

NOTE

Ecological significance of benthic foraminifera: ¹³C labelling experiments

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ABSTRACT: We examined the ability of foraminifera in taking up freshly deposited algal carbon in intertidal estuarine sediments. Lyophilized ¹³C-labelled axenic *Chlorella* was added to intact sediment cores containing natural benthic biota. The response of the system as a whole was rapid; ~5% of the added carbon was respired to CO₂ within 6 h. Bacteria assimilated ~2 to 4% of the added carbon within 12 h. Among the foraminifera, the dominant foraminifer *Ammonia* exhibited rapid uptake and it is estimated that ~1 to 7% of the added carbon was ingested within 3 to 53 h. This rapid, substantial uptake by *Ammonia* and the significant contribution of foraminifera to meiobenthic abundance and biomass (37 and 47% respectively) suggest that foraminifera play an important role in the carbon cycle in these sediments.

KEY WORDS: Meiobenthos · Benthic foraminifera · Bacterial biomarkers · Algal carbon · Carbon cycle · CO₂ · ¹³C labelling

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Benthic foraminifera are heterotrophic, amoeboid protozoa, characterized by the presence of granulo-reticulate pseudopodia and a test (shell) with one or more chambers. They are widespread in modern oceans and have colonized a wide range of habitats since their first appearance in the Cambrian. Because of the fossilization potential of foraminifera, most foraminiferal studies have been carried out by geologists, leading to a vast literature on shell taxonomy and broad-scale distribution patterns (Boltovskoy & Wright 1976, Murray 1991). In recent years, foraminifera increasingly have been found to be dominant members of benthic communities in both shallow and deep-sea environments (e.g. Widbom 1988, Alongi 1992, Gooday et al. 1992 and references therein, Piepenburg et al. 1997, Moodley et al. 1998). This suggests that they may play an important role in the carbon cycle

(Altenbach 1992, Gooday et al. 1992, Graf 1992, Linke et al. 1995).

Sedimentation of organic material from phytoplankton blooms often represents a considerable fraction of the annual benthic organic matter input (e.g. Graf 1992), and this phytodetritus may play an important role in the nutrition of some foraminifera (Gooday 1988, Gooday & Lamshead 1989). Field experiments have qualitatively documented the uptake of phytodetritus by benthic foraminifera (Heeger 1990, Rivkin & DeLaca 1990, Linke 1992, Gooday 1993, Goldstein & Corliss 1994, Levin et al. 1999) and quantitatively shown that foraminifera may be responsible for substantial uptake of a phytodetritus deposit (Altenbach 1992, Linke et al. 1995). In this study we examined the ability of foraminifera in taking up fresh algal carbon in estuarine sediments containing the natural benthic biota using ¹³C-enriched algal carbon as a tracer (Blair et al. 1996, Levin et al. 1997, 1999). The response of the benthic system as a whole, in terms of processing algal carbon, was examined by measuring the amount of algal carbon respired, as quantified by carbon-isotopic analysis of ΣCO₂. Bacterial assimilation was separately quantified by carbon-isotope analysis of polar lipid derived fatty acids (PLFA) specific for bacteria.

Material and methods. An axenic clone of the green algae *Chlorella* (CCMP 243, Provasoli-Guillard National Center for Culture of Marine Phytoplankton, Bigelow Laboratory) was cultured at 20°C in an artificial seawater medium amended with f/2 medium and 4 mM NaHCO₃ (Levin et al. 1997) containing 30% ¹³C-enriched bicarbonate (99% ¹³C-enriched NaHCO₃, Cambridge Isotope Laboratories). This produced algal carbon that consisted of 25 ± 1% ¹³C (mean ± 1 SD, calculated from the δ¹³C of direct measurements and *Chlorella*-specific PLFA). Algal material was extracted

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by centrifugation, rinsed with an isotone solution and dried *in vacuo*. Just prior to centrifugation, the axenic state of the *Chlorella* culture was verified by incubating a few drops of the culture, in the dark, in agar plates containing the culture medium and glucose.

Sediment (~15 cm deep) was collected in 6 Perspex cores (78 cm²) during ebb from an intertidal flat in the Oosterschelde Estuary (The Netherlands) on 9 October 1998. A column of ~15 cm of ambient seawater was added and maintained at *in situ* temperature (10°C) in the dark. After a few hours, allowing for stabilization, 30 mg of *Chlorella* (~0.95 g C m⁻², the organic carbon content of the algae was measured using a Carlo Erba CN Analyser) was added to the water column in 4 cores. The remaining 2 cores were used to isolate foraminifera to determine their average biomass and background $\delta^{13}\text{C}_{\text{org}}$ values. In order to establish if foraminifera are capable of rapid uptake of phytodetritus, the 4 experimental cores, which were continuously aerated, were used to examine foraminifera after 3, 6, 12 and 53 h incubation. The upper centimeter was sliced off and passed through a 63 μm sieve to remove fine sediment and algal cells. The >63 μm sediment fraction was then transferred to petri dishes filled with seawater and allowed to settle for at least 30 min. Living foraminifera were then readily recognized by the concentration of particles around the mouth opening or the entire test. This method of isolating living specimens was verified by observing cytoplasmic activity under an inverted microscope (Moodley et al. 1997). Living specimens (50 to 75 individuals of each genus per core) were picked out and stored in petri dishes at -20°C. Prior to analysis, specimens were transferred to Milli-Q water and cleaned vigorously of any adhering particles with a brush under the microscope. Cleaned specimens were then transferred to pre-combusted silver boats, decalcified with 2.5% HCl and then dried *in vacuo*. Fifteen to 20 specimens were used for individual $\delta^{13}\text{C}_{\text{org}}$ measurements.

For the carbon mineralization and bacterial uptake study, 2 cores (165 cm²) were taken and processed as described above, except that 45 mg *Chlorella* (~0.75 g C m⁻²) was added and the cores were sealed off with a lid containing a magnetic stirrer. The algal carbon added in both experiments represented $1 \pm 0.2\%$ of the total particulate organic carbon (POC) content in the 0 to 1 cm interval of the sediment (87 ± 11 g C m⁻², calculated from the % POC and porosity assuming a dry density of 2.55 g cm⁻³ for sediment). After 6 h incubation, water samples were taken with a silicon tube and dispensed directly into glass vials (23 ml volume) and sealed with aluminum caps fitted with a rubber septum. A headspace was created by injecting 3 ml of nitrogen gas and the sample was then acidified. The $\delta^{13}\text{CO}_2$ in the headspace was measured directly and the $\delta^{13}\text{C}(\Sigma\text{CO}_2)$ was calculated according to Yoshii et

al. (1995). The concentration of CO₂ in the headspace was measured directly using a Carlo Erba MEGA 5340 gas chromatograph and $[\Sigma\text{CO}_2]$ was calculated using thermodynamic constants.

After 12 h, sub-cores (10 cm²) were taken and 3 g wet weight of sediment from the upper centimeter was stored frozen. Lipid extraction and carbon-isotopic analysis of PLFA were done according to Boschker et al. (1999). For background values, sediment samples were taken from an untreated core and 0 h incubation samples were processed within 1.5 h.

The $\delta^{13}\text{CO}_2$ in the headspace and $\delta^{13}\text{C}_{\text{org}}$ of foraminifera were measured using a Carlo Erba 1106 Elemental Analyser coupled online with a Finnigan Delta S isotope ratio mass spectrometer. Carbon isotopes are expressed in the delta notation ($\delta^{13}\text{C}$) relative to Vienna PDB: $\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}}/({}^{13}\text{C}/{}^{12}\text{C})_{\text{ref}} - 1] \times 1000$. Incorporation of ¹³C is reflected as excess (above background) ¹³C and is expressed in terms of specific uptake (i.e. $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{background}}$) as well as total uptake (*I*). *I* was calculated as the product of excess ¹³C (*E*) and biomass, concentration CO₂ or PLFA carbon. *E* is the difference between the fraction ¹³C of the background ($F_{\text{background}}$) and the samples (F_{sample}): $E = F_{\text{sample}} - F_{\text{background}}$, where $F = {}^{13}\text{C}/({}^{13}\text{C} + {}^{12}\text{C}) = R/(R + 1)$ and *R* = the carbon isotope ratio. For the $F_{\text{background}}$ of CO₂, we used the $\delta^{13}(\Sigma\text{CO}_2)$ measured in water samples taken from an independent control (0 h) incubation without sediment. *R* was derived from the measured $\delta^{13}\text{C}$ values as: $R = (\delta^{13}\text{C}/1000 + 1) \times R_{\text{VPDB}}$, where $R_{\text{VPDB}} = 0.0112$. The uptake of total added algal carbon (¹²C + ¹³C) was calculated as the quotient of *I* and the fractional abundance of ¹³C in the algae (0.25).

The biomass (organic carbon content) of foraminifera and other meiofauna taxa was measured using a Carlo Erba CN Analyser. Twenty to 100 specimens of the dominant meiofauna taxa or foraminifera genus per core were used for biomass measurements. The absolute organic carbon content of a sample can be calculated from the area counts of a standard (i.e. of a known carbon content) and the area counts of the sample containing a number of decalcified specimens of foraminifera or other meiofauna taxa. Specimens for biomass measurements were cleaned of adhering debris, rinsed with Milli-Q, and then frozen and dried *in vacuo* in pre-combusted silver boats. The samples were analyzed after removal of carbonate by *in situ* acidification with HCl (Nieuwenhuize et al. 1994). We used silver boats rather than cups to visually verify the removal of carbonate.

The total standing stock of macrofauna (abundance, >300 μm) and meiofauna (abundance and biomass, >63 μm) in the upper centimeter was determined from 3 cores (3, 6 and 53 h cores). Sediment for this purpose was preserved in a Rose Bengal alcohol solution.

Results and discussion. The macrofauna in the upper centimeter ($17\,111 \pm 7900$ ind. m^{-2}) consisted mainly of gastropods (59%), oligochaetes (25.6%), polychaetes (8.8%) and bivalves (5.8%). The permanent meiofauna assemblage in the upper centimeter ($2.9 \pm 0.5 \times 10^6$ ind. m^{-2}) consisted of nematodes (46.5%), foraminifera (37.1%), copepods (15.5%) and ostracods (0.9%). Soft-shelled foraminifera were not abundant at this time of the year. The stained assemblage of hard-shelled foraminifera consisted primarily of *Ammonia* (56.6%), *Haynesina* (20.8%) and *Elphidium* (21.1%), a typical estuarine assemblage (Murray 1991). The average meiobenthic biomass was estimated at 2623 ± 399 mg C m^{-2} , with foraminifera and nematodes accounting for, on average, 47 and 23% respectively.

Our estimates of individual foraminifera biomass are in good agreement with other studies based on direct measurements of organic carbon content (wet oxidation method; Altenbach 1987, 1992, Thomsen & Altenbach 1993). We found an average biomass value of $0.75 \mu\text{g C ind.}^{-1}$ for *Elphidium* with an average length of $268 \mu\text{m}$, $1.10 \mu\text{g C ind.}^{-1}$ for *Ammonia* with an average length of $325 \mu\text{m}$ and $1.48 \mu\text{g C ind.}^{-1}$ for *Haynesina* with an average length of $381 \mu\text{m}$. The method we used is a simple application of an apparatus common in most laboratories, and acidification in the boats or cups prevents loss of organic material and eliminates reweighting procedures (Nieuwenhuize et al. 1994). Estimates of foraminifera biomass based on volume calculations are often complicated due to variation in thickness of the shell and in filling of the individual chambers (Altenbach 1987). We measured average biomass values of 0.44, 1.67 and $2.22 \mu\text{g C ind.}^{-1}$ for nematodes, copepods and ostracods respectively. These values are well within the range recorded for these taxa (e.g. Widbom 1984).

The algal cells settled rapidly and a distinct green layer was visible on the sediment surface within <10 min. Within <1 h, a large part of this layer had disappeared and was either ingested or mixed into deeper layers of the sediment.

PLFA typical of green algae (e.g. 16:0 and 18:3 ω 3) and specific for *Chlorella* used in this study (16:4, this PLFA was not present in background sediment) were successfully enriched in ^{13}C and due to uptake, degradation and transport out of the 0 to 1 cm layer, a clear decrease in ^{13}C content with time was seen (Fig. 1A). After 12 h incubation, the label was clearly incorporated into fatty acids such as i14:0, i15:0, a15:0 and i16:0, which are characteristic of heterotrophic bacteria (Fig. 1B). The PLFA 18:1 ω 7c, which is predominantly present in bacteria, was also enriched in ^{13}C in the 0 h samples but decreased in concentration after 12 h (Fig. 1C). This indicates that the PLFA 18:1 ω 7c was also part of the fatty acids in the *Chlorella* clone

used in this study as found for some green algae (Volkman et al. 1989, Ahlgren et al. 1992). This blurs the use of this PLFA as a unique signal of bacterial incorporation. However the decrease in ^{13}C content ($\sim 30\%$) is much less than that calculated for typical algal biomarkers ($\sim 75\%$, Fig. 1A). Therefore, the relatively low decrease in concentration of this PLFA can be explained by bacterial incorporation. Bacterial biomass in the upper centimeter was estimated at 5.79 ± 1.5 and 4.27 ± 1.68 g C m^{-2} , with and without PLFA 18:1 ω 7c, respectively. For the above calculations, the average fraction of specific bacterial PLFA concentration encountered in sediments was taken as 0.28 ± 0.04 and 0.14 ± 0.07 , with and without PLFA 18:1 ω 7c, respectively (Middelburg et al. 2000).

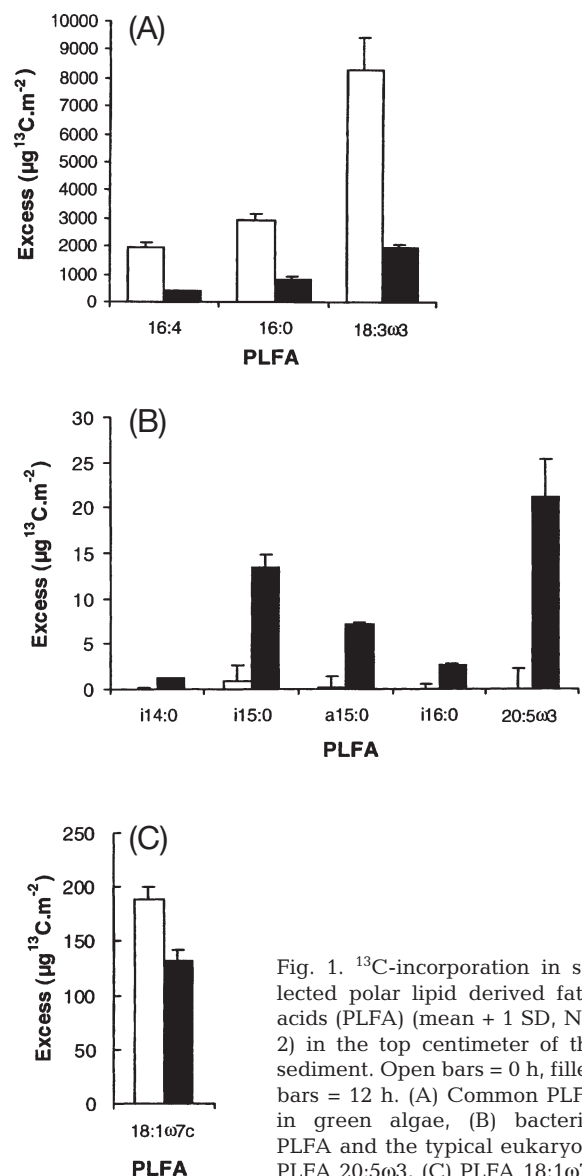


Fig. 1. ^{13}C -incorporation in selected polar lipid derived fatty acids (PLFA) (mean + 1 SD, N = 2) in the top centimeter of the sediment. Open bars = 0 h, filled bars = 12 h. (A) Common PLFA in green algae, (B) bacterial PLFA and the typical eukaryote PLFA 20:5 ω 3, (C) PLFA 18:1 ω 7c

The response of the system as a whole was rapid. After an incubation period of 6 h, we measured a $\Delta\delta^{13}\text{C}$ of $181 \pm 5.5\%$ for ΣCO_2 in the water column and it is estimated that approximately $4.9 \pm 0.2\%$ of the added algal carbon was respired. Few studies have examined carbon mineralization at such short time intervals. Carbon dioxide from a labelled carbon source was found after a few hours in marine sediment (Blair et al. 1996) and freshwater sediment (Gullberg et al. 1997). Using sediment from the Baltic Sea, Olafsson et al. (1999) reported that 34% of the added algal carbon was respired to CO_2 within 1 mo, but half of this was measured at the first sampling time (after 7 d). Although the respiration measured within 6 h is the sum of all benthic compartments, a key role in the turnover of organic carbon is usually attributed to bacteria (e.g. Rowe & Deming 1985). Accordingly, a rapid response of bacteria was recorded. Based on ^{13}C -incorporation into bacteria-specific PLFA, it is estimated that $4.0 \pm 0.4\%$ of the algal carbon was incorporated into bacterial biomass within 12 h. If calculations are restricted to unique bacterial biomarkers (i14:0, i15:0, a15:0 and i16:0), this value drops to $1.7 \pm 0.1\%$. The actual amount processed by bacteria was inevitably larger because growth efficiencies of bacteria are less than 1. In an *in situ* labelling experiment, bacteria assimilated about 2% of microphytobenthos carbon within 4 h (Middelburg et al. 2000).

Of the 3 genera of foraminifera examined, *Ammonia* exhibited a clear and rapid uptake of algal carbon, reaching a $\Delta\delta^{13}\text{C}$ of $240 \pm 22\%$ within 3 h of incubation (Fig. 2). An independent 0 h check was not performed for foraminifera, but the possibility that the enrichment in ^{13}C of *Ammonia* was due to adhesion of the algal cells can be discounted as great care was taken to remove adhering particles from freeze-killed specimens. In contrast to reproductive cysts, feeding cysts (aggregates of particles around the test) are readily removed (Goldstein & Moodley 1993), especially in dead specimens. Additionally, after decalcification, algae were clearly visible inside the different chambers. The increase in $\Delta\delta^{13}\text{C}$ with time for *Ammonia* (Fig. 2) indicates active and preferential uptake, and this was also evident in the colour change of the cytoplasm in progressive chambers of the organism (Fig. 3). There was no distinct colour change in the other 2 genera (*Elphidium* and *Haynesina*), and *Haynesina* additionally had a natural greenish brown coloured cytoplasm in these sediments at this time of the year. Limited ^{13}C enrichment was recorded for these 2 genera compared to *Ammonia*, and large variation among individuals was observed (Fig. 2). This suggests a preference for other carbon sources (e.g. locally produced diatoms or more refractory material), which implicates resource partitioning within the upper centimeter as

also observed for nematodes (Olafsson et al. 1999). In shallow environments, different sources of carbon may promote selective feeding and benthic diatoms form an important source of carbon for foraminifera (Lee 1980 and references therein, Hohenegger et al. 1989). Different populations in different places may also vary in their response to a phytodetrital input. Using radio-labelled phytodetritus, foraminifera in the mid Narragansett bay (7 m water depth) have been observed to show a low preference for fresh material (Rudnick 1989, Widbom & Frithsen 1995). However, these analyses of the total foraminiferal assemblage may have masked the response on the species or generic level; *Ammonia* and *Elphidium* were the dominant calcareous foraminifera in sediments of the Narragansett bay

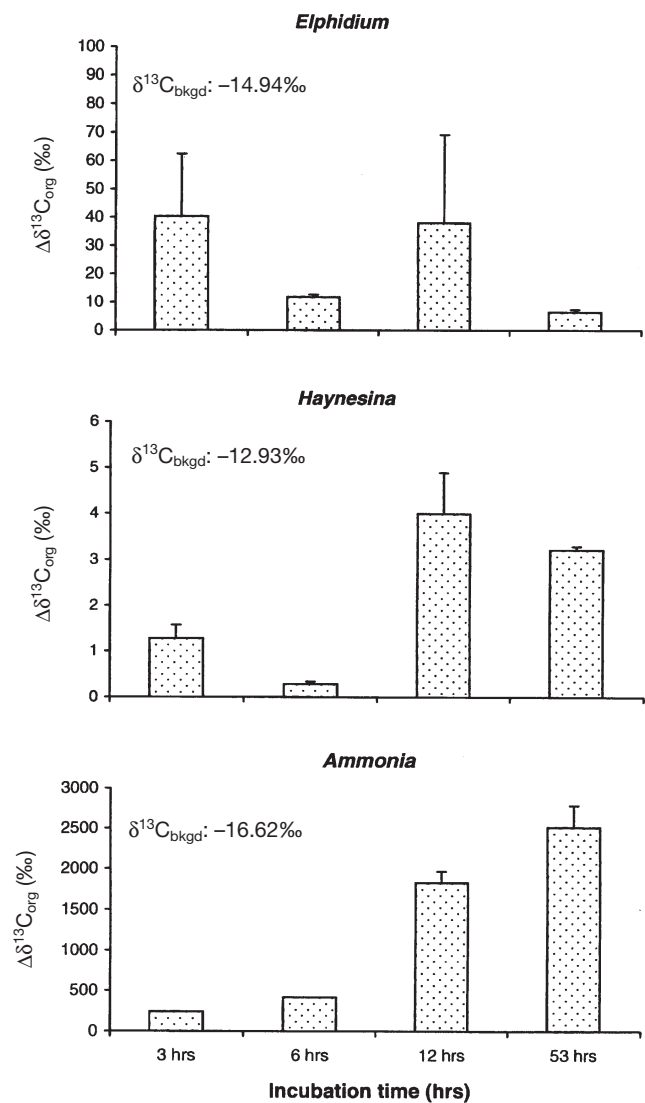


Fig. 2. $\Delta\delta^{13}\text{C}_{\text{org}}$ of the 3 dominant genera of hard-shelled foraminifera in the top centimeter of sediment after different periods of incubation (mean + 1 SD, N = 2)

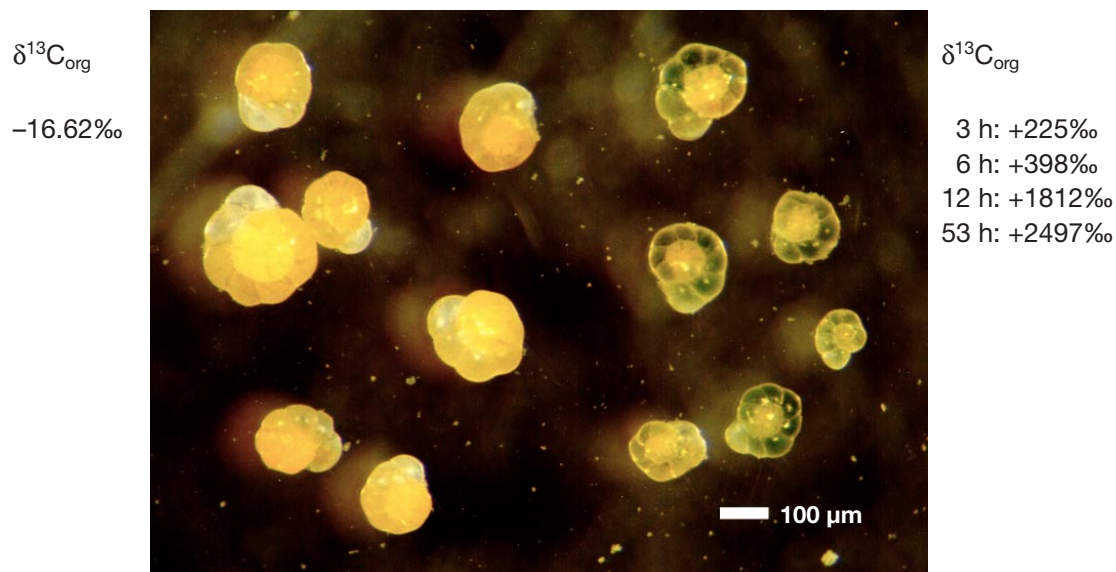


Fig. 3. Micrograph and average $\delta^{13}\text{C}_{\text{org}}$ of *Ammonia* ($N = 2$). On the left, yellow coloured cytoplasm in specimens from the background core and on the right, green coloured cytoplasm visible in the different chambers of specimens from a 12 h experimental core

(Widbom & Frithsen 1995). Alternatively, the uptake of freshly deposited material may also be affected by the life stage of the species (Lee 1980) or the general size and structure of the benthic community. In the Oosterschelde Estuary, uptake by *Ammonia* was evidently not inhibited by a relatively rich meio- and macrofaunal community.

Due to the absence of distinct uptake by *Elphidium* and *Haynesina*, calculation of phytodetritus uptake by foraminifera was restricted to *Ammonia*. This genus had an average biomass of $0.61 \pm 0.2 \text{ g C m}^{-2}$ and it is estimated that this dominant foraminifer ingested ~ 0.7 to 7 % of the added carbon within 5 to 53 h (Fig. 4). Uptake by *Ammonia* appeared linear during the first few hours and then seemed to level off (Fig. 4). A similar pattern of microphytobenthos uptake by nematodes was observed by Middelburg et al. (2000). Levelling off of *Ammonia* ingestion may reflect satiation, but a more detailed study is required to examine the dynamics of temporal uptake. Measurements of individual time series were pseudo-replicates. However, if we ignored the trend of increase with time in ^{13}C enrichment and used the 3, 6 and 12 h samples as true replicates, we still recorded a rapid and significant uptake of $\sim 2.3\%$ within 12 h. The granuloreticulate pseudopodia of foraminifera can form long, extensive networks (Travis & Bowser 1991) which constitute an extremely efficient system for trapping, gathering and accumulating food particles (Bowser et al. 1992, Gooday et al. 1996). This mode of food collection is similar for both shallow and deep-sea foraminifera (Goldstein & Corliss 1994). Evidently, a significant portion of the algal carbon was

rapidly ingested by *Ammonia* and a large part was probably also assimilated, as foraminifera have been reported to rapidly assimilate ingested algal carbon (within hours; Rivkin & DeLaca 1990). Evidence for the assimilation of the added carbon by eukaryotes may be traced in the specific fatty acids. The PLFA 20:5 ω 3 is predominantly found in eukaryotes including diatoms but is generally absent in most green algae (Volkman et al. 1989, Ahlgren et al. 1992), with the exception of some marine *Chlorella* that can have up to 30 % of 20:5 ω 3 (Watanabe et al. 1983). However, the PLFA 20:5 ω 3 was not enriched in ^{13}C in the 0 h sample, which indicates that PLFA 20:5 ω 3 was not part of the *Chlorella* clone used in this study (Fig. 1B). Therefore, the significant ^{13}C enrichment measured in the PLFA 20:5 ω 3 after 12 h (Fig. 1B) suggests that indeed a part of the added carbon was assimilated by eukaryotes.

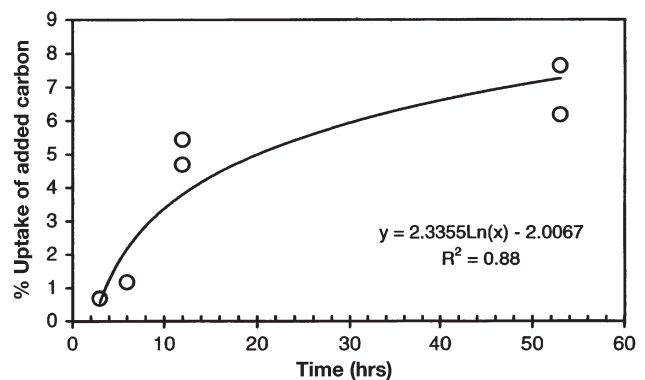


Fig. 4. Uptake of added algal carbon by *Ammonia* versus time ($N = 2$)

Observations made in this study indicate that labile carbon entering the benthic environment can be rapidly processed (within hours; Graf 1992, Goedkoop et al. 1997, Middelburg et al. 2000) and that some foraminifera play an important role in the breakdown of a phytodetritus deposit. Clearly, a large portion of incoming labile carbon was rapidly respired. It is not possible to directly compare uptake by bacteria and *Ammonia*. Uptake by bacteria measured through PLFA represents assimilation (2 to 4% within 12 h) so that the actual amount processed by bacteria was inevitably larger and, given the rapid turnover of bacteria, a large part of the CO₂ production was probably bacteria mediated. In the case of the *Ammonia*, uptake probably predominantly reflects ingestion of the added carbon. Irrespectively, some foraminifera may be potential competitors for phytodetritus. Although the cosmopolitan foraminifer *Ammonia* has been reported to feed on bacteria (Chandler 1989), the high $\Delta\delta^{13}\text{C}_{\text{org}}$ measured in the foraminifera (+240 to +1828‰ within 3 to 12 h), compared to bacteria PLFA (+17 to +61‰) and the green colour (Fig. 3), indicate that the enrichment measured in *Ammonia* was primarily due to direct uptake of phytodetritus. In this study the use of *Chlorella* as a source of labile carbon to follow the response in the selected components was evidently successful. This study also demonstrates selective feeding among foraminifera and the next step would be to use locally dominant diatoms.

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LITERATURE CITED

- Ahlgren G, Gustafsson IB, Boberg M (1992) Fatty acid content and chemical composition of freshwater algae. *J Phycol* 28:37–50
- Alongi DM (1992) Bathymetric patterns of deep-sea benthic communities from bathyal depths in the western South Pacific (Solomon and Coral Seas). *Deep-Sea Res* 39:549–565
- Altenbach AV (1987) The measurement of organic carbon in foraminifera. *J Foraminifer Res* 17:106–109
- Altenbach AV (1992) Short-term processes and patterns in the foraminiferal response to organic flux rates. *Mar Micropaleontol* 19:119–129
- Blair NE, Levin LA, DeMaster DJ, Plaia G (1996) The short-term fate of fresh algal carbon in continental slope sediments. *Limnol Oceanogr* 41:1208–1219
- Boltovskoy E, Wright R (1976) Recent foraminifera. Dr W Junk Publishers, The Hague
- Boschker HTS, De Brouwer JFC, Cappenberg TE (1999) The contribution of macrophyte derived organic matter in microbial biomass in salt marsh sediments: stable carbon-isotope analysis of microbial biomarkers. *Limnol Oceanogr* 44:309–319
- Bowser SS, Alexander SP, Stockton WL, Delaca TE (1992) Extracellular matrix augments mechanical properties of pseudopodia in the carnivorous foraminiferan *Astrammia rara*: role in prey capture. *J Protozool* 39:724–732
- Chandler GT (1989) Foraminifera may structure meiobenthic communities. *Oecologia* 81:354–360
- Goedkoop W, Gullberg KR, Johnson RK, Ahlgren I (1997) Microbial response of a freshwater benthic community to a simulated diatom sedimentation event: interactive effects of benthic fauna. *Microb Ecol* 34:131–143
- Goldstein ST, Corliss BH (1994) Deposit feeding in selected deep-sea and shallow-water benthic foraminifera. *Deep-Sea Res* 41:229–241
- Goldstein ST, Moodley L (1993) Gametogenesis and the life cycle of the foraminifer *Ammonia beccarii* (linne) forma *tepida* (Cushman). *J Foraminifer Res* 23:213–220
- Goody AJ (1988) A response by benthic foraminifera to the deposition of phytodetritus in the deep-sea. *Nature* 332:70–73
- Goody AJ (1993) Deep-sea benthic foraminiferal species which exploit phytodetritus: characteristic features and controls on distribution. *Mar Micropaleontol* 22:187–205
- Goody AJ, Lamshead PJD (1989) Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Mar Ecol Prog Ser* 58:53–67
- Goody AJ, Levin LA, Linke P, Heeger T (1992) The role of benthic foraminifera in deep-sea food webs and carbon cycling. In: Rowe GT, Pariente V (eds) *Deep-sea food chains and the global carbon cycle*. Kluwer Academic Publishers, Dordrecht, p 63–91
- Goody AJ, Pfannkuche O, Lamshead PJD (1996) An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic. *J Mar Biol Assoc UK* 76:297–310
- Graf G (1992) Benthic-pelagic coupling: a benthic review. *Oceanogr Mar Biol Annu Rev* 30:149–190
- Gullberg KR, Goedkoop W, Johnson RK (1997) The fate of diatom carbon within a freshwater benthic community—a microcosm study. *Limnol Oceanogr* 42:452–460
- Heeger T (1990) Elektronenmikroskopische Untersuchungen zur Ernährungsbiologie benthischer Foraminiferen. *Berichte aus dem Sonderforschungsbereich* 313, 31:1–139
- Hohenegger J, Piller W, Baal C (1989) Reasons for spatial microdistributions of foraminifers in an intertidal pool (northern Adriatic Sea). *PSZN I: Mar Ecol* 10:43–78
- Lee JJ (1980) Nutrition and physiology of the foraminifera. In: Levansowsky M, Hunters SH (eds) *Biochemistry and physiology of protozoa*. Academic Press, New York, p 43–66
- Levin LA, Blair NE, DeMaster DJ, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina Slope. *J Mar Res* 55:595–611
- Levin LA, Blair NE, Martin CM, DeMaster DJ, Plaia G, Thomas CJ (1999) Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *in situ* experiments using ¹³C-labeled diatoms. *Mar Ecol Prog Ser* 182:37–54
- Linke P (1992) Metabolic adaptations of deep-sea benthic foraminifera to seasonally varying food input. *Mar Ecol Prog Ser* 81:51–63
- Linke P, Altenbach AV, Graf G, Heeger T (1995) Responses of deep-sea benthic foraminifera to a simulated sedimentation event. *J Foraminifer Res* 25:75–82

- Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an in situ ^{13}C labelling experiment. *Limnol Oceanogr* (in press)
- Moodley L, van der Zwaan GJ, Herman PMJ, Kempers L, van Breugel P (1997) Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina). *Mar Ecol Prog Ser* 158:151–163
- Moodley L, Heip CHR, Middelburg JJ (1998) Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics. *J Sea Res* 40:263–280
- Murray JW (1991) Ecology and palaeoecology of benthic foraminifera. Longman Scientific & Technical, Harlow
- Nieuwenhuize J, Maas YEM, Middelburg JJ (1994) Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar Chem* 45:217–224
- Olafsson E, Modig H, van de Bund WJ (1999) Species specific uptake of radio-labelled phytodetritus by benthic meiofauna from the Baltic Sea. *Mar Ecol Prog Ser* 177:63–72
- Piepenburg D, Ambrose WG, Brandt A, Renaud PE, Ahrens MJ, Jensen P (1997) Benthic community patterns reflect water column processes in the Northeast Water polynya (Greenland). *J Mar Syst* 10:467–482
- Rivkin RB, DeLaca TE (1990) Trophic dynamics in antarctic benthic communities. I. In situ ingestion of microalgae by foraminifera and metazoan meiofauna. *Mar Ecol Prog Ser* 64:129–136
- Rowe GT, Deming JW (1985) The role of bacteria in the turnover of organic carbon in deep-sea sediments. *J Mar Res* 43:925–950
- Rudnick DT (1989) Time lags between the deposition and meiobenthic assimilation of phytodetritus. *Mar Ecol Prog Ser* 50:231–240
- Thomsen L, Altenbach AV (1993) Vertical and areal distribution of foraminiferal abundance and biomass in microhabitats around tubes of marine echinurids. *Mar Micropaleontol* 20:303–309
- Travis JL, Bowser SS (1991) The motility of foraminifera. In: Lee JJ, Anderson OR (eds) *Biology of foraminifera*. Academic Press, London, p 91–155
- Volkman JK, Jeffrey SW, Nichols PD, Rogers GI, Garland CD (1989) Fatty acid and lipid composition of 10 species of microalgae used in mariculture. *J Exp Mar Biol Ecol* 128: 219–240
- Watanabe T, Kitajima C, Fujita S (1983) Nutritional values of live organisms used in Japan for the mass propagation of fish: a review. *Aquaculture* 34:115–143
- Widbom B (1984) Determination of average individual dry weights and ash-free dry weights in different sieve fractions of marine meiofauna. *Mar Biol* 84:101–184
- Widbom B (1988) The benthic meiofauna of three coastal areas: structure, seasonal dynamics and response to environmental perturbations. Doctoral thesis, University of Stockholm
- Widbom B, Frithsen JB (1995) Structuring factors in a marine soft bottom community during eutrophication—an experiment with radio-labelled phytodetritus. *Oecologia* 101: 156–168
- Yoshii K, Koitabashi T, Wada E (1995) Determining the stable isotope ratio of total dissolved inorganic carbon in lake water by GC/C/IRMS. *Limnol Oceanogr* 40:994–1000

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