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Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments

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Abstract

We measured organic carbon uptake rates by deep-sea benthic foraminifera and studied differences among species, living depth, and seasons to investigate how these protists contribute to carbon consumption on the deep-sea floor. In situ feeding experiments using ^{13}C-labeled algae were carried out in the central part of Sagami Bay from 24 to 29 November 2001 and 1 to 12 April 2002. Our results indicate that carbon assimilation rates were higher in shallow infaunal species (*Uvigerina akitaensis, Bulimina aculeata*) and lower in intermediate (*Textularia kattegatensis*) and deep infaunal species (*Chilostomella ovoidea*). Some shallow and intermediate infaunal species showed higher carbon uptake in spring than in autumn. In total, benthic foraminifera assimilated C at 5.8 $\pm$ 4.8 mg m^{-2} and 2.0 $\pm$ 1.3 mg m^{-2} (in spring and in autumn, respectively) of labeled algae within 2 d, which was more than that by total metazoans (1.5 $\pm$ 0.4 mg m^{-2} and 0.4 $\pm$ 0.1 mg m^{-2}, respectively). Deep-sea benthic foraminifera rapidly ingest large amounts of carbon and may play an important role in carbon consumption on the deep-sea floor. Different responses to algal carbon among species may explain foraminiferal assemblages and shifts after environmental changes, such as seasonal pulses of organic matter supply.

The sinking organic matter produced at the oceanic surface to the seafloor is affected by various physical and biochemical transformations in the water column. This phytodetritus and its more labile components are the main food sources for benthic organisms (Gooday and Lambshead 1989; Gage 1990; Altenbach 1992), suggesting that benthic activity controls carbon budgets on the deep seafloor. Additionally, metazoan macrofauna mix surface sediments through bioturbation, thereby burying labile and decomposed organic materials. It is necessary to clarify the fate of deposited phytodetritus by biological as well as geochemical processes to understand the carbon budget on the deep seafloor.

Benthic foraminifera are one of the most abundant components of deep-sea benthic communities and important proxies for paleoenvironment reconstructions because they have a well-documented fossil record. They sometimes comprise more than 50% of the benthic biomass (Snider et al. 1984; Gooday et al. 1992) and therefore should play a significant role in the deep-sea carbon budget. However, deep-sea benthic foraminiferal feeding behavior and metabolic activity in relation to the carbon budget are poorly understood

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(Linke 1992; Linke et al. 1995). Most previous field investigations focused on changes in foraminiferal population size before and after phytodetritus deposition (e.g., Gooday 1988; Drazen et al. 1998; Gooday and Rathburn 1999). Experimental approaches are necessary to understand the short-term responses of benthic foraminifera to phytodetritus deposition, particularly in deep-sea settings. Stable isotopes are useful tracers for following the fate of labeled material over short to long time scales and for examining quantitatively the ingestion rates of benthic organisms (Blair et al. 1996; Levin et al. 1999; Middelburg et al. 2000). Levin et al. (1999) carried out an in situ experiment at a water depth of 850 m using ^{13}C-labeled algae to investigate food ingestion by annelids, other macrofaunal metazoans, and large benthic foraminifera. They observed the effects of an artificial food supply over both short (1.5-d) and long (14-month) time scales and concluded that labile organic matter was consumed by benthic foraminifera within 1.5 d. Moodley et al. (2002) also reported that benthic foraminifera were responsible for 30% of the organic carbon processed by the total benthic community on a day scale at a water depth of 2,170 m. It is clear from these studies that deep-sea benthic foraminifera can utilize deposited organic carbon very quickly, within 1 d, and thus play a very important role in the early stages of consumption of organic carbon on the seafloor.

In contrast, Witte et al. (2003) reported that metazoan macrofauna are more important than protozoans during the early diagenesis of organic matter at a water depth of 4,800 m. In their studies, the macrofaunal response was very high after 2 d of incubation, whereas foraminifera and bacteria showed a retarded reaction. Their study suggested that the dominant taxa in the food web differ between abyssal areas and the continental slope. However, these differences between the findings of Moodley et al. (2002) and Witte et al. (2003) may be caused by differences in the behavior of benthic taxa. Aberle and Witte (2003) reported that different types of uptake occurred among the same metazoan taxa depending on their feeding strategy. In laboratory studies, we found differential responses to a simulated food supply in benthic foraminiferal species obtained from Sagami Bay (Nomaki unpubl. data). Shallow and intermediate infaunal species showed clear reactions to food materials under experimental conditions, in contrast to some deep infauna. We suggest that these species differences might affect the deep-sea carbon budget. Shallow infaunal species such as *Uvigerina akitaensis* or *Bulimina aculeata* may process large amount of carbon, whereas some deep infaunal species (*Chilostomella ovoidea*) may process only a little. Additionally, these differences may reveal the paleoproductivity preserved in the foraminiferal fossil record.

Therefore, organic carbon uptake experiments are needed to address benthic foraminifera at the species level. It has also been reported that foraminiferal species composition changes seasonally in Sagami Bay as a result of the seasonality of phytodetritus deposition (Kitazato and Ohga 1995; Ohga and Kitazato 1997; Kitazato et al. 2000). This may be caused by differences in species responses, indicating that some benthic foraminiferal activity is high in spring, when large amounts of phytodetritus is deposited on the seafloor, and low in autumn, when limited phytodetritus is deposited (Nakatsuka et al. 2003). In particular, some shallow infaunal species that showed distinct seasonality in their abundance should show larger carbon uptake in spring than in other seasons. Seasonal variations of carbon uptake have not yet been examined through in situ experiments, although seasonal variations in trophic conditions influence foraminiferal metabolism (Linke 1992) and assemblages (e.g., Ohga and Kitazato 1997) and their importance in carbon consumptions.

In this study, we investigated how organic carbon is consumed by benthic foraminifera and metazoans in a deep-sea area. In particular, we focused on the following questions: (1) Is there a differential uptake among foraminiferal species in relation to living depth in the sediment? (2) Are there any seasonal variations in benthos carbon uptake? (3) Which taxa play the most important role in early diagenesis? For this purpose, experiments were designed using stable isotope (^{13}C)-labeled algae in both autumn and spring. Temporal and vertical sediment sampling was carried out to investigate the amount of added organic carbon ingested by foraminifera on a species level. Assimilation rates of organic carbon calculated for the dominant foraminiferal species were analyzed to examine which taxa mainly contribute to organic carbon consumption on the deep seafloor. These data were compared with those of metazoans in the feeding experiment, and the importance of protozoans in the deep-sea carbon budget is discussed.

Materials and methods

Study site—In situ carbon uptake experiments were carried out in the central part of Sagami Bay (Sta. OBB2, water depth 1,449 m), central Japan, during autumn (November 2001) and spring (April 2002). In Sagami Bay, the spring bloom occurs from mid-February to May when the chlorophyll concentration is higher than 70 mg m^{-2} in the surface 50 m (Kanda et al. 2003), and high organic carbon (200–500 mg m^{-2} d^{-1}) and pheopigment fluxes are observed at the sediment trap moored 20 m above bottom (Kitazato et al. 2000; Kitazato et al. 2003*a*, Nakatsuka et al. 2003). Some meiobenthic organisms, including benthic foraminifera, react to these pulses (Kitazato et al. 2000; Shimanaga and Shirayama 2000). The spring experiment should represent benthic foraminiferal consumption of organic matter under eutrophic conditions, and the autumn experiment should represent responses during a less trophic season. ^{13}C-labeled algae were used as the source of organic matter. Assimilation rates of organic carbon were calculated by measuring the δ^{13}C values in foraminiferal protoplasm. Bottom-water physicochemical parameters around Sta. OBB2 are stable throughout the year with a temperature of 2.33°C ± 0.1°C, salinity of 34.5 ± 0.2‰ and dissolved oxygen concentration of 1.1 ± 0.2 ml L^{-1} (46 ± 8 μmol L^{-1}) (Ohga and Kitazato 1997).

Production of ^{13}C-labeled algae—The unicellular algae *Dunaliella tertiolecta*, originally provided by the Institute of Biology, Tuebingen University, and maintained in the laboratory at Shizuoka University, was used as food material. *D. tertiolecta* was incubated at 20°C with sterilized prefiltered

natural seawater that contained f/2 medium and approximately 0.1 mol L^{-1} of additional $NaHCO_3$ that contained enriched 99.9% ^{13}C (Shoko Tsusyo). The final concentration of ^{13}C in the algal carbon was 5.23 atom% in the autumn experiment and 4.49 atom% in the spring experiment. The algae were centrifuged at 4000 *g* for 10 min and extracted from the cultured seawater. Extracted algae were rinsed with non-^{13}C-labeled sterilized seawater to remove inorganic carbon labeled with ^{13}C and were then frozen at −20°C until used in the in situ culture experiment.

Experimental procedure—The autumn culture experiment was carried out from 23 November through 29 November 2001, during the RV *Natsushima* cruise NT01–11. On 23 November, five incubation cores (5 cm in inner diameter; Kitazato et al. 2003*b*) were prepared and placed on the undisturbed seafloor a few meters from Sta. OBB2 by the manipulator arm of the manned submersible *Shinkai 2000*. Each incubation core was equipped with two syringes, each storing 5 ml of labeled algae. The volume of overlying seawater in the inner incubation core was approximately 100 cm^3, and the core was also connected to exterior seawater with a silicon valve. After inserting the incubation cores to a depth of 30 cm, each syringe was triggered and the algal slurry was deposited on the sediment surface. The amount of added algae was 1.03 g m^{-2}, corresponding to two- to fivefold the daily total organic carbon flux at the center of Sagami Bay, and also corresponding to 3% of bulk total organic carbon in surface 0 to 1 cm sediment. After a few minutes on the seafloor, one of the incubation cores (A-2h) was recovered by the manipulator and brought immediately on board (it arrived on board 2 h after recovery). The time at which this core was examined was taken as the time 0 control to determine what types of changes occurred in the other incubation cores during the experimental procedure. However, one of the two syringes on the A-2h core was not triggered because of a mechanical problem. The subsequent two cores (A-2d-a, A-2d-b) were recovered 2 d after the start of the experiment (25 November), and the remaining two (A-6d-a, -b) after 6 d (29 November). On 25 November, one additional core (A-4d) was placed on the seafloor and then recovered after 4 d (29 November). At the same time, three push-core samples (4.2 cm in inner diameter) were taken to document the natural background abundance, distribution, and ^{13}C% of foraminifera (A-B).

The spring culture experiment was carried out from 1 April to 12 April 2002, during an RV *Natsushima* training cruise and cruise NT02–05. On 1 April, four incubation cores were again placed on the undisturbed seafloor and labeled algae were introduced as described above. The amount of algae added, 1.00 g m^{-2}, coincides to that of autumn experiment. Two of the incubation cores (S-3h-a, -b) were recovered after a few minutes on the seafloor and the other two (S-11d-a, -b) after 11 d (12 April). On April 10, the subsequent two incubation cores (S-2d-a, -b) were placed on the seafloor and recovered 2 d later (12 April). A push-core sample (4.2 cm in diameter) was also taken to document the natural background abundance, distribution, and ^{13}C% of foraminifera in spring (S-B).

The recovered incubation cores were immediately processed in the shipboard laboratory within a few hours after arriving on deck. Each core was sliced into 1-cm-thick layers from the surface to a depth of 5 cm. Both A-2h and A-2d-b from the autumn experiment were sampled to a depth of only 3 cm. A subsample (0.5 cm^2) of every sliced sediment fraction was used to analyze the ^{13}C concentration in the sediment. These subsamples were kept frozen at −20°C until analyzed. The remaining sediment samples were used for measurement of the ^{13}C content in organisms and for isotopic and elemental analysis. They were sieved on a 63-μm mesh using artificial seawater and then preserved at −20°C before the selection of living foraminiferal individuals and metazoan meiofauna.

Sample preparation—Some metazoan meiofauna and macrofauna (nematodes, harpacticoids, other copepods, bivalves, and polychaetes) and all foraminifera of which the test cavity was filled with definite cytoplasm were selected from the sediment residues under a binocular microscope and sorted into species. Organism samples were cleaned with artificial seawater to remove sediment particles around their bodies, transferred to a Petri dish, and frozen again until isotope analysis. Sediment samples were dried at 50°C to measure the dry weight. About 5 to 10 mg of dried sediment was transferred into silver cups for analysis in a mass spectrometer. Living individuals of each species were also transferred into silver cups and dried at 50°C. Both sediment and organism samples were decalcified with 20% HCl.

Total organic carbon concentrations were measured using an elemental analyzer (NA-1500, Fisons Instrument). $^{13}C/^{12}C$ ratios were determined using an isotope ratio monitoring mass spectrometer (Delta plus, Thermo Quest) connected to an elemental analyzer at the Institute of Low Temperature Science, Hokkaido University, and shown as δ-notation against the Vienna Pee Dee Belemnite standard ($\delta^{13}C = [(^{13}C/^{12}C)\ \text{sample}/(^{13}C/^{12}C)\ \text{PDB} - 1] \times 1000$) (Web appendix 1 at http://www.aslo.org/lo/toc/vol_50/issue_1/0134a1.pdf). Blank cups that contained no sample but had been treated in the same manner as the sample cups were also measured for each analysis. Total organic carbon in the blank cups ranged from 0.78 to 3.62 μg of C, (mean: 1.38 ± 0.50 μg of C) in autumn and from 1.91 to 4.25 μg of C (mean: 3.06 ± 0.68 μg of C) in spring. Sample data were subtracted from the blank cup data for each measurement run.

Calculation of added carbon concentration in benthic foraminifera—Concentration of ''added labeled carbon'' in organic carbon were calculated using the following formula:

$$\text{Added carbon \%} = \text{Excess } ^{13}C/(^{12}C + ^{13}C)_{\text{sample}} \times 100 \div \text{Excess } ^{13}C/(^{12}C + ^{13}C)_{\text{algae}}$$

Excess $^{13}C/(^{12}C + ^{13}C)$ values were calculated from the difference in the $^{13}C/(^{12}C + ^{13}C)$ values of each sample and the labeled algae from the background samples. If the sample did not contain labeled algae, the $^{13}C/(^{12}C + ^{13}C)$ value was the same as that of the background sample and the labeled algal carbon percentage was zero. If all the carbon in the sample was derived from the labeled algae, the $^{13}C/(^{12}C + ^{13}C)$ value was the same as that of the labeled algal sample,

Table 1. Foraminiferal biomass (mg C m^{-2}) in the surface 0 to 3 cm of sediment in each experimental core sample.

	Autumn					Spring			
Species	A-B	A-2h	A-2d-a, b	A-4d	A-6d-a, b	S-B-a, b	S-3h	S-2d-a, b	S-11d-a, b
Uvigerina akitaensis	10.6	7.0	24.4±8.7	11.3	40.4±26.9	22.4±3.5	4.7	11.4±0.7	26.0±6.8
Bulimina aculeata	1.5	0.0	4.9±3.2	2.2	6.9±4.4	2.4±0.5	1.4	3.0±2.1	6.6±1.8
Bolivina spissa	2.5	2.5	3.8±0.2	1.1	18.2±17.2	0.8±0.8	0.0	2.8±1.1	4.6±2.3
Bolivina pacifica	4.1	0.6	3.9±2.1	0.9	2.0±0.3	2.3±1.4	0.4	4.7±3.0	5.5±3.6
Textularia kattegatensis	5.9	1.5	5.0±1.6	0.0	5.3±2.6	9.3±1.4	7.4	4.1±0.5	9.5±4.0
Globobulimina affinis	5.2	10.2	38.5±32.5	1.1	54.2±29.1	36.4±9.4	108.9	223.8±189.5	62.6±18.0
Chilostomella ovoidea	5.6	3.7	10.7±3.5	0.9	16.8±13.3	4.2±0.5	10.8	18.0±11.3	14.3±5.3
Cyclammina cancellata	85.6	0.0	110.3±50.7	18.2	81.4±54.9	88.3±78.1	17.4	14.8±12.7	46.3±17.3
Other	27.2	13.0	10.6±4.4	5.8	29.4±21.4	41.4±1.0	19.6	15.6±7.1	35.3±9.1
Total foraminifera	148.3	38.5	212.1±106.9	41.5	254.7±170.0	207.5±65.4	170.6	298.1±228.1	210.8±32.2

and the added carbon = 100%. Here, we assumed that the $^{13}C/(^{12}C + ^{13}C)$ value of the background samples and of the blank cups that were treated in the same manner as the sample cups were the same, because of distinctly lower values in comparison with the $^{13}C/(^{12}C + ^{13}C)$ values of labeled organic carbon. Thus, we can model the data using two sources: labeled organic carbon and others. Using this notation, we can directly compare the concentrations of labeled algae in samples from autumn and spring even though the absolute $\delta^{13}C$ values of the labeled algae were different. The assimilation of organic carbon by foraminifera was also estimated from the $^{13}C/(^{12}C + ^{13}C)$ data using the following calculation, where TOC = total organic carbon = biomass of foraminifera (Table 1, Web Appendix 1):

$$\text{Assimilated orgain carbon (mg C)} = \text{TOC}_{\text{foraminifera}}\ \text{(mg C)} \times \text{added carbon \%}$$

Some of the samples analyzed had a low organic carbon content compared with the blank cups and therefore yielded unreliable $\delta^{13}C$ data. We only used samples with more than twofold the organic carbon content of the blank samples. However, the assimilation rate of organic carbon is not as strongly affected by the blanks if we assume that the $\delta^{13}C$ values of the blank samples were almost the same as those of the background samples. Even though the sample amounts were low, high $\delta^{13}C$ values indicate that labeled algae were included in the analyzed samples. If the $\delta^{13}C$ values were low, the difference between the background $\delta^{13}C$ and the blank $\delta^{13}C$ values was largely responsible for the calculated amounts of assimilated carbon. Therefore, we calculated assimilation rates for all the data that showed sufficient organic carbon or high $\delta^{13}C$ values compared with the background data.

The assimilated organic carbon content of the metazoan animals was calculated both from the $\delta^{13}C$ values obtained from the in situ experiments and from the natural biomass values reported in previous Sagami Bay studies (Table 2; Shimanaga and Shirayama 2000). Assimilated organic carbon for harpacticoids were calculated with copepods biomass, and assimilated organic carbon for polychaetes and bivalves were calculated with others biomass.

Results

$\delta^{13}C$ in sediment—$\delta^{13}C$ values in the surface sediment, which directly reflect the amounts of added algae mixed into the sediment (food accessibility for the sediment community), changed in response to the input of algae (Fig. 1). Background sediments showed constant $\delta^{13}C$ values (about −20‰) throughout the sediment in both autumn and spring. In autumn, the $\delta^{13}C$ ratio rose to −5‰ in the top 0.5-cm layer 2 h after the addition of labeled algae (core A-2h), although one of the labeled algae syringes was not injected. In core A-2d-a, $\delta^{13}C$ values increased to 80‰ in the top 0.5 cm. Added algae were mixed to a depth of 1.5 to 2.0 cm within 2 d of incubation, and to a sediment depth of 4 to 5 cm within 4 d of incubation, while the $\delta^{13}C$ value at the sediment surface decreased to 2‰. In general, similar trends were observed in the spring, but the mixing of labeled carbon was more active (Fig. 1). Three hours after the algal release, labeled algae were already found down to a depth of 2 to 3 cm in the sediment. During the 2-d incubation, labeled algae mixed into the sediment at a depth of 4 to 5 cm in spring. Eleven days after feeding, maximum values of $\delta^{13}C$ (16‰) were observed at a depth of 1 to 1.5 cm, indicating that more organic carbon from the labeled algae was being transported into deeper layers.

Vertical foraminiferal distribution—Previous investigations in Sagami Bay described vertical microhabitat segregations in foraminiferal species (Ohga and Kitazato 1997; Nomaki unpubl. data). This vertical distribution pattern was

Table 2. Metazoan biomass (mg C m^{-2}) in the surface 0 to 5 cm of sediment observed in Sagami Bay through the year (Shimanaga and Shirayama 2000).

	Nematodes	Copepods	Others	Total metazoans
Biomass (mg C m^{-2})	61.8±22.9	101.1±38.9	76.5±31.0	239.5±72.3

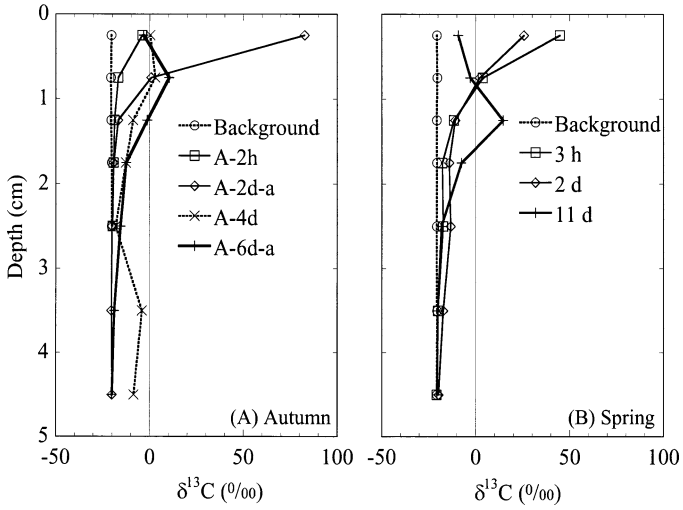

Fig. 1. Depth distribution of δ^{13}C of bulk total organic carbon within the sediment. (A) Autumn experiment (November 2001); (B) spring experiment (April 2002).

also observed in our incubation core sediments (Figs. 2 and 3). *U. akitaensis* and *B. aculeata* are categorized as shallow infaunal species and are abundant at sediment depths of between 0 to 2 cm. These species prefer fresh phytodetritus as a food source. *Bolivina spissa* is also categorized in this group (Web Appendix 1). *Bolivina pacifica* and *Textularia kattegatensis* are intermediate infaunal species, mainly found at sediment depths of between 1 cm and 3 cm, corresponding to the oxygen penetration depth (Nomaki unpubl. data). *Globobulimina affinis* and *C. ovoidea* are deep infaunal species, and can be found below 1 or 2 cm with a maximum in deeper layers.

Foraminifera δ^{13}C values—Changes in δ^{13}C values in foraminiferal cytoplasm clearly show ingestion of labeled algae during the incubation period (Figs. 2 and 3). In general, shallow infaunal species (*U. akitaensis, B. aculeata*) showed a rapid increase in abundance and higher values of δ^{13}C. Intermediate infaunal species (*T. kattegatensis* and *B. pacifica*) and deep infaunal species (*G. affinis* and *C. ovoidea*) showed a slower increase in δ^{13}C values and had lower δ^{13}C values in comparison with shallow infaunal species.

Autumn in situ experiment: B. aculeata was the most reactive species for the labeled algae supply. The δ^{13}C value of *B. aculeata* was about 850 ± 260‰ after 2 d of incubation and rose to 1,665‰ within 4 d in the 0- to 1-cm layer. *U. akitaensis* also exhibited a rapid uptake in δ^{13}C down to a depth of 3 cm within 4 d: δ^{13}C values were 282‰ in the upper 1 cm and 593‰ at a depth of 2 to 3 cm. *B. pacifica, T. kattegatensis,* and *G. affinis* showed a slight increase in δ^{13}C values (17‰, 3.5‰, and −18 ± 7‰ in the surface or 1 to 2 cm, respectively) within 2 d, but δ^{13}C values rose after 6 d of incubation to 463‰, 188 ± 133‰, and 579‰, respectively. *C. ovoidea* was the only species that did not show a distinct δ^{13}C increase during 2 d of incubation. Uptake was observed in the surface sediments after 6 d with a δ^{13}C value of 36 ± 10‰, but at a lower level than the other species.

Spring in situ experiment: B. aculeata and *U. akitaensis* showed quick responses to labeled food during the spring experiment. δ^{13}C values of *U. akitaensis* and *B. aculeata* in the surface layer were 883‰ and 1,078‰, respectively after 2 d of incubation. δ^{13}C values of *U. akitaensis* were about eightfold higher than those in the autumn experiment (117‰), whereas *B. aculeata* showed comparable δ^{13}C values. Even *U. akitaensis* living in the 4- to 5-cm layer apparently ingested labeled algae (42‰) after 2 d of incubation. δ^{13}C values for *T. kattegatensis* and *C. ovoidea* in the surface layer were lower than those of the sediment organic carbon (+25‰), at −3‰ and −17 ± 3‰, respectively. After 11 d of incubation, all the species at every depth interval, except for *B. aculeata* in the surface 1 cm, exhibited higher δ^{13}C values than after 2 d of incubation. *T. kattegatensis* clearly ingested more labeled algae after 11 d in the spring than during the autumn 6-d incubation. However, *C. ovoidea* was as inactive with respect to the labeled algae as in the autumn experiment.

Carbon concentrations originating from labeled algae—Figure 4 shows the amount of organic carbon originating from labeled algae as a percentage of the total foraminiferal biomass. These data indicate not only the rapid uptake rate but also the turnover rate of organic carbon in protoplasm. There were clear differences in labeled carbon concentrations derived from labeled algae from different microhabitats and species.

B. aculeata ingested labeled carbon rapidly, and labeled carbon concentrations in their bodies accounted for up to 16% ± 14% and 18% ± 10% after the 2-d incubation period in autumn and spring, respectively. After 6 d and 11 d, nearly one-third of their biomass was composed of labeled algal carbon (29% ± 17% at 6 d and 28% ± 4.9% at 11 d). *U. akitaensis* also showed high concentrations after 6 and 11 d of 22% ± 15% and 40% ± 8.8%, respectively. Concentrations after 2 d of incubation were also high in spring (16% ± 11%) but low in autumn (2.9% ± 1.9%). The concentration in *B. pacifica* also increased to 33% ± 4.5% after 11 d of incubation, but showed only a low level of labeling after 2 d of incubation. Marked carbon concentrations in other intermediate and deep infaunal species were low in comparison with those in *B. aculeata* and *U. akitaensis* after 2 d of incubation (approximately 0.5%). However, they increased consistently with time during the experiment in *B. pacifica, T. kattegatensis,* and *G. affinis,* although the rates were different for each species: 13% ± 7.4% of the *G. affinis* biomass and 5.3% ± 2.2% of the *T. kattegatensis* biomass originated from labeled algae after 11 d of incubation. For *C. ovoidea,* the labeled carbon concentration was less than 1% during the entire experimental period. In total, after 6 d and 11 d of incubation, the labeled algal uptake was responsible for 6.4% ± 5.7% and 15% ± 2.8%, respectively, of the foraminiferal biomass.

Comparing the spring and autumn data after 2 d of incubation, seasonal variations in uptake were observed in *U. akitaensis* and *B. pacifica.* Markedly high labeled carbon concentrations were found in spring (16% ± 11% in spring vs. 2.9% ± 1.9% in autumn for *U. akitaensis*; 5.3% ± 0.1% in spring and 0.7% ± 0.4% in autumn for *B. pacifica*).

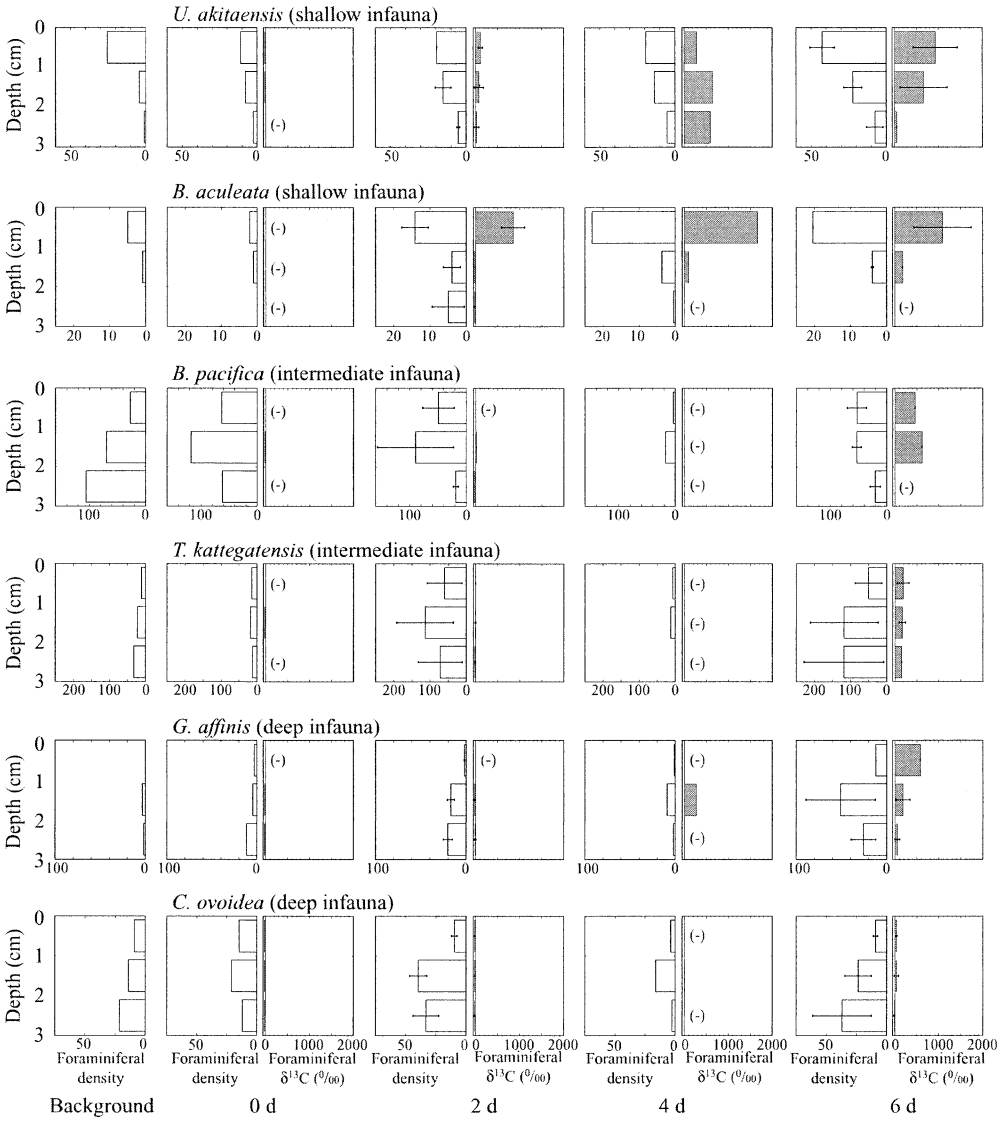

Fig. 2. $\delta^{13}C$ values in foraminiferal biomass for six dominant species in the autumn in situ experiment. (-) indicates that organic carbon content of the sample was lower than twofold the organic carbon content of the blank samples. See method for further explanation.

Total assimilated organic carbon—The amounts of assimilated organic carbon differed between species and seasons and consistently increased over time during the incubation periods (Table 3, Fig. 5). For the comparison between autumn and spring data directly, assimilated carbon was represented for the total of 0 to 3 cm sediment depth. In autumn, 2.0 ± 1.3 mg m^{-2} of organic carbon was ingested by the total foraminiferal assemblage within 2 d. By day 6, a total of 15 ± 4.6 mg m^{-2} of organic carbon, corresponding to up to 2% of the added algae, was assimilated by the total foraminiferal assemblage. Both *U. akitaensis* and *B. aculeata* ingested large amounts (7.2 ± 2.4 mg m^{-2} and 1.7 ± 0.4 mg m^{-2}, respectively) of organic carbon. In addition to these two shallow infaunal species, the deep infaunal *G. affinis* ingested 2.9 ± 0.7 mg m^{-2} of labeled carbon. Other foraminiferal species also showed higher uptakes by day 6, although they were low in comparison with those of *U. akitaensis*, *B. aculeata*, and *G. affinis*, and therefore are not visible on the scale used in Fig. 5.

In spring, a total of 5.8 ± 4.8 mg m^{-2} C was assimilated by benthic foraminifera after 2 d of incubation. *G. affinis* (deep infauna) showed the highest assimilation of organic carbon (2.1 ± 2.0 mg m^{-2}) after 2 d. Among shallow infaunal species, *U. akitaensis* and *B. aculeata* also assimilated large amounts of labeled organic carbon in this time period (1.9 ± 1.4 mg m^{-2} and 0.8 ± 0.7 mg m^{-2}, respectively). After 11 d of incubation, a total of 31 ± 13 mg m^{-2} C, corresponding to up to 4% of the added algae, was ingested by benthic foraminifera. More than half of the assimilated carbon was taken up by *U. akitaensis* and *G. affinis*, since

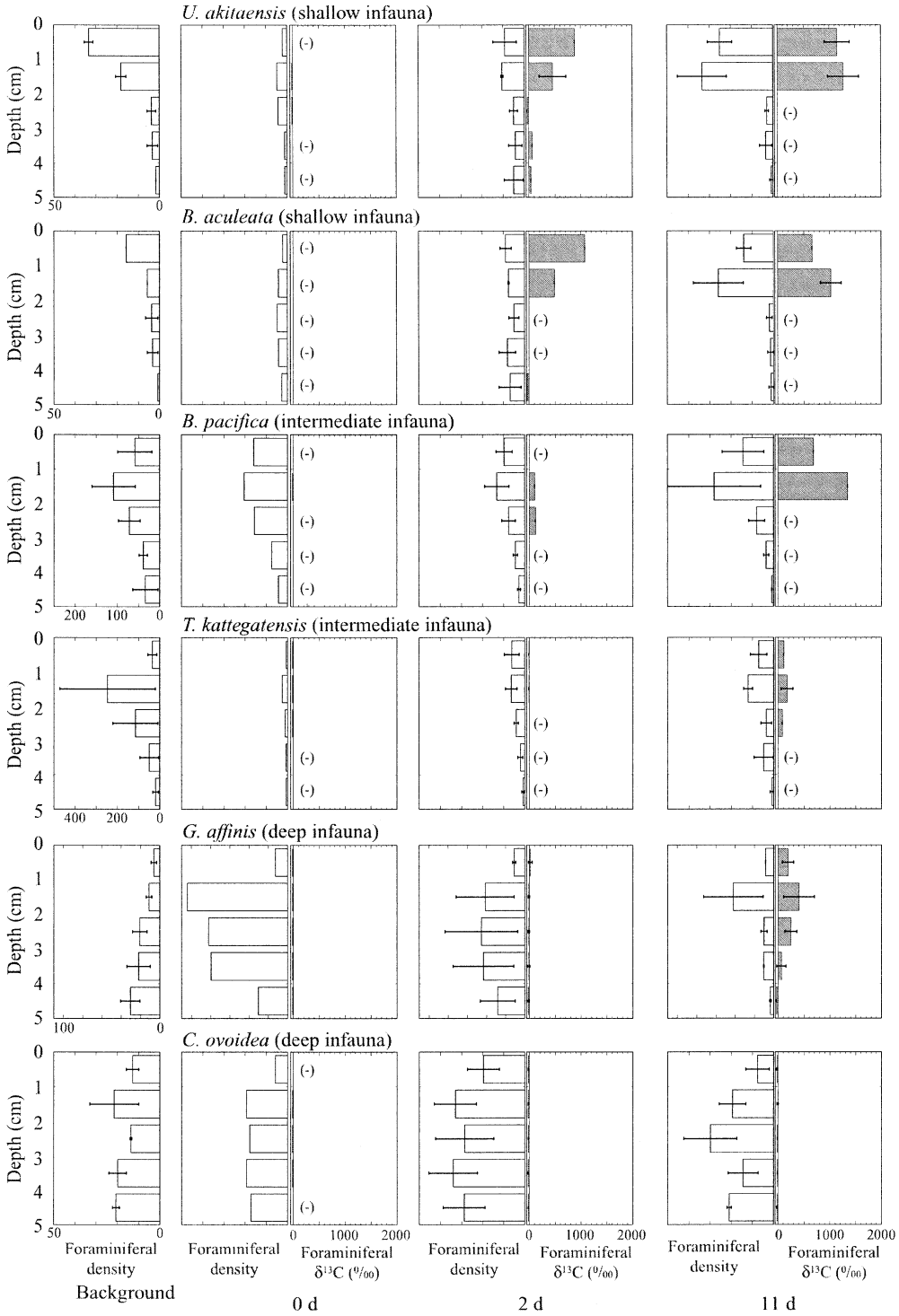

Fig. 3. δ^{13}C values in foraminiferal biomass for six dominant species in the spring in situ experiment. (-) indicates that organic carbon content of the sample was lower than twofold the organic carbon content of the blank samples. See method further explanation.

each species assimilated 11 ± 5.1 mg m^{-2} C and 6.8 ± 2.3 mg m^{-2} C, respectively.

Metazoan δ^{13}C and carbon assimilation—Metazoan meiofauna and macrofauna did not exhibit large changes in cytoplasmic δ^{13}C values in either autumn or spring (Web Appendix 2 at http://www.aslo.org/lo/toc/vol_50/issue_1/0134a2.pdf). In autumn, only harpacticoids in the surface 1-cm layer on day 2 showed somewhat higher values (18‰), although these changes were quite small compared to those

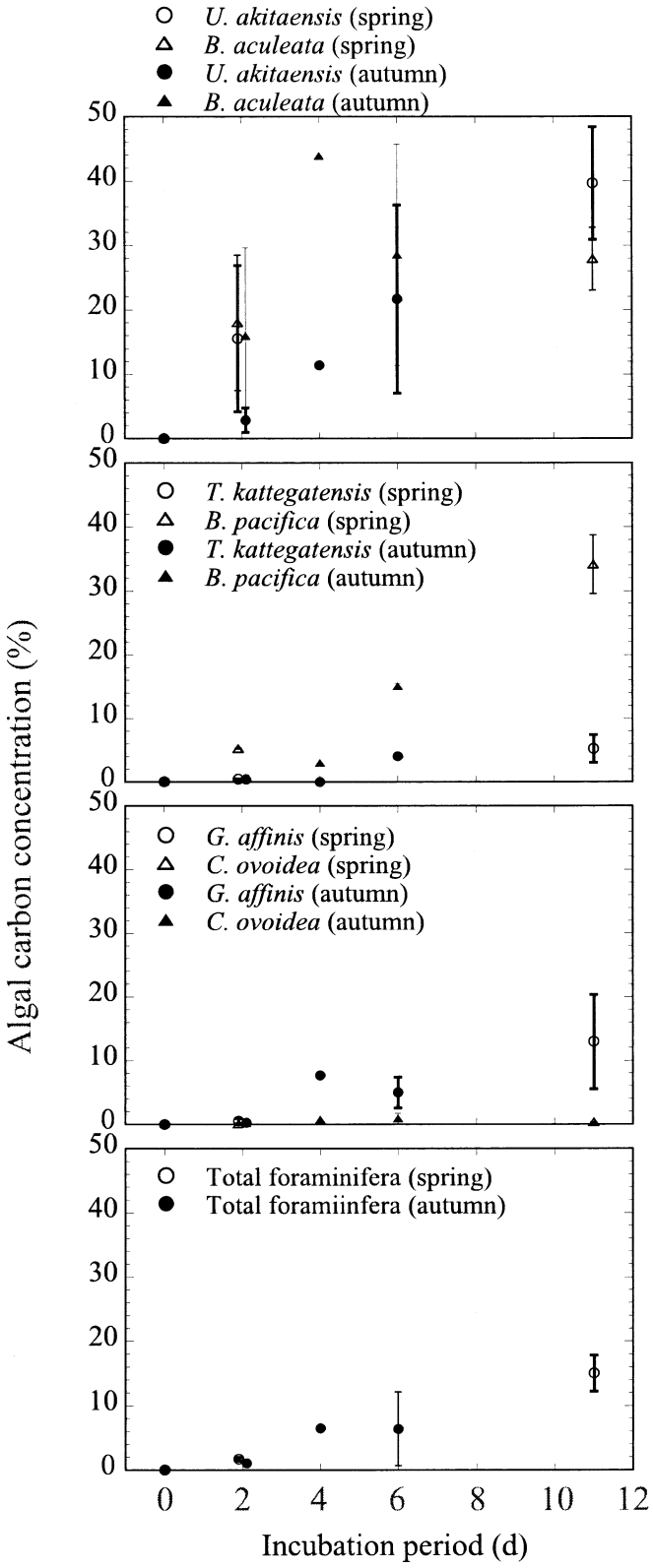

Fig. 4. Contribution of added carbon to foraminiferal biomass with time. Data for two shallow infaunal species (*U. akitaensis, B. aculeate*), two intermediate infaunal species (*T. kattegatensis, B. pacifica*), two deep infaunal species (*G. affinis, C. ovoidea*), and the total foraminiferal fauna are shown.

in foraminifera. The $\delta^{13}C$ values of other metazoan species, for example, nematodes, polychaetes, copepods, and bivalves, ranged between −10‰ to −30‰ and showed no distinct difference in comparison with the background sediment. In spring, clear increases in $\delta^{13}C$ were observed in polychaetes (64‰) and harpacticoids (62‰) in the surface sediment on day 2. These were comparable to the $\delta^{13}C$ values of the surface sediment on day 2. No increased values were measured after 11 d.

Total metazoan meiofauna and macrofauna exhibited lower carbon assimilation (1.5 ± 0.4 mg m^{-2} in spring and 0.4 ± 0.1 mg m^{-2} in autumn) than foraminifera (Fig. 5), although they had comparable biomass in Sagami Bay (Tables 1 and 2).

Discussion

Experimental limitations—In Sagami Bay, there is a sharp spring peak in the flux of chlorophyll *a* transported from the ocean surface to the seafloor (Nakatsuka et al. 2003). In our experiment, labeled unicellular algae (*D. tertiolecta*, which is absent from Sagami Bay) were added to simulate the sinking of organic carbon. In our other ^{13}C-labeling experiment, the response of foraminifera to *D. tertiolecta* was mostly comparable to *Chaetoceros sociale*, which is a common alga in this area (Nomaki, unpubl. data). However, as the experimental period progressed, the source of the labeled carbon became increasingly unclear. Moodley et al. (2002) indicated that the labeled algal carbon used in their experiments was incorporated and degraded by bacteria within 35 h. The same process must have occurred in our experiments, making it uncertain whether the increases in $\delta^{13}C$ reflected direct ingestion of algae, bacteria, or degraded organic matter, especially after 11 d. Thus, our data may not reflect the actual ingestion of phytoplankton on the seafloor. However, they do illustrate the fate of organic carbon contained in phytoplankton on the seafloor. The protoplasmic color change to green in several incubated specimens indicates the uptake of algal material, for example, Chl *a* (Kitazato et al. 2003*a*).

Foraminiferal biomass was markedly different among all core samples (Table 1). These differences were mainly caused by the heterogeneity of the benthic foraminiferal abundance in the sediment. Our incubation core was relatively small (5 cm in diameter) to obtain common biomass data on benthic foraminifera. However, heterogeneity was covered to a certain extent with replicates, and the reactions to algal carbon were similar in replicate cores. This indicates that species responses to simulated phytodetritus were well represented by the small amount of sediment samples, although the foraminiferal abundance was not constant among core samples.

Different responses to sinking organic carbon by foraminiferal species—The responses of deep-sea benthic foraminifera to the addition of organic material varied from species to species and in relation to microhabitat preferences. For example, the shallow infauna *U. akitaensis* and *B. aculeata* showed high labeled carbon concentrations in comparison with most intermediate and deep infaunal species (Fig. 4). Kitazato and Ohga (1995) carried out laboratory feeding

Table 3. Assimilated carbon by benthic foraminifera (mg C m^{-2}, sum of 0–3 cm sediment depth) calculated from biomass and $\delta^{13}C$ data. Data for the 0–5 cm sediment depth are also presented for the spring experiment.

	Autumn			Spring			
Species	A-2d-a, b	A-4d	A-6d-a, b	S-2d-a, b	(0–5cm)	S-11d-a, b	(0–5 cm)
Uvigerina akitaensis	0.88±0.56	2.49	7.15±2.36	1.88±1.43	1.99±1.30	11.06±5.05	11.07±5.03
Bulimina aculeata	0.57±0.38	1.90	1.74±0.44	0.78±0.70	0.78±0.70	1.94±0.84	1.94±0.84
Bolivina spissa	0.03±0.03	0.10	0.51±0.27	0.13±0.08	0.13±0.08	0.88±0.48	0.88±0.48
Bolivina pacifica	0.03±0.01	0.05	0.43±0.08	0.25±0.15	0.25±0.15	2.07±1.50	2.08±1.50
Textularia kattegatensis	0.03±0.01	0.00	0.27±0.07	0.02±0.00	0.02±0.00	0.59±0.42	0.59±0.42
Globobulimina affinis	0.05±0.02	0.16	2.86±0.70	2.05±2.01	3.63±3.51	6.83±2.31	7.02±2.37
Chilostomella ovoidea	0.03±0.01	0.02	0.08±0.04	0.01±0.01	0.01±0.01	0.05±0.03	0.06±0.04
Cyclammina cancellata	0.13±0.13	0.04	0.40±0.24	0.03±0.02	0.03±0.02	0.30±0.26	0.30±0.26
Other	0.23±0.12	0.44	1.66±0.11	0.60±0.34	0.79±0.53	7.33±1.62	7.44±1.63
Total	1.99±1.26	5.20	15.09±4.64	5.76±4.75	7.60±6.21	31.04±12.51	31.38±12.57

experiments and found that deep infaunal species apparently prefer to ingest altered food. Rudnick (1989) conducted feeding experiments involving metazoan meiobenthos and reported that the time necessary for food assimilation differed between surface-living meiobenthos and sediment-dwelling meiobenthos. Olafsson et al. (1999) also reported different rates of food assimilation of labeled carbon among some benthic meiofauna. They speculated that these differences may be caused by vertical microhabitat distribution. In our experiments, we observed that shallow infaunal species ingested labeled carbon more rapidly than intermediate and deep infaunal species. These results coincide with the results of Rudnick (1989) and Olafsson et al. (1999). However, it is difficult to determine why the deep-dwelling species ingested deposited food more slowly. Is it because they are in deeper layers and need more time to reach the food? Or are they unable to react as quickly even if sufficient food is present because of their food preference?

Our investigations showed that within one vertical microhabitat, there were clear variations in response from species to species. It may indicate that not only vertical microhabitat segregation, but also food preferences of each species influences more to their carbon assimilation. Two of the three shallow infaunal species studied, *B. aculeata* and *U. akitaensis,* showed rapid ingestion of labeled algae in comparison with most intermediate or deep infaunal species. But another shallow infaunal species, *B. spissa,* had an ingestion rate similar to that of *B. pacifica,* an intermediate infaunal species. Another intermediate infaunal species, *T. kattegatensis,* exhibited ingestion rates that were even lower than those of deep infaunal species such as *G. affinis.* The two deep infaunal species, *G. affinis* and *C. ovoidea,* showed diverse responses to added algae. *C. ovoidea* rarely assimilated algae in either autumn or spring. In contrast, *G. affinis* clearly assimilated algae during both sets of in situ culture experiments (autumn and spring). This trend coincides well with the results of laboratory culture experiments (Nomaki unpubl. data). These two species may have different life habits or food preferences, even though they show similar habitat segregation patterns within the sediment. Different scales and timing of responses to labeled algae were probably controlled by food preferences in each species. In addition, these food preferences seem to affect their vertical microhabitat in the sediment. These different types of responses to freshly sedimented organic matter are important for our understanding of the trophic structure of benthic organisms within the sediment.

The mixing of labeled algae deep into the sediment (food availability) must also be considered when discussing different responses to food material in different sediment layers. Changes in food availability with sediment depth probably affect the ingestion of food by benthic foraminifera. There are clear differences in foraminiferal protoplasmic $\delta^{13}C$ values in cells from different sediment depths collected on the same day for the same species. After 11 d of incubation in spring, the highest $\delta^{13}C$ values were obtained for *G. affinis, B. aculeata,* and *T. kattegatensis* at a depth of 1 to 2 cm, where the organic carbon in the sediment also showed the highest $\delta^{13}C$ values (compare Fig. 1 and Fig. 3). In autumn, higher assimilation rates of labeled carbon occurred in the surface 1-cm layer in *B. aculeata* rather than in deeper sediment. The amount of labeled carbon available within each layer influenced the concentration of labeled carbon in the foraminiferal cells.

However, differences between species, probably caused by variable food preferences, are still more important for the variability. Shallow infaunal species (*U. akitaensis* and *B. aculeata*) ingested larger amounts of labeled carbon than intermediate or deep infaunal species living at the same sediment depth, especially during short incubations (e.g., surface sediment on day 2 core samples in spring). *B. pacifica, T. kattegatensis, G. affinis,* and *C. ovoidea* from a depth of 0 to 2 cm had lower $\delta^{13}C$ values, although the concentration of labeled carbon (food availability) in the sediment was the same as for the shallow infaunal species. Moreover, *U. akitaensis* at a sediment depth of 4 to 5 cm exhibited higher $\delta^{13}C$ values than other deep-dwelling species. These differences were not caused by food availability in the sediment, but probably by different species food preferences or response times to fresh organic matter. We conclude that assimilation rates varied first with foraminiferal behavior in reaction to fresh organic matter, and then with food availability in different sediment layers, as caused by mixing.

Genus *Uvigerina* and *Bulimina* are found in eutrophic conditions in recent assemblages (Loubere and Fariduddin 1999; Fontanier et al. 2003) and are thought to be indicator

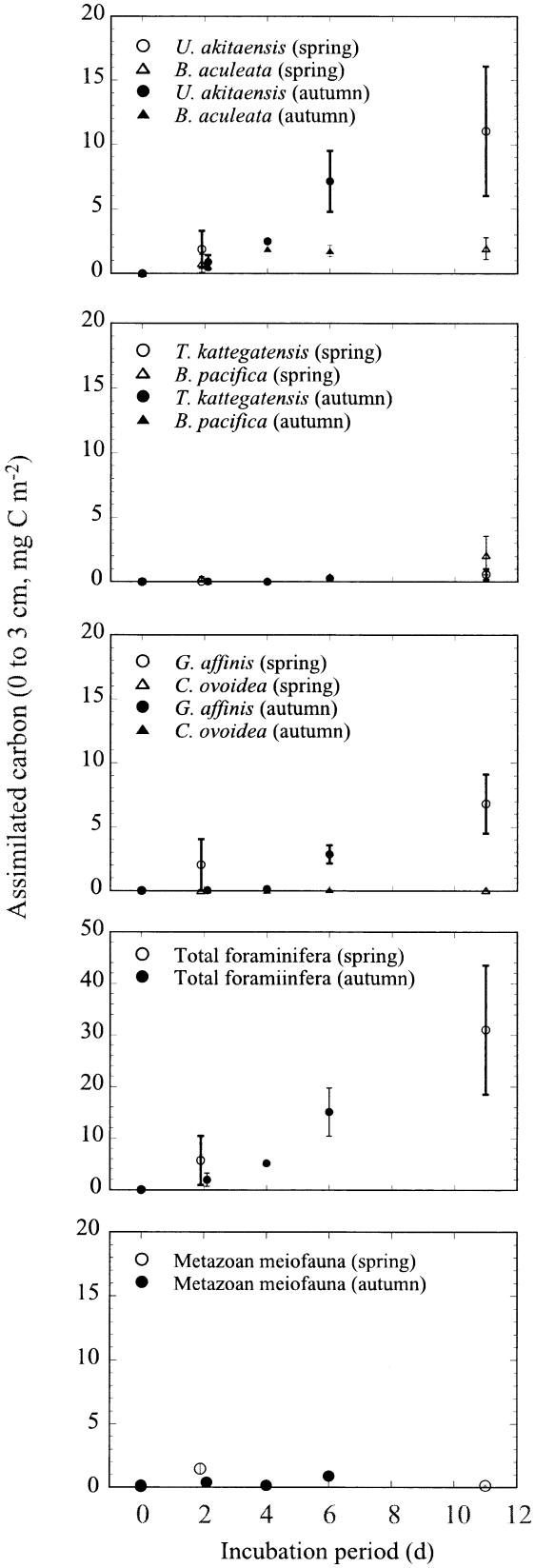

Fig. 5. Carbon assimilation by foraminifera and metazoans after different incubation times. Data for two shallow infaunal species, two intermediate infaunal species, two deep infaunal species, total foraminiferal fauna, and total metazoan data are shown.

species for eutrophic conditions both in recent and paleoenvironment investigations. This is accordance with our results that *U. akitaensis* and *B. aculeata* quickly reacted to algal deposition. They may dominate in high productivity areas because they mostly utilize freshly delivered phytodetritus, and are useful indicators for eutrophic environment.

The ecology of *Globobulimina* and its role in benthic trophic nets is still poorly understood. Some authors group *Globobulimina* in high productivity assemblages (Loubere 1984; Fariduddin and Loubere 1997; Loubere and Fariduddin 1999). Others report that its bathymetric distribution is not influenced by downward organic flux (De Rijk et al. 2000). It is not clear which kind of food *Globobulimina* can use. It was described that this species not obviously ingests phytodetritus such as diatoms but is a deposit feeder that prefers sediment particles (Goldstein and Corliss 1994). Kitazato and Ohga (1995) showed in culture experiments the preference of *Globobulimina* individuals for dried algae compared to fresh algae. Because it belongs to the deep infauna, it was proposed that they may feed on bacterial consortia that concentrate around deep redox fronts or they may use slowly degraded resistant organic matter buried in deeper sediment layers (Jorissen et al. 1998; Fontanier et al. 2002). Fontanier et al. (2002) suggest that *Globobulimina* is not able to compete for labile food particles with very opportunistic taxa living in superficial sediment layers. They described *Nonion scaphum* and *C. oolina* as very opportunistic. All these statements are in contrast to our results where we can show that *Globobulimina* can quickly respond to fresh labile organic matter, whereas *Chilostomella* is not ingesting fresh food.

Are there seasonal differences in the foraminiferal response to food pulses?—We performed in situ carbon uptake experiments in autumn and spring to explore seasonal variations in organic carbon consumption. We suspected that foraminiferal responses to sedimented organic carbon could differ in different seasons. There were some seasonal differences in our experimental results, indicating that more active carbon consumption occurred in spring. The first difference was food mixing within the sediment. The depth at which food materials existed was deeper in spring compared with autumn on the same time scale. We cannot clearly distinguish sediment mixing from eventual transport via burrowing tubes based on the $\delta^{13}C$ data (high $\delta^{13}C$ values in deeper layers on day 4 in autumn are assumed to be due to transport via burrows). Food availability within the sediment resulting from both mixing and transportation differed between seasons.

The second difference was more rapid uptake of labeled carbon in spring by *U. akitaensis* and *B. pacifica* at 2 d of incubation. The $\delta^{13}C$ values of *U. akitaensis* and *B. pacifica* were eight- and sixfold higher in spring than in autumn, respectively. Other species showed no clear differences in the uptake of labeled algae. *U. akitaensis* and *B. pacifica* may have a distinct seasonality in their metabolism. However, their total abundance in Sagami Bay did not show as much clear seasonality in comparison with the other species (Ohga and Kitazato 1997). This suggests that metabolic seasonality is not directly related to the seasonal abundance of foraminifera.

The third difference was higher carbon assimilation in spring. Not only *U. akitaensis* and *B. pacifica,* which showed high labeled carbon concentrations, but also *G. affinis* assimilated larger amounts of labeled carbon within 2 d in spring. Total carbon assimilation is therefore higher in spring (5.8 ± 4.8 mg m^{-2}) than in autumn (2.0 ± 1.3 mg m^{-2}) after 2 d.

Metazoan meiofauna and macrofauna also showed higher carbon uptake as represented by that of $\delta^{13}C$ in spring, e.g., polychaetes (64‰) and harpacticoids (62‰) on day 2, whereas in autumn, a distinct $\delta^{13}C$ increase above the background level was only found in harpacticoids (18‰). As a result, carbon assimilated by total metazoans was high in spring (1.5 ± 0.4 mg m^{-2}) compared with autumn (0.4 ± 0.1 mg m^{-2}).

To summarize our observations, in spring, deposited carbon is rapidly transported into the deeper part of the sediment by bioturbation and is quickly available to deep-dwelling animals. Some foraminiferal species and metazoans may have higher metabolisms and show higher uptake of deposited food. In total, the benthic community assimilated more carbon in spring than in autumn.

Importance of benthic foraminifera in deep-sea carbon cycling—In our experiments, benthic foraminifera responded to deposited organic matter within 2 d (Figs. 2–5). In particular, *B. aculeata* and *U. akitaensis* ingested high amounts of labeled material in relation to their body size. It has already been suggested that benthic foraminifera quickly reacted organic matter when it is deposited on the seafloor (Gooday 1988; Drazen et al. 1998). Rapid ingestion of organic carbon by benthic foraminifera was also reported by Moodley et al. (2000, 2002) using ^{13}C-labeled algae. Moodley et al. (2002) proposed that benthic foraminifera play an important role in carbon processing comparable to bacteria on the deep seafloor, even though the foraminiferal biomass is substantially less than the bacterial biomass. According to the results of Moodley et al. (2002), total benthic communities processed up to 6 mg m^{-2} (1.4% of added carbon) within 35 h, including carbon respired as CO_2, off the northwest coast of Spain, at a water depth of 2,170 m. In our experiments, total carbon assimilation by benthic foraminifera accounted for 2.0 ± 1.3 to 5.8 ± 4.8 mg m^{-2} (up to 1% of added carbon) within 2 d, which coincides well with the figure of Moodley et al. (2002). Respired carbon as CO_2 and carbon that escaped were not included in our data, although respired carbon makes up a large portion (45%) of total processed carbon (Moodley et al. 2002). When these pathways are included, approximately up to 20 mg m^{-2} of organic carbon (2% of added carbon) was processed by benthic foraminifera alone. Because they quickly ingest considerable amounts of fresh phytodetritus into their cells, benthic foraminifera must play an important role in the early decomposition of sinking organic carbon on continental slopes. The retarded response of benthic foraminifera in an abyssal area in the northeast Atlantic (Witte et al. 2003) can be explained by the difference in species composition between the two study areas. Rapidly reacting species, such as *U. akitaensis* or *B. aculeata* in Sagami Bay, were not abundant in the abyssal area studied. Additionally, the northeast Atlantic is a very oligotrophic area, and the addition of food may first lead to the time-consuming activation of metabolism, which is not the case in Sagami Bay, which has high trophic conditions throughout the year. Different water depths (1,450 m to 4,800 m) may also cause a lag in the response to organic carbon, since benthic foraminiferal metabolism may decrease with water depth. We found species-specific reactions to organic carbon input and its seasonal variation. More studies are necessary to clarify what determines the reactions to organic carbon uptake, such as water depth, oxygen concentration, or the composition of organic matter.

In contrast to benthic foraminifera, metazoan meiofauna and macrofauna did not assimilate large amounts of labeled carbon in our experiments (Fig. 5). Only harpacticoids (in autumn) and harpacticoids and polychaetes (in spring) showed higher values of $\delta^{13}C$ after 2 d, but the changes were very small compared with those in the foraminiferal samples. One of the reasons may be that the small metazoans analyzed in this study have different food preferences compared with the foraminifera. Deep-sea benthic foraminifera are known to ingest algae originating from the ocean surface quickly (Gooday 1988; Moodley et al. 2002) and are, therefore, presumably herbivores, which can utilize sedimented algae directly. However, metazoan meiofaunal taxa show varieties of food preferences. Metazoan organisms were highly enriched by labeled organic carbon compared to benthic foraminifera during long-term experiments (Rudnick 1989; Widbom and Frithsen 1995; Aberle and Witte 2003). Widbom and Frithsen (1995) reported that suspension feeders and surface deposit feeders showed high amounts of ^{14}C-labeled organic carbon in comparison with scavengers and subsurface deposit feeders at shallow water area. In our experiments, all animals were combined into higher taxa. Although the water depth was totally different from Widbom and Frithsen (1995), species-specific response to phytodetritus may occur in our studied area like foraminiferal responses. Species-level analyses are needed to document fully the metazoan response to organic carbon deposition.

Although metazoan macrofauna did not assimilate large amounts of organic carbon in our study, some previous studies showed that metazoan macrofauna play an important role in carbon cycling on the deep seafloor as both consumers and transporters of organic materials (Levin et al. 1997, 1999; Witte et al. 2003). In our study, rapid mixing of labeled carbon could be seen in the $\delta^{13}C$ sediment data. On day 4 of the autumn experiment, two subsurface peaks of $\delta^{13}C$ were recognized at sediment depths of 0.5 to 1.0 and 3 to 4 cm. The higher peak in $\delta^{13}C$ may be the result of macrofaunal disturbance of the sediment, such as polychaete tubes. Burrows of metazoan macrofauna transport organic material into the sediment, and their motions also mix organic material in the sediment. They are an important component in the primitive decomposition of organic matter in the sediment surface and its mixing into the deep parts of the sediment, which enables organisms living deeper in the sediment like foraminifera to respond quickly to fresh organic matter.

We concluded our study as following four points: (1) Benthic foraminifera assimilated 5.8 ± 4.8 mg m^{-2} of labeled carbon within 2 d and 31 ± 13 mg m^{-2} within 11 d in spring.

Deep-sea benthic foraminifera can thus utilize large amounts of labile organic carbon on the time scale of 1 d. (2) Benthic foraminiferal responses to supplied algae varied between species. *B. aculeata* and *U. akitaensis* were the most responsive species. Intermediate infaunal species and deep infaunal species such as *B. pacifica* and *G. affinis* also ingested significant amounts of labeled algae. However, the deep infaunal species *C. ovoidea* ingested only small amounts of labeled algae. These different responses may reflect contrasting food preferences, not only food availability in the sediment. These different food preferences may have been recorded in the foraminiferal fossil record as proxies for paleoproductivity. (3) Active carbon consumption occurred in spring, when seasonal organic carbon sedimentation is observed. In spring, deposited carbon was rapidly transported into deeper parts of the sediment by bioturbation and was quickly available to deep-dwelling animals. Benthic foraminifera and some metazoan meiofauna assimilated more carbon in spring than in autumn. Benthic activity has some relation to seasonal carbon deposition in Sagami Bay. (4) Carbon assimilation was higher in benthic foraminifera than in metazoan meiofauna in this area. Benthic foraminifera probably play a more important role in the short-term processing of carbon on the deep seafloor than metazoans of similar size.

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