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Processing of ^{13}C-labelled phytoplankton in a fine-grained sandy-shelf sediment (North Sea): relative importance of different macrofauna species

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ABSTRACT: On-board and *in situ* experiments with ^{13}C-labelled diatoms were carried out to investigate the processing of algal carbon by the macrofauna community of a fine sandy-shelf site in the southern German Bight (North Sea). The time series (12, 30, 32 and 132 h incubations) was supplemented by additional laboratory experiments on the role of the dominant macrofauna organism, the bivalve *Fabulina fabula* (Bivalvia: Tellinidae), for particulate organic matter subduction to deeper sediment layers. The specific uptake of algal ^{13}C by macrofauna organisms was visible after 12 h and constantly increased during the incubation periods. *F. fabula*, a facultative (surface) deposit- and suspension-feeder, *Lanice conchilega* (Polychaeta: Terebellidae), a suspension-feeder and the (surface) deposit-feeder *Echinocardium cordatum* (Echinodermata: Spatangidae) were responsible for the majority of macrofaunal carbon processing. Predatory macrofauna organisms like *Nephtys* spp. (Polychaeta: Nephtyidae) also quickly became labelled. The rapid subduction of fresh organic matter by *F. fabula* down to ca. 4 to 7 cm sediment depth could be demonstrated, and it is suggested that entrainment by macrofauna in this fine-grained sand is much more efficient than advective transport.

KEY WORDS: Carbon processing · Macrofauna · Sandy sediments · ^{13}C labelling · Stable isotopes · North Sea · German Bight

INTRODUCTION

Shelf areas such as the North Sea cover approximately 7.5% of the total ocean area (Wollast 2003) and 70% of the shelf is covered by sandy deposits (Emery 1968). This comparably small area has a very high biological productivity, which amounts to 30% of the total oceanic primary production (Jørgensen 1996). Despite this, sandy-shelf sediments contain a low amount of organic matter (Shum & Sundby 1996) and low bacterial standing stocks (Llobet-Brossa et al. 1998). The low organic carbon content may be a result of high turnover rates, rather than low activity; the high permeability of most sands is thought to allow advective percolation of the upper sediment layers. Advection, however, has been shown to result in an effective exchange of pore water (Huettel et al. 2003), to rapidly transport particulate organic matter (POM) into permeable sediments (Huettel & Rusch 2000), and to enhance the remineralisation and nutrient release in comparison to non-permeable sediments (Ehrenhauss et al. 2004b).

In addition, the activities of macrofauna can significantly affect the transport of solutes and particulates across the sediment–water interface (Graf & Rosenberg 1997). For example, bioirrigation by tube-building worms is responsible for rapid water pumping; bioturbation is well known to enhance the particle transport within the sediment (Forster & Graf 1995, Ziebis et al. 1996). The macrofauna community of the North Sea shelf consists mainly of bivalves, polychaetes, crustaceans and echinoderms (Salzwedel et al. 1985). The infaunal suspension and (surface) deposit-feeders in particular, such as the bivalve *Fabulina fabula* and the polychaete *Lanice conchilega*, both common at our study site, may have immediate access to a

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fresh organic carbon source and may be responsible for fast transport of this POM into deeper sediment layers by bioirrigation, bioturbation or defecation. This matter is thus available for other benthic organisms, living in deeper sediment layers. Carnivorous macrofauna organisms are expected to have a delayed access to a fresh carbon source but can nevertheless contribute to sediment mixing by bioturbation due to hunting activities.

In recent years, pulse-chase experiments with isotopically labelled substrates have been established as a useful tool for following and quantifying the processing and remineralisation of fresh organic carbon in a variety of marine sedimentary habitats (e.g. Levin et al. 1997, Middelburg 2000, Aberle & Witte 2003, Witte et al. 2003a). However, information on the benthic processing of fresh POM in sandy-shelf environments is still scarce. We therefore carried out a series of on-board and *in situ* pulse-chase experiments in North Sea sandy sediments and followed the entrainment, processing and degradation of algal carbon by the benthic community. Within the project, not only the macrofauna but also bacterial carbon processing was studied (Bühring et al. 2004) as well as the entrainment and degradation of diatoms into the sediment (Ehrenhauss et al. 2004a,b).

This contribution focuses on the importance of macrofauna for carbon transport processes in a fine-grained, sandy North Sea sediment. We investigated the composition, abundance and biomass of the macrofauna community as well as the processing of added, labelled diatom carbon by the different macrofauna taxa. We report on the potential of *Fabulina fabula*, the dominant macrofauna organism, for POM subduction, and discuss the relative importance of bioturbation and advective transport.

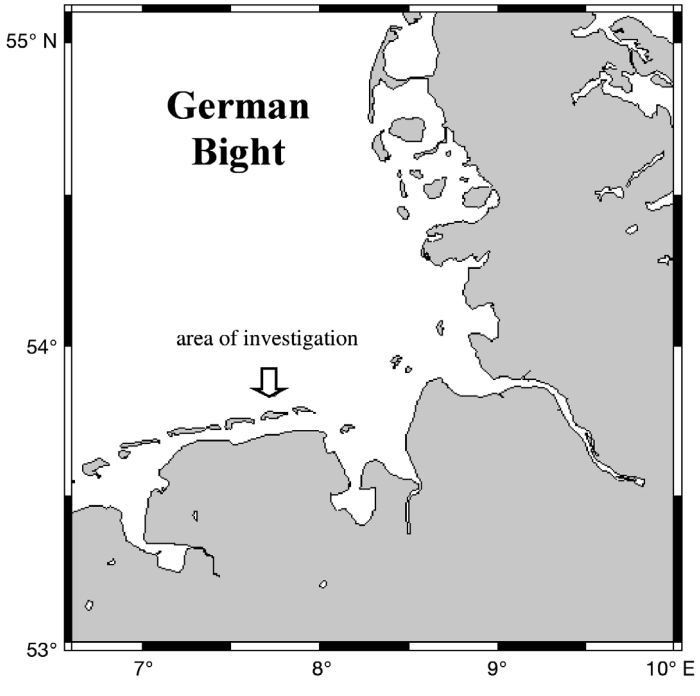

Fig. 1. Area of investigation in the southern German Bight (North Sea)

MATERIALS AND METHODS

Area of investigation. The study site was situated in the southern German Bight (North Sea), seaward of the East Frisian island Spiekeroog (53° 51′ N, 007° 44′ E) (Fig. 1). The water depth in this area was 19 m with a tidal range about 2 m. Salinity was 31 to 32 and the mean water temperature was 9°C in April and 13°C in June. The sediment type is fine sand with a grain size of 163 ± 20 µm and a permeability of 3.0 ± 1.7×10^{-12} m^2 (Janssen et al. 2005).

The experiments and sampling took place during Expeditions HE 145 in April 2001 (on-board and laboratory experiments) and HE 148 in June 2001 (*in situ* experiments) of the RV 'Heincke'.

Cultivation of labelled phytoplankton. *Ditylum brightwellii* (Bacillariophyceae: Biddulphiales) was cultured with *F*/2 medium (Guillard & Ryther 1962) in sterile artificial seawater (Grasshoff et al. 1999) with a salinity of 33. The diatoms were labelled with ^{13}C by replacing 25% of the $NaHCO_3$ in the formula by $NaH^{13}CO_3$ (99%; Cambridge Isotope Laboratories). The algae were incubated for 10 d at 25°C under a light:dark cycle of 16:8 h and a light intensity of 34.9 µmol photons m^{-2} s^{-1}. The algal carbon produced consisted of 15 at.% ^{13}C (on-board experiments) and 9 at.% ^{13}C (*in situ* experiments).

For the laboratory experiments we used *Chlorella* sp. (Chlorophyceae: Chlorococcales). The algal carbon of *Chlorella* sp. consisted of >60 at.% ^{13}C.

Sampling and determination of macrofauna for natural abundance and biomass. For the determination of the natural abundance and biomass of macrofauna, sediment samples were collected with a van Veen grab (surface area 0.1 m^2). Each haul (9 during the cruise in April and 10 in June) was separately sieved (1.0 mm-mesh aperture), and the sieve contents were preserved in 4% formaldehyde buffered with sodium tetraborate until taxonomic identification under a stereomicroscope. The wet weight (g WW m^{-2}) for each taxonomic group was determined in the laboratory in Bremen.

Sampling of macrofauna for natural isotope signatures. The macrofauna samples for the measurements of the natural isotope signatures ($\delta^{13}C$) were also taken with a van Veen grab, but after sorting the individuals were immediately frozen at –20°C, as fixation with

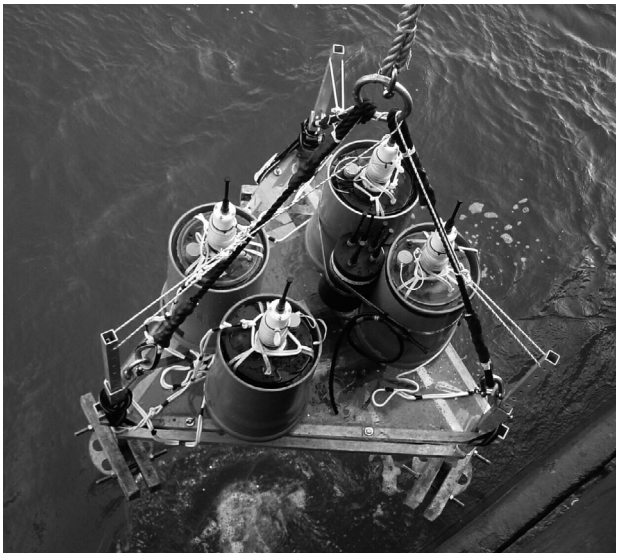

Fig. 2. Experimental chambers within their frame

formaldehyde would change the natural isotope signatures (Kaehler & Pakhomov 2001). Measurements of $\delta^{13}C$ were made with an isotope ratio mass spectrometer (IRMS) (see subsection 'Measurements').

On-board and *in situ* experiments. The experiments were conducted in cylindrical acrylic chambers (31 cm high, 19 cm diameter) with a horizontally rotating disk. The rotating water column generates a radial pressure gradient of approximately 1.5 Pa cm^{-1} that induces advective pore-water flows in permeable sediments (Huettel & Rusch 2000). These chambers were attached to a frame, lowered to the seafloor (Fig. 2), and carefully inserted approximately 15 cm deep into the sediment by divers, with minimum disturbance of the natural stratification of the sediment. For the *in situ* experiments, labelled *Ditylum brightwellii* (0.31 g C m^{-2}) was immediately injected into 2 chambers by divers, and incubated for 32 h. For the on-board experiments, the chambers were brought back directly to the research vessel after they were filled with the natural sediment and incubated with labelled *D. brightwellii* (0.36 g C m^{-2}) for 12, 30 and 132 h, with 2 replicates each. Incubation was conducted under *in situ* conditions at a temperature of 8°C in the dark. After incubation, the macrofauna from 4 different horizons (0 to 2, 2 to 5, 5 to 10 and >10 cm) was sieved using a 0.5 mm-mesh aperture to include juveniles, and then individually frozen (–20°C). For taxonomic identification, individuals were thawed and identified under a stereomicroscope in the laboratory in Bremen; throughout, the samples were cooled to avoid decomposition. Subsequently, bivalve shells and calcareous structures of *Echinocardium cordatum* were removed and all individual organisms immediately dried at a temperature of 60°C. Before determination of the $\delta^{13}C$ signatures, the dry weights (DW) of each individual was determined (g DW $ind.^{-1}$). Often the organisms had to be homogenised, and a subsample (approximately 0.5 to 1.5 mg) was transferred into tin cups for measurement. Organisms were pooled when their individual dry weight was <0.5 mg.

Laboratory experiments. The experimental chambers used for the laboratory experiments were similar to those used for the *in situ* and on-board experiments. Sediment and *Fabulina fabula* organisms were sampled with a van Veen grab. The sediment was sieved to remove macrofauna organisms and stored at 4°C. *F. fabula* were kept in an aquarium at *in situ* temperature (9°C).

Prior to the experiments, the chambers were filled with the sediment (18 cm). The surface water from the area of investigation was sampled with a water sampler. *Fabulina fabula* were put into the sediment cores in abundances of 0 and 14 individuals per core (2 replicates each) and allowed to settle in the sediment for 1 wk. The experiments were initiated by injecting the chambers with labelled *Chlorella* sp. (equivalent to 1 g C m^{-2}), and ran for 132 h. After incubation, the sediment of the chambers was sliced at 0.5 cm intervals for the first 1 cm and at 1 cm intervals to a depth of 10 cm, followed by a 10 to 12.5 cm and then a 12.5 to 18 cm layer. *F. fabula* were picked out, and a carefully homogenised subsample of the sediment from each sediment horizon was frozen immediately at –20°C until treatment. For determination of $TO^{13}C$ (total organic ^{13}carbon) signatures, ~2 g of this sediment was thawed and dried for 48 h at 60°C and pre-treated with approximately 10 ml 2 M HCl overnight to remove inorganic carbon compounds. Sediments were then centrifuged (2800 × *g*, 10 min), washed 3 times with distilled water, and then centrifuged and dried again. After this, approximately 100 mg of the sediment was weighed into tin cups for isotope ratio measurement.

Measurements. For measurement of the isotope ratios, the carbon was combusted to CO_2 in a CHN-analyser (CE Instruments) connected via an interface using the carrier gas He (ThermoFinnigan) to an isotope ratio mass spectrometer (IRMS; ThermoFinnigan). $\delta^{13}C$ was determined relative to Vienna PDB ($^{13}C/^{12}C_{VPDB}$: 0.0112372) (Peterson & Fry 1987) and calculated according to McKinney et al. (1950):

$$\delta^{13}C_{sample}\,(‰) = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \qquad (1)$$

where R = isotope ratio (^{13}C:^{12}C). The specific uptake of the ^{13}C by macrofauna organisms ($\Delta\delta^{13}C$, ‰) was calculated according to:

$$\Delta\delta^{13}C = \delta^{13}C_{sample} - \delta^{13}C_{natural\ isotope\ signature\ of\ taxa} \qquad (2)$$

Table 1. Natural isotope signatures ($\delta^{13}C$). n: number of individuals pooled for 1 measurement. Natural $\delta TO^{13}C$ (total organic ^{13}carbon) signature of the sediment was –21.67 ± 0.54‰ (Expedition HE 145) with no notable difference between sediment layers (S. Ehrenhauss unpubl. data). –: no data

Organism	n	$\delta^{13}C$ (‰) HE 145	HE 148
Fabulina fabula	10	–16.75	–17.63
Montacuta bidentata	9	–17.39	–
Montacuta ferruginosa	2	–17.65	–
Spisula spp.	2	–18.49	–
Nephtys spp.	10	–15.14	–15.19
Spionidae	1	–	–17.73
Magelona mirabilis	1	–17.28	–
Lanice conchilega	5	–16.48	–16.31
Ophelia limacina	3	–15.90	–
Aphroditidae	1	–	–15.86
Urothoe poseidonis	3	–	–15.63
Gammaridea	2	–15.82	–
Echinocardium cordatum	1	–17.68	–
Actinaria	1	–	–18.21

The specific labelling of the ^{13}C into the sediment ($\Delta\delta TO^{13}C$) was calculated according to:

$$\Delta\delta TO^{13}C = \delta TO^{13}C_{sample} - \delta TO^{13}C_{natural\ isotope\ signature\ of\ sediment} \quad (3)$$

The natural isotope signatures used for the equations are shown in Table 1.

RESULTS

Macrofauna abundance and biomass

The mean abundance of the macrofauna in the study area varied between 771 ± 287 (SD) ind. m^{-2} in April and 1531 ± 292 ind. m^{-2} in June (Table 2). During both cruises the most frequently observed taxa were bivalves, with 514 ± 188 and 1026 ± 82 ind. m^{-2} for April and June, respectively (dominance in terms of individuals was 67% during both cruises). In addition, polychaetes, crustaceans and echinoderms were frequently found. The dominant species in this area was the bivalve *Fabulina fabula* with 311 ± 162 ind. m^{-2} in April and 928 ± 101 ind. m^{-2} in June (dominance in terms of individuals was 40% in April and 61% in June). Furthermore the bivalves *Montacuta bidentata* and *M. ferruginosa* (Montacutidae), the polychaetes *Nephtys* spp. (Nephtyidae) and the crustacean *Urothoe poseidonis* (Haustoriidae) were widespread in the area of investigation (Table 2).

The mean biomass of the macrofauna was 243.8 ± 236 g WW m^{-2} in April and 351.3 ± 73 g WW m^{-2} in June (Table 2). The biomass of the bivalves increased from 56.5 ± 35.6 g WW m^{-2} in April to 230.5 ± 30.4 g WW m^{-2} in June. The biomass of the echinoderms reached 156.0 ± 223.8 g WW m^{-2} in April and 97.6 ± 86.8 g WW m^{-2} in June. The large sea urchin *Echinocardium cordatum* (Spatangidae), which can be considered a megafaunal rather than macrofaunal organism, occurred at relatively high densities (approximately 16 ind. m^{-2}) and accounted for >95% of echinoderm biomass. The biomass of the polychaetes was 29.8 ± 35.4 g WW m^{-2} in April and 22.4 ± 5.2 g WW m^{-2} in June. Crustacean biomass was low, as only small individuals occurred in this area. Again, *Fabulina fabula* had the highest biomass of the bivalves (88% in April and 97% in June); the biomass of other bivalves was low. Within the polychaetes, *Nephtys* spp. reached the highest biomass (80% in April and 88% in June).

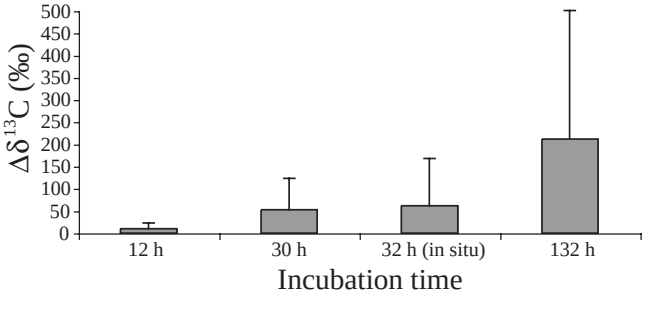

Fig. 3. Mean (+SD) specific uptake of ^{13}C after different incubation times by all macrofauna organisms ($\Delta\delta^{13}C$) in on-board and *in situ* (32 h) experiments (both replicates). High standard deviations reflect strong individual differences

Specific uptake of labelled algal carbon by macrofauna organisms (on-board and *in situ* experiments)

The mean specific uptake of ^{13}C by the total macrofauna continually increased in the time series experiments from 10.2 ± 12.8‰ after 12 h to 211.9 ± 288.9‰ after 132 h (Fig. 3; linear regression of averaged values, $r^2 = 0.98$). However, strong differences in labelling patterns occurred among the different taxa (Fig. 4). The highest $\Delta\delta^{13}C$ enrichment occurred within the bivalves, the polychaete *Lanice conchilega* (Terebellidae) and the echinoderm *Echinocardium cordatum*. *Fabulina fabula*, found in all investigated cores, showed a $\Delta\delta^{13}C$ value of 16.6 ± 15.6‰ after 12 h, which increased to 291.2 ± 323.0‰ after 132 h. *L. conchilega* showed its highest value (376.5 ± 225.1‰) after 132 h. The specific uptake of ^{13}C by a single *E. cordatum* was 13.0‰ after 12 h. Low specific uptakes were found for most of the other polychaetes, especially *Nephtys* spp., and for the crustaceans. Like *F. fabula*, *Nephtys* spp. were found in all cores. The specific uptake of ^{13}C by *Nephtys* spp. increased from 0.4 ± 0.3‰ at 12 h to

Table 2. Abundances (ind. m^{-2}) and biomasses (g wet wt m^{-2}; without shells) of taxa during Expedition HE 145 in April and Expedition HE 148 in June 2001. Data are averages ± SD

Organism	HE 145				HE 148			
	Abundance		Biomass		Abundance		Biomass	
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD
Bivalvia[a]	**514**	**188**	**56.5**	**35.6**	**1026**	**82**	**230.5**	**30.4**
Fabulina fabula	311	162	49.8	33.4	928	101	224.7	28.7
Montacuta bidentata	167	109	0.9	0.6	26	30	0.2	0.3
Montacuta ferruginosa	19	16	0.3	0.3	62	69	0.4	0.5
Abra alba	12	15	4.6	5.4	3	5	0.9	1.5
Macoma balthica	1	3	<0.1	<0.1	6	7	4.2	12.1
Spisula spp.	2	4	0.9	2.6	1	3	>0.1	0.1
Nucula spp.	2	7	<0.1	0.1				
Polychaeta	**146**	**60**	**29.8**	**35.4**	**209**	**38**	**22.4**	**5.2**
Nephtys spp.[b]	87	45	23.8	27.4	130	36	19.6	3.8
Spiophanes bombyx	7	7	<0.1	< 0.1	31	29	0.1	0.1
Magelona mirabilis	23	36	0.1	0.1	11	12	0.1	0.1
Lanice conchilega	19	19	2.4	2.5	4	5	0.8	1.4
Eumida bahusiensis					13	16	>0.1	0.1
Pygospio elegans	1	3	<0.1	< 0.1	10	11	>0.1	>0.1
Hediste spp.	2	4	3.0	7.4	2	4	1.2	3.4
Goniadidae	2	4	0.1	0.1	2	4	0.1	0.4
Cirratulidae					3	7	>0.1	>0.1
Capitellidae	2	4	0.2	0.6				
Other Spionidae	1	3	<0.1	<0.1	1	3	>0.1	>0.1
Scoloplos armiger	1	3	<0.1	<0.1	1	3	>0.1	0.1
Harmothoe sp.					1	3	>0.1	>0.1
Rest of biomass			0.2	0.3			0.4	0.4
Crustacea	**89**	**95**	**1.4**	**3.8**	**283**	**251**	**0.8**	**0.5**
Urothoe poseidonis	61	95	0.1	0.2	249	239	0.5	0.4
Other Gammaridea	12	10	<0.1	<0.1	22	27	>0.1	>0.1
Diastylis rathkei	11	12	<0.1	0.1	7	8	0.1	0.1
Iphinoe trispinosa					4	10	>0.1	>0.1
Mysidacea	2	4	<0.1	<0.1				
Processa edulis					1	3	0.1	0.3
Crangon crangon	1	3	1.2	3.5				
Pinnotheres pisum	1	3	0.1	0.3				
Echinodermata	**22**	**21**	**156.0**	**223.8**	**13**	**11**	**97.6**	**86.8**
Echinocardium cordatum	18	19	137.8	216.5	13	11	97.6	86.8
Ophiura ophiura	3	7	3.0	8.9				
Ophiura juvenile	1	3	<0.1	<0.1				

[a]In addition, fragments of *Ensis* cf. *americanus* were found
[b]In spot checks we were able to classify *Nephtys* spp. as *N. caeca* and *N. hombergii*

6.7 ± 8.0‰ at 132 h. The highest specific uptake of ^{13}C was found in a single individual of *Spisula* sp. (Bivalvia: Mactridae) with 457.0‰ after 32 h (Fig. 4).

Altogether, specific labelling patterns were determined for 83 individuals of *Fabulina fabula*, ranging from 0.2 to 57.0 mg DW $ind.^{-1}$ in biomass. A trend for higher specific uptake of ^{13}C by smaller individuals was apparent (Fig. 5).

The vertical distribution of macrofauna $\Delta\delta^{13}C$ signatures within the sediment is given in Fig. 6. Within 30 h, macrofauna throughout the whole sampling column had ingested tracer carbon, but signatures below 10 cm sediment depth were lower than those above. In each sediment horizon, $\Delta\delta^{13}C$ signatures increased over time.

Subduction of $PO^{13}C$ into sediment (laboratory experiments)

As expected, $\Delta\delta TO^{13}C$ signatures were highest at the sediment surface (Fig. 7). Pronounced subsurface maxima between approximately 4 and 7 cm sediment depth developed in the *Fabulina fabula* cores (Fig. 7B).

DISCUSSION

The investigated increase in macrofauna abundance and biomass from April to June (Table 2) is in accordance with seasonal trends described for the German

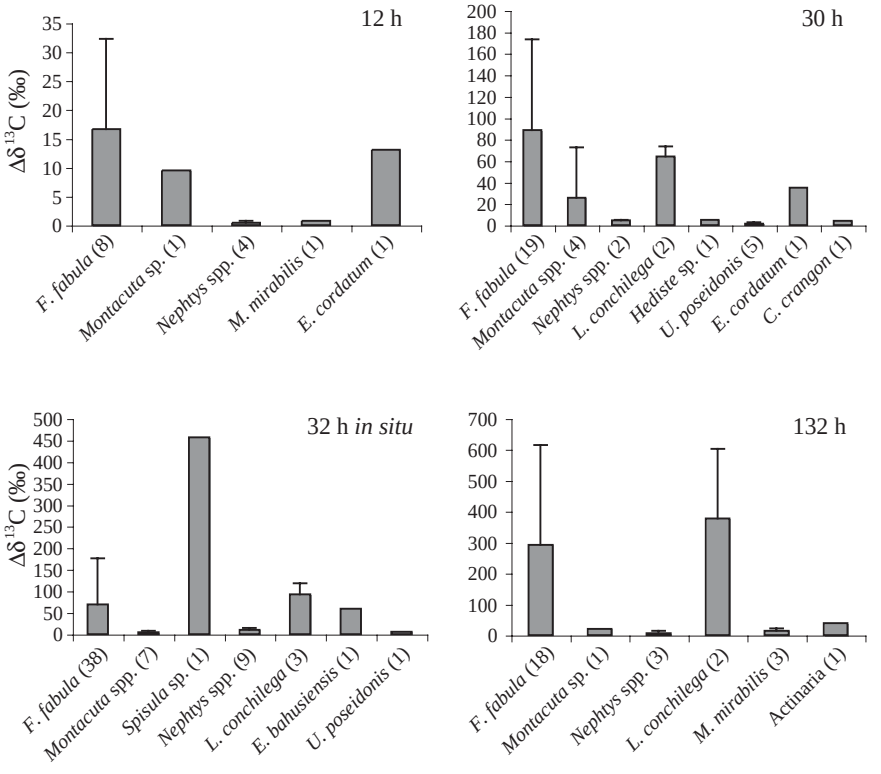

Fig. 4. Mean (+SD) specific uptake of ^{13}C by macrofauna organisms ($\Delta\delta^{13}C$) in on-board and *in situ* experiments (both replicates). High standard deviations reflect strong individual differences. Number of individuals is given in parentheses. Note different ordinate scales for the different incubation times. When organisms of different species had to be pooled because of their low biomass, their data were not included in this figure (< 0.04 % of total biomass)

Bight: in general, there is a minimum of abundance and biomass in the late winter or early spring, and a maximum in summer and autumn (Dörjes et al. 1986, Michaelis & Reise 1994). Salzwedel et al. (1985) reported a mean macrofauna abundance of 2377 ind. m^{-2} in October for an area of 24 000 km^2, covering nearly the whole sublittoral area of the German Bight. Furthermore, Salzwedel et al. (1985) demonstrated that, with respect to macrofauna community composition, the German Bight could be divided into 4 to 5 macrofauna community areas. The macrofauna community of the largest of these regions (12 000 km^2), in which our area of investigation was located, is dominated by the tellinid bivalve *Fabulina fabula* (former *Tellina fabula*), and is accordingly named the '*F. fabula* association'.

In our study we describe 32 species or taxa. Salzwedel et al. (1985) detected a mean of 34 species for the *Fabulina fabula* community, in good agreement with our number. The community composition of our investigation differs somewhat from the study from Salzwedel et al. (1985), perhaps due to shifts in species occurrence between the investigations. As is typical for the *F. fabula* community and for the German Bight in general, polychaetes showed the highest diversity, with 14 different species or taxa (Salzwedel et al. 1985, Dörjes et al. 1986).

Among the polychaetes, *Nephtys* spp. comprised the most frequently observed taxa in terms of both abundance and biomass (approximately 10 % of total macrofauna). The tube-building polychaete *Lanice conchilega* contributed approximately 1 % of the total biomass. However, we found that many intact tubes were empty, which may indicate that *L. conchilega* successfully escaped the sampling process, leading to an underestimation of its biomass.

With 8 % of all individuals in April and 16 % in June, the crustacean *Urothoe poseidonis* is important in terms of abundance, but less so with respect to biomass because of the comparatively small size of these Haustoriidae. This is well in accordance with the investigation of Salzwedel et al. (1985), in which 7 % of all individuals belonged to *U. poseidonis* (former *U. grimaldeii*) within the *Fabulina fabula* community. The most important species within the echinoderms is *Echinocardium cordatum*, with the highest individual biomass in our study area.

The rapid and continuous specific uptake of added, fresh organic matter by benthic organisms in our study (Fig. 3) has also been shown in other investigations with isotopic labelled matter from a variety of marine sedimentary habitats (Levin et al. 1997, 1999, Middelburg et al. 2000, Moodley et al. 2000, Aberle & Witte

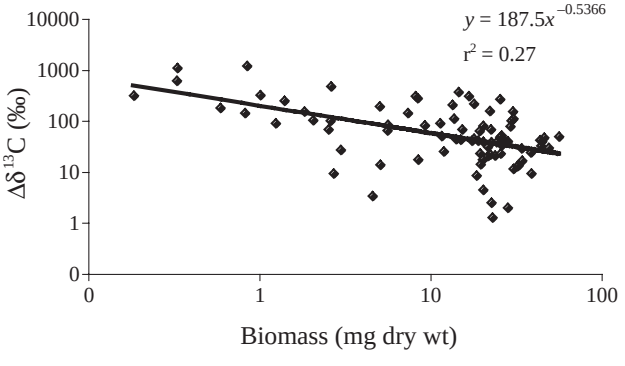

Fig. 5. *Fabulina fabula*. Individual response in on-board and *in situ* experiments to fresh carbon source (both replicates), showing specific uptake of ^{13}C ($\Delta\delta^{13}C$) as a function of size. Note logarithmic scales

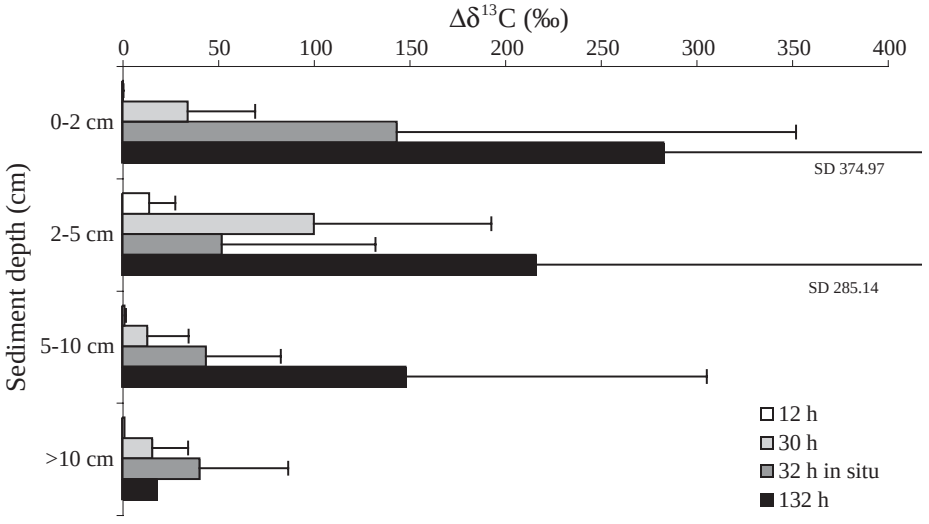

Fig. 6. Mean (+SD) specific uptake of ^{13}C after different incubation times by all macrofauna organisms as a function of sediment depth ($\Delta\delta^{13}C$) in on-board and *in situ* experiments (both replicates). High standard deviations reflect strong individual differences

2003, Witte et al. 2003b). For a North Sea tidal flat, Middelburg et al. (2000) showed very rapid label transfers through the benthic food web. After only a few hours, a predatory nematode was already significantly labelled. Moodley et al. (2000) showed rapid label transfer from algal matter to foraminiferans. At continental slope depths (800 m), maldanid polychaetes were found to subduct fresh organic matter so rapidly, that deep-dwelling meiofauna were able to ingest the labelled matter after only 1.5 d (Levin et al. 1997); even at abyssal depths (4800 m), 70% of the macrofauna organisms accessed a labelled phytodetritus pulse within 2.5 d (Witte et al. 2003b). In the latter study, the macrofauna initially processed much more carbon than the bacteria, and Witte et al. (2003b) speculated that much of the fresh particulate organic carbon (POC) reaching the deep-sea floor passes through the gut systems of larger organisms before becoming available to unicellular individuals.

Within the macrofauna in our study, the very abundant bivalve *Fabulina fabula*, the tube-building worm *Lanice conchilega* and the sea urchin *Echinocardium cordatum* most rapidly ingested the fresh carbon source (Fig. 4). A study by Herman et al. (2000) in the eulittoral of a Dutch estuary confirmed comparably rapid specific uptakes of labelled carbon by the bivalve *Macoma balthica*, which is very abundant in this area. According to Meyer el al. (1994), *M. balthica* is able to suck the surface to ingest detritus and phytoplankton, and this ability was also observed during our laboratory experiments for *F. fabula*. Thus, both species are (surface) deposit-feeders. Arruda et al. (2003) also confirmed this for both *Macoma* spp. and *Fabulina* spp. However, bivalves that feed directly on deposits also take up a good deal of suspended matter with the inhalant flow (Arruda et al. 2003), and are thus more accurately named facultative suspension and (surface) deposit-feeders, as reported by Herman et al. (2000) for *M. balthica* and by Køie & Kristiansen (2001) for Tellinidae in general. Because of their feeding habits, Tellinidae are among the primary consumers within the food chain. The tube-building worm *L. conchilega* was sampled only from 3 cores, most probably because of its ability to escape (see above). However, those individuals collected showed very high specific labelling patterns (Fig. 4). *L. conchilega* is a suspension-feeder (Buhr 1976), and

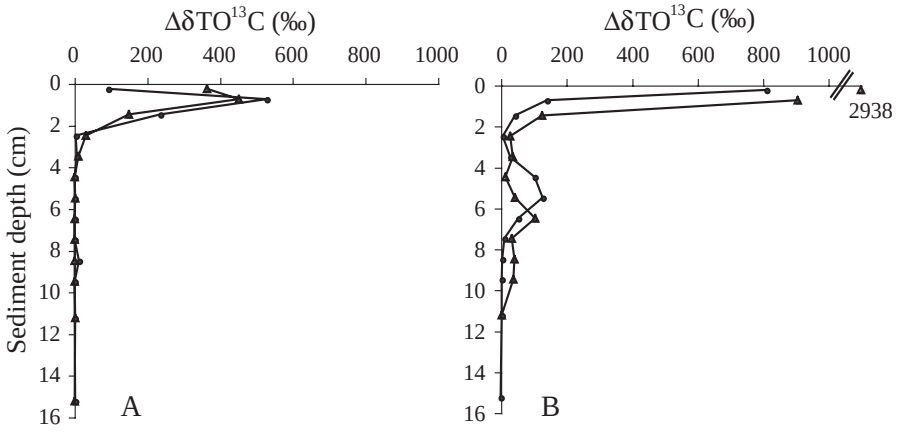

Fig. 7. Specific labelling of total organic (TO) ^{13}C in the sediment ($\Delta\delta TO^{13}C$) in laboratory experiments after 132 h. (A) Experiments without *Fabulina fabula*; B: experiments with 14 *F. fabula*. (▲) Replicate a; (●) replicate b

this confirms the hypothesis that suspension-feeders play a very important role in the initial processing of fresh organic matter. Furthermore, this species is able to grow to a length of up to 25 cm and lives in deep-reaching tubes (Meyer et al. 1994), which renders it a prime candidate for the rapid subduction of organics by bioturbation and bioirrigation (Forster & Graf 1995). The sampled (surface) deposit-feeder *E. cordatum* (Hollertz et al. 1998) also showed an initial and high specific uptake of ^{13}C (Fig. 4), which underlines that both feeding types (suspension- and deposit-feeding) allow rapid ingestion of fresh organic matter. In addition, *E. cordatum* is very mobile, and thus probably causes strong sediment mixing.

In contrast, the polychaetes *Nephtys* spp. showed a contrasting labelling pattern: initial ^{13}C uptake was almost negligible and the label then continually accumulated throughout the time series. This pattern is in good agreement with the data of Herman et al. (2000) and has been shown for predators in general by Aberle & Witte (2003). Our results confirm the classification of *Nephtys* spp. as mainly carnivores (Hartmann-Schröder 1996) and a fast carbon transfer between trophic levels.

The investigated trend for higher specific uptake of ^{13}C by smaller *Fabulina fabula* individuals (Fig. 5) could be due to different feeding attributes of juveniles and adults. Such ontogenetic variation was reported for the tellinid bivalve *Macoma balthica* by Rossi et al. (2004). Juvenile *M. balthica* feed entirely on microphytobenthos, while there is a gradual tendency for larger sized individuals to feed more on microphytoplankton.

During our on-board and *in situ* experiments, the pathway of settling POC through the benthic food web was also investigated with respect to bacterial community and remineralisation rates (Bühring et al. 2004). Bühring et al. (2004) showed that initial carbon processing (12 h) was dominated by the bacteria, but after longer incubation times (30 and 32 h *in situ*) the macrofauna gained in importance until, after 132 h, the greatest fraction of the added ^{13}C was mineralised to CO_2. The initial uptake of fresh organic matter by bacteria could have been due to the specific uptake of dissolved organic carbon (DOC), which was already present in the added algal matter (Ehrenhauss et al. 2004a). Middelburg et al. (2000) also found fast uptake by bacteria, during an experiment at an intertidal site in an estuary, where they sprayed ^{13}C-bicarbonate on the surface and followed its pathway through the benthic food web. Middelburg et al. (2000) found evidence for photosynthetically fixed ^{13}C entering the microbial food web within hours and maximum labelling of bacteria after 1 d. In this regard, it is probable that our macrofaunal deposit-feeders also ingested some labelled bacteria during incubation.

The quaternary sandy deposits at our study site have a permeability of $3.0 \pm 1.7 \times 10^{-12}$ m^2 (Janssen et al. 2005). According to Huettel & Gust (1992), transport processes down to 2 cm sediment depth can be expected to be dominated by advection at this permeability. This hypothesis was confirmed by our laboratory experiments with pre-sieved sediments, where our particulate tracer was mixed down to 2 cm into the sediment even in those cores with no macrofauna present (Fig. 7A). For the upper 2 cm, no distinction between advective and bioturbative particle transport could be made. Below this depth, however, particle transport clearly depends on macrofauna activity. Mixing into deeper layers occurred only in those cores with *Fabulina fabula* present. Here, clear subsurface maxima developed at approximately 4 to 7 cm sediment depth, the actual burrowing depth of *F. fabula* in the cores, indicating non-local mixing by the bivalves. Sun et al. (1999), who carried out similar laboratory experiments with the (surface) deposit-feeder *Yoldia limatula* (Bivalvia: Nuculanidae), also found a penetration of POC into deeper sediment layers when *Y. limatula* was abundant, but a penetration into the uppermost sediment layers only, when physical processes alone were involved. Ehrenhauss et al. (2004a) found that in our on-board and *in situ* experiments, the labelled algal carbon was mixed into the sediment down to 6 cm; here, it could not be easily distinguished between advective and organism-mediated mixing. In another *in situ* chamber study at the same station, Janssen et al. (2005) did not detect significant changes of sediment community oxygen consumption in the presence and absence of horizontal pressure gradients, and concluded that, due to the relatively low permeability of the fine sand, advective solute transport is of minor importance compared to molecular diffusion and bioirrigation. Therefore, the subduction of particulate carbon into the sandy sediment of the study area would be almost exclusively due to bioturbation. The advective entrainment of tracer particles into the upper sediment layer during our laboratory experiments would then be a result of the disruption of the natural sediment texture during sediment treatment (sampling, sieving and storing). In any case we can conclude that the transport of POM down to more than 2 cm sediment depth is a result of macrofauna activity. The importance of this bioturbative transport is confirmed by investigations of microbial activity: both the incorporation of ^{13}C into bacterial biomarkers and the concentration of $^{13}CO_2$ in the pore water show subsurface peaks at the respective sediment depths (Bühring et al. 2004). Macrofauna thus rapidly supply deep-dwelling, small organisms (bacteria, meiofauna) with fresh organic matter.

CONCLUSIONS

In conclusion we investigated the relative importance of different macrofauna species for carbon processing and subduction in a fine sandy sediment. To date, sandy sediments have been poorly studied marine habitats, and our on-board and *in situ* experiments give the first insights into the macrofaunal response to a fresh carbon source in this particular environment. We found strong interspecific differences in the rates of specific uptake of labelled organic matter related to the feeding types of the macrofauna. The most rapid ingestion of freshly deposited organic carbon was observed in suspension- and deposit-feeders, but mainly predatory organisms also quickly became labelled. Additional laboratory experiments with the dominant facultative (surface) deposit- and suspension-feeder *Fabulina fabula* demonstrated the ability of macrofauna for the fast subduction of organic matter into deeper sediment layers. Because of its high abundance and feeding type, *F. fabula* is able to subduct large amounts of fresh organic matter, and thus pronouncedly affects carbon transport processes in fine sandy sediments.

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