standards (Sigma-Aldrich, Matreya). Repeated analysis of a 28 component standard sample gave a mean % SD across all peaks of 1.02%.

FAME stable carbon isotope ratios. The isotopic composition of individual FAME was determined using a GC Trace Ultra with combustion column attached via a GC Combustion III to a Delta V Advantage isotope ratio mass spectrometer (all Thermo Finnigan). Samples (2 µl) were injected in splitless mode onto a J&W Scientific HP-5 column, 50 m length, 0.2 mm i.d. with a film thickness of 0.33 µm (Agilent Technologies). Running conditions were as described by Paterson et al. (2006). The C isotope ratios were calculated with respect to a CO_2 reference gas injected with every sample and traceable to IAEA reference material NBS 19 TS-Limestone. Repeated analysis, over a 2 mo period, of the $\delta^{13}C$ value of a C_{19} FAME internal standard gave a SD of 1.11‰ (n = 18).

Calculations. Carbon isotopes are expressed in the delta notation (δ ‰) relative to a reference according to:

$$\delta^{13}C\ (‰) = R_{sample}/R_{VPDB} \times 1000 \quad (1)$$

where R_{sample} and R_{VPDB} are the ^{13}C:^{12}C ratios of the sample and the international reference material for carbon (VPDB) respectively (R_{VPDB} = 0.0112372). In order to obtain the actual PLFA $\delta^{13}C$ values, the isotope ratios of FAME were corrected for the extra C in the methyl group that was added during derivatization according to Crossman et al. (2004).

The absolute amount of incorporated ^{13}C (total uptake, I) was calculated as the product of excess ^{13}C (E) and concentration of DIC, specimen biomass or specific bacterial PLFA concentration. Excess ^{13}C (E) is given by the difference in the fraction ^{13}C in the sample (F_{sample}) and the background ($F_{background}$):

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

where $$F = \frac{^{13}C}{^{13}C + ^{12}C} = \frac{R}{R+1}$$

and $$R = \left(\frac{\delta^{13}C}{1000} + 1\right) \times R_{VPDB}$$

The background $\delta^{13}C$ of DIC was taken as the value measured at Time 0 in the experimental cores in order to correct for any contamination of ^{13}C-bicarbonate by the added diatoms (Moodley et al. 2005).

Label incorporation into bacterial biomass, was based on the ^{13}C labelling of the most common bacterial PLFA in all cores and depth horizons (i15:0, a15:0, and i16:0) (Boschker & Middelburg 2002). The fatty

acid 18:1(n-7) is considered to be primarily of bacterial origin; however, it is also present in *Chaetoceros radicans* (D. J. Mayor unpubl. data). The effect of incorporating 18:1(n-7) into the calculations of bacterial uptake is examined. For each bacterial fatty acid, label incorporation was calculated as:

$$I_{PLFA} = E_{PLFA} \times PFLA_{concentration} \quad (3)$$

Subsequently, incorporation into bacterial biomass was calculated based on Middelburg et al. (2000) as:

$$I = \sum \frac{I_{PLFA}}{a \times b} \quad (4)$$

where a is the average PLFA concentration in bacteria (0.056 g PLFA C g^{-1} of C biomass; Brinch-Iversen & King 1990) and b is the fraction of the bacterial PLFA considered here that are encountered in sediments from the FSC (0.11; calculated from the % of i15:0, a15:0, i16:0 in the present study, data not shown). The total algal C ($^{12}C + {}^{13}C$) recovered from bacteria, fauna, and the DIC pool was calculated as the quotient of the total uptake I and the fractional abundance of ^{13}C in the algae (0.46). Bacterial biomass was calculated from the concentration of bacteria-specific biomarkers (i15:0, a15:0, i16:0) and the conversion factors used in Eq. (4).

Bacterial growth efficiency (BGE). BGE is defined as the fraction of assimilated OC that is channelled towards growth according to:

$$BGE = \frac{BP}{BP+BR} \quad (5)$$

where BP is bacterial production and BR the bacterial respiration. In the present study, BGE was calculated based on ^{13}C uptake data and represents the growth efficiency when bacteria consume the added material. BP is thus the total algal C uptake (see 'Calculations' above) and BR is the bacterial respiration of algal C (= total algal DIC – algal DIC due to faunal respiration). Macrofaunal and nematode biomass-specific respiration rates (R_{macro} and R_{nem}) were estimated using the allometric equations: $R_{macro} = 7.4 \times 10^{-3} \times W^{-0.24}$ (Mahaut et al. 1995) and $R_{nem} = 0.0164 \times W^{-0.1456}$ (Soetaert et al. 1997, Heip et al. 2001), respectively, where W is the individual organism weight (mg C). Corrections for temperature were based on Gillooly et al. (2001).

Statistical analysis. The oxygen flux within each core was calculated from the slope of the linear regression of oxygen concentration against time (0, 2, 3, 6 d) (Fig. 2). Due to analytical problems encountered on Days 1 and 4, data from these days were excluded from the analysis.

The increase in algal-derived DIC concentration with time was best described by an exponential curve ($y = b \times e^{ax}$). The effect of time on algal-derived DIC production was tested by means of linear regression after the natural log transformation of the DIC concentration data. Statistical tests (ANOVA or the non-parametric equivalent where the ANOVA assumptions were not met) were carried out using SigmaStat® 11.0 (Systat Software). Values are given as means ± SD.

RESULTS

Sediment community oxygen consumption (SCOC)

The bottom water oxygen content obtained from the control and experimental cores (before initiation of the incubation) averaged 306 ± 6.3 µmol O_2 l^{-1} (n = 15). Background SCOC, as determined from the 3 control cores averaged 2.0 ± 1.5 mmol m^{-2} d^{-1} (n = 3). SCOC in experimental cores (3.2 ± 1.4 mmol m^{-2} d^{-1}, n = 6) after 6 d of incubation was not significantly different from the SCOC in controls (Kruskal-Wallis test, p = 0.381).

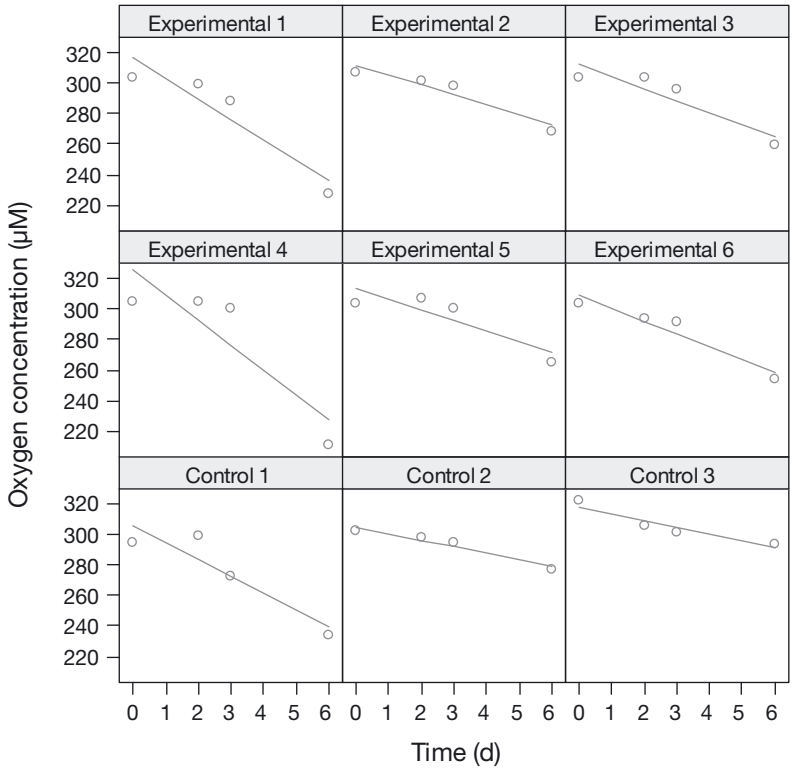

Fig. 2. Decrease in oxygen concentration (µM) with time in control and experimental replicate cores. The slope of each linear regression was used to calculate the oxygen flux (mmol O_2 m^{-2} d^{-1}) within each core

Algal C mineralization and uptake

The quantity of the algal-derived C that was mineralized increased significantly ($F = 171.1$, df = 1, $p < 0.001$) over the duration of the experiment (Fig. 3). In quantitative terms, a total of 3.77 mg C m^{-2} (0.75%) and 43.66 mg C m^{-2} (9%) of the added C was released as DIC after 3 and 6 d of incubation, respectively (Table 1).

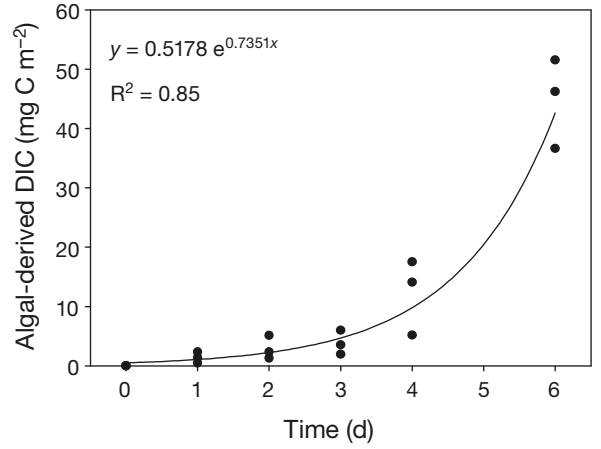

Fig. 3. Release of dissolved inorganic carbon (DIC) deriving from the consumption of the added diatoms with time

Table 1. Total amount of algal C (means ± SD) incorporated in bacteria, meiofauna, and macrofauna (mg C m^{-2}), total respiration (mg C m^{-2}), and respiration partitioning among the measured food-web compartments (%). Data on macrofaunal uptake are from Gontikaki et al. (in press). The biomass (means ± SD) of each investigated compartment is given for comparison: bacteria 4.0 ± 0.2 g C m^{-2} (0 to 10 cm), meiofauna 0.04 ± 0.02 g C m^{-2} (0 to 2 cm), macrofauna 0.7 ± 0.6 g C m^{-2} (0 to 10 cm)

	Algal C budget (mg C m^{-2}) 3 d	6 d	Respiration (%)
Bacteria	14.9 ± 7.2	17.5 ± 3.0	90.1
Meiofauna	0.01 ± 0.01	0.02 ± 0.01	1.2
Macrofauna	0.8 ± 0.9	2.0 ± 1.9	8.7
Total respiration	3.8 ± 2.0	43.7 ± 7.4	

The total amount of added C that was mineralized and incorporated into bacterial and faunal biomass (hereafter mentioned as total processed C) reached 19.5 and 63 mg C m^{-2} after 3 and 6 d, representing 3.9 and 12.6% of the total added C respectively. The majority of processed C after 3 d (~77%) was incorporated into bacterial biomass, whereas the bulk of the processed C after 6 d of incubation (~69%) was retrieved from the DIC pool (Fig. 4). The total amount of added C that was recovered from the investigated food web compartments is presented in Table 1. Bacterial uptake averaged 14.9 ± 7 and 17.5 ± 3 mg C m^{-2} after 3 and 6 d, respectively (15.3 ± 5.8 and 16.6 ± 4.2 mg C m^{-2} after 3 and 6 d when 18:1(n-7) is included in the calculations) (Table 1). The difference in bacterial uptake between Days 3 and 6 was not significant (Kruskal-Wallis test, $p = 0.667$). Approximately 95% of the total bacterial uptake took place at 0 to 0.5 cm in both experimental times, although uptake was detectable down to 2 cm. Incorporation of ^{13}C into the bacterial biomarkers i15:0, a15:0, and i16:0 is presented in Fig. 5.

Among meiofaunal taxa, only nematodes from 0 to 2 cm were analysed for ^{13}C uptake. Nematode abundance averaged 306 ± 74 ind. 10 cm^{-2}. The abundance of other metazoan meiofaunal taxa was extremely low (only 3 to 4 ind. recovered from each sample), and thus their contribution to C processing was considered to be negligible. Foraminifera and other protozoa were not included in the analysis, and thus their contribution to the total processed C is unknown. Nematode uptake contributed 0.05 and 0.02% to the total processed algal C after 3 and 6 d, respectively (Fig. 4). The difference in nematode uptake between the 2 sampling times was not statistically significant ($F = 0.427$, df = 1, $p = 0.56$). Macrofauna were responsible for 99% of the metazoan uptake; however, the overall contribution of metazoan fauna to C processing was relatively low (4.2 and 3.2% of the total processed algal-derived C on Days 3 and 6, respectively). Macrofaunal uptake on Day 3 was not significantly different from that on Day 6 (Gontikaki et al. in press).

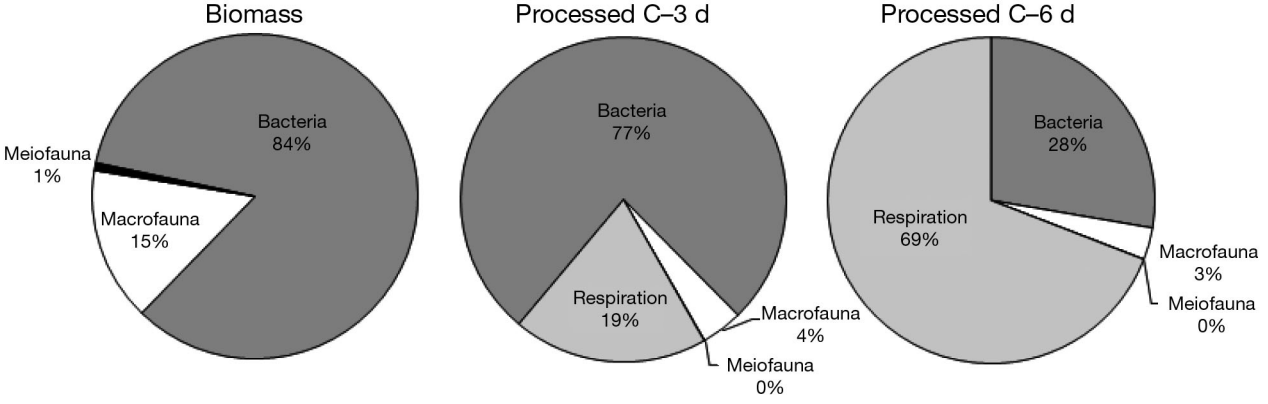

Fig. 4. Proportional division of biomass and processed carbon (C) after 3 and 6 d among the different benthic compartments

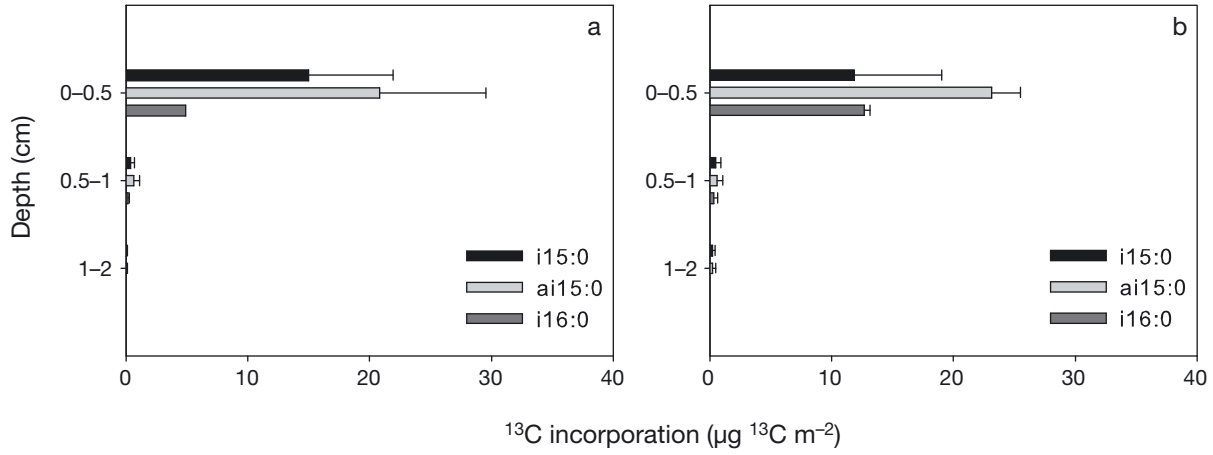

Fig. 5. Incorporation of ^{13}C into bacterial phospholipid fatty acids (PLFA) at 0 to 0.5, 0.5 to 1, and 1 to 2 cm after (a) 3 d and (b) 6 d of incubation. No tracer was detected in bacterial PLFA at deeper horizons. Error bars represent ± SD (n = 3)

Faunal respiration and BGE

Macrofaunal and nematode biomass-specific respiration rates were 2.84 and 0.35 mg C m^{-2} d^{-1}, respectively. These values represented 8.7 and 1.2% of SCOC in experimental cores (SCOC was converted to C units assuming a respiratory quotient RQ = 0.85; Smith 1987). Accordingly, the macrofaunal and nematode algal C respiration for each experimental time was assumed to be 8.7 and 1.2% of the total algal-derived DIC production, respectively. Bacterial respiration was thus assumed to account for the remaining 90.1% of the total respiration. It should be noted that this is a maximum value since not all faunal compartments are considered in the analysis. The BGE estimated from the bacterial algal C uptake and respiration after 3 d was 0.8 ± 0.04. This value dropped to 0.3 ± 0.07 when calculated from the bacterial processed C budget after 6 d.

DISCUSSION

Methodological considerations

It is acknowledged that *ex situ* incubations may involve artefacts related to core warming and decompression during core retrieval (Glud et al. 1994, 1998, Hall et al. 2007). The extremely cold temperatures prevailing in much of the water overlying the FSC (<2°C below 450 m) in combination with rapid onboard handling (typically ~15 min for 8 cores) ensured minimal warming of the sediment cores during their collection and retrieval. Decompression effects are more pronounced in sediments >2000 m, and it is generally accepted that at or above 1000 m core recovery artefacts seem to be more or less negligible (Hensen et al. 2006). Labelling experiments conducted both *in situ* and *ex situ* did not show any systematic differences down to ~1000 m depth in the Arabian Sea (Woulds et al. 2007, Andersson et al. 2008). We are therefore confident that the sampling procedures and experimental conditions did not introduce major errors into the results of the present study.

Benthic mineralization

The background SCOC averaged 2.06 mmol O_2 m^{-2} d^{-1}. Individual rates ranged from 1.12 to 3.90 mmol O_2 m^{-2} d^{-1} indicating a high degree of heterogeneity among replicates. Our oxygen uptake rates fall within the range of published SCOC rates in other warmer slope regions (1.1 to 2.5 mmol O_2 m^{-2} d^{-1} at ~1000 m and 9°C in the Goban Spur: Lohse et al. 1998; 2.6 to 3.4 mmol O_2 m^{-2} d^{-1} at 1300 m and 3.5°C in the North Pacific: Smith 1987; 2.4 mmol O_2 m^{-2} d^{-1} at 330 to 915 m and 13 to 14°C in the western Mediterranean: Accornero et al. 2003), suggesting that, similar to the cold Arctic shelf sediments (Arnosti 1998, Glud et al. 1998, Kostka et al. 1999), low temperatures in the FSC do not inhibit OM mineralization rates.

The difference in SCOC between control and experimental cores was not statistically significant, possibly due to inter-core variability. However, there was an increasing trend in oxygen consumption in experimental cores, and an average of 45% more oxygen was consumed in the experimental cores compared to the controls after 6 d of incubation. If the elevated oxygen consumption in experimental cores was due to the

remineralisation of the added material, then the difference between control and experimental cores should approximate the algal-derived DIC release. The difference in oxygen consumption between control and treatment cores equates to an average of 67 mg C m^{-2} after 6 d, while the DIC release attributed to the added material was 44 ± 7 mg C m^{-2}. This result suggests that the mineralization of the added substrate was responsible for the major part of the increase in oxygen consumption in experimental cores. A possible contribution to the difference between control and treatment could be due to priming effects (PE), i.e. the acceleration of the decomposition of stable (refractory) OM due to the addition of labile OM (Kuzyakov et al. 2000). The existence of PE in marine sediments has only recently been demonstrated experimentally in shallow-water ecosystems (van Nugteren et al. 2009). However, the enhancement of PE in oligotrophic systems (Guenet et al. 2010) means that these processes could also be of major importance in deep-sea ecosystems and merit further attention in future studies on C and nutrient cycling.

Community response

Comparison of total C processing rates, measured in different pulse-chase experiments, is problematic owing to different methodologies (e.g. amount of added OM) and data analysis (i.e. which faunal groups were included in the C budget) in each study. However, rough comparisons are allowed based on that: (1) the amount of added OM in most pulse-chase experiments is in excess, and thus comparisons between benthic communities are based on their maximum capacity for C processing; and (2) total C processing rates are dominated by respiration rates, and thus the exclusion of uptake by a faunal group in the analysis is not expected to produce a significant error in the community C budget.

The total C processing rates in the FSC varied between 6.5 and 14.6 mg C m^{-2} d^{-1}, as estimated from the C budget at 0 to 3 and 3 to 6 d, respectively (10.5 mg C m^{-2} estimated from the whole duration of the experiment). Witte et al. (2003b) found processing rates ranging between 4 and 8.4 mg C m^{-2} d^{-1} in the Porcupine Abyssal Plain (PAP) calculated after 2.5, 8, and 23 d of experiment. A similar range of C processing rates has been observed in other cold (<4°C) and deep settings: 4.2 and 7.9 mg C m^{-2} d^{-1} at ~2150 m in the NE Atlantic (Moodley et al. 2002, 2005); 6.9 mg C m^{-2} d^{-1} at 1200, and 10.36 mg C m^{-2} d^{-1} at 1850 m in the Pakistan margin (Woulds et al. 2009). Higher processing rates have been observed at bathyal settings in the very productive Benguela upwelling system (12 to 25 mg C m^{-2} d^{-1}; Aspetsberger et al. 2007) and under warm bottom water conditions such as the Sognefjord (7°C, 17 to 19 mg C m^{-2} d^{-1}; Witte et al. 2003a) and the eastern Mediterranean Sea (13 to 14°C, 47 to 68 mg C m^{-2} d^{-1}; Moodley et al. 2005, Bühring et al. 2006). An exception was observed when a very low OM pulse was added to sediments from the bathyal eastern Mediterranean: in that case the total C processing rate (6 mg C m^{-2} d^{-1}) resembled the rates measured in cold bathyal and abyssal environments (Bühring et al. 2006).

The importance of meiofauna in benthic C and energy flows has been acknowledged in several earlier studies (Kuipers et al. 1981, Heip et al. 1985, Coull 1999). Recent pulse-chase experiment studies, however, indicate a limited direct contribution of metazoan meiofauna (nematodes) to the short-term processing of fresh OM in both intertidal (Urban-Malinga & Moens 2006, Franco et al. 2008) and deep-sea settings (Moodley et al. 2002, Witte et al. 2003b, Moens et al. 2007, Ingels et al. 2010). In the present study, the incorporation of diatom-derived OM into nematode biomass (15 µg C m^{-2} in 6 d) was in the range of uptake rates calculated by Ingels et al. (2010) for a bacterial-derived food source (11 µg C m^{-2} after 7 d in Antarctic sediments). Differences between nematode C uptake in the aforementioned studies possibly arise due to differences in the organic substrates added (see Ingels et al. 2010). They may also be attributable to differences in sample processing techniques (e.g Moens et al. 1999), as well as the structure and functional diversity of nematode communities. It is apparent that the lack of knowledge on the life cycles, energy requirements, and food preferences of deep-sea nematodes has so far hampered the full exploitation of stable isotope labelling techniques in understanding the role of these organisms in deep-sea C cycling.

Macrofauna tend to rapidly ingest labelled material during the initial stages of pulse-chase experiments, after which the net content of ^{13}C may not increase (Woulds et al. 2009). As a result, uptake rates may appear artificially greater for shorter experiments. Comparisons between experiments may be allowed when the timescales considered are similar but should be regarded with caution (Gontikaki et al. in press). In the FSC, macrofaunal C uptake (0.8 mg C m^{-2} after 3 d) was evidently higher than macrofaunal uptake in Korsfjord (0.04 mg C m^{-2} after 2 d at 7°C; Sweetman & Witte 2008) despite the similar macrofaunal biomass estimates between the 2 sites. In contrast, macrofaunal uptake in this study was 9× lower than that measured at similar depth in Sognefjord (7.2 mg C m^{-2} after 3 d at 7°C; Witte et al. 2003a), although macrofaunal biomass was 3× lower in the latter location. These results demonstrate that total biomass and temperature differences between experimental sites can-

not explain sufficiently macrofaunal reaction patterns to OM addition. Differences in the community structure and species composition as well as seasonal and ontogenetic variations in metabolic rates may help explain the observed variability in macrofaunal response.

The total quantity of algal C attributed to bacterial community respiration after 3 d (3.4 ± 1.9 mg C m^{-2}) was lower than their C uptake (14.9 ± 7.0 mg C m^{-2}). This response pattern can be explained based on bacterial energetics. The BGE of deep water bacteria is thought to relate to OM quality, with BGE being highest when the bacterial community is fuelled by labile compounds (Tamburini et al. 2003). Low BGE has been observed when bacteria are consuming refractory compounds and is thought to reflect the energy requirements of enzyme production for the hydrolysis of these compounds (Tamburini et al. 2003). The introduction of labelled algae to the sediment in our experiment potentially involves the simultaneous addition of labile low molecular weight DOC (LMW-DOC), which is assimilated directly by bacteria resulting in high BGE. Indeed, the BGE estimated from ^{13}C-uptake after 3 d averaged 0.81 (± 0.04). Similarly high bacterial growth efficiencies have been calculated for marine bacterioplankton feeding on dissolved OM excreted by phytoplankton (0.5 to 0.8; del Giorgio & Cole 1998). The second half of our experiment was characterised by increased ^{13}C-respiration without a significant increase in the quantity of ^{13}C incorporated into bacterial biomass. The BGE estimated from the algal-derived processed C after 6 d (0.32 ± 0.07) is typical for marine bacterioplankton feeding on phytoplanktonic detritus (0.07 to 0.5; del Giorgio & Cole 1998). The hydrolysis of large compounds within the detritus pool by extracellular enzymes is a necessary step for the utilization of polymers by bacteria and has been suggested to represent a major expenditure of bacteria in natural aquatic systems (del Giorgio & Cole 2000). The decrease in BGE in the second half of our experiment could possibly be explained by an increase in bacterial energy demand associated with the production of extracellular hydrolytic enzymes (Middelboe & Sondergaard 1993, Middelboe et al. 1996). Supporting evidence towards this suggestion come from batch cultures of bacterioplankton in which the extracellular enzyme production increased when most of the labile DOC was consumed and larger particle fractions were increasingly utilized (Middelboe & Sondergaard 1995). Assuming a low contribution of DOC to the total added algal C (~5%; Andersson et al. 2008), the amount of added DOC (25 mg C m^{-2}) would be within the range of bacterial algal-derived C processing observed over the first 3 d of experimentation (Table 1).

The pattern of low respiration-high assimilation observed in the FSC after 3 d has only been observed before in the Cretan Sea, when a low C load was added to the system (Bühring et al. 2006). In that case, however, the experiment was terminated after 1.5 d, and a possible change in the reaction pattern from enhanced growth to enhanced respiration could not be confirmed. The change in BGE observed at the 2 sampling intervals in the present study more likely represents a continuum rather than an abrupt change and is probably universal during the initial stages of the OM degradation process. It seems that factors such as the amount of added OM (Bühring et al. 2006) and/or low temperature (the present study) may have resulted in the extension of the transition from high to low BGE so that it was captured in the aforementioned pulse-chase experiments. The present study showed that a relatively large part of bacterial metabolism may be directed towards growth in the initial steps of the degradation process of labile OM and that the timing of sampling is crucial for identifying such patterns. A change in the pattern of energy and C allocation would have direct consequences for the amount of energy available to higher trophic levels. However, the regulation of BGE in natural systems remains perplexing both at the cellular and the community level. For example, BGE has been shown to differ along gradients of productivity but also with the phylogenetic composition of the community (del Giorgio & Cole 2000). Future pulse-chase experiments should thus cover a wide range of locations of differing environmental and trophic regimes, combining substrates of various quantities and qualities with various sampling times in order to provide further insight on the combination of factors that drive C processing in benthic communities.

CONCLUSIONS

A 2 phase sampling strategy provided important insights into how deep-sea bacteria respond to an influx of OM: BGE was apparently high during the first 3 d. This was attributed to the consumption of the most labile, readily utilizable substrates provided at the outset of the experiment. The BGE estimated at the end of the experiment was much lower, potentially reflecting the increased energy requirements associated with the production of hydrolytic enzymes. We hypothesise that a transition from high to low BGE following the addition of OM is a common occurrence in deep-sea sediments. The rate of change is expected to be influenced by the local environment (e.g. temperature and productivity) and the nature of the organic substrate.

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