Experimental *in-situ* phytodetritus pulses: response and assemblage of benthic deep-sea foraminifera

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät

der Eberhard Karls Universität Tübingen

zur Erlangung des Grades eines Doktors der Naturwissenschaften

(Dr. rer. nat.)

vorgelegt von

Annekatrin Julie Enge

aus Berlin

Tübingen

2012

Tag der mündlichen Qualifikation:	26.10.2012
Dekan:	Prof. Dr. Wolfgang Rosenstiel
1. Berichterstatter:	PD Dr. Petra Heinz
2. Berichterstatter:	Prof. Dr. Michal Kucera

TABLE OF CONTENTS

Author's contribution to the publications 1-3 iii

Abstract v

Zusammenfassung vii

Introduction 1

1 Benthic foraminifera 1

2 Foraminiferal assemblages in marine environments 2

3 Food availability in the deep sea 4

4 Response to phytodetritus by deep-sea foraminifera 7

5 Isotope labeling experiments 11

6 Findings of previous *in-situ* feeding experiments in the deep sea 14

Focus of included research papers 17

Conclusions and outlook 22

References 27

Acknowledgments 35

Publication 1: Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific

Publication 2: Diversity and microhabitats of living benthic foraminifera in the abyssal Northeast Pacific

Publication 3: Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin

AUTHOR'S CONTRIBUTION TO THE PUBLICATIONS 1-3

1. *Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific.*
Annekatrin J. Enge, Hidetaka Nomaki, Nanako O. Ogawa, Ursula Witte, Markus M. Moeseneder, Gaute Lavik, Naohiko Ohkouchi, Hiroshi Kitazato, Michal Kucera, Petra Heinz, (2011). Marine Ecology-Progress Series 438, 129-142.

Own contributions:	
Scientific ideas:	30 %
Data generation:	80 %
Analysis and interpretation:	80 %
Paper writing:	85 %

2. *Diversity and microhabitat preferences of benthic foraminifera in the abyssal Northeast Pacific*.
Annekatrin J. Enge, Michal Kucera, Petra Heinz, (2012). Marine Micropaleontology 96-97, 84-104.

Scientific ideas:	80 %
Data generation:	90 %
Analysis and interpretation:	90 %
Paper writing:	90 %

3. *Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin*.
Annekatrin J. Enge, Ursula Witte, Michal Kucera, Petra Heinz. To be submitted to Biogeoscienes.

Scientific ideas:	30 %
Data generation:	90 %
Analysis and interpretation:	90 %
Paper writing:	90 %

ABSTRACT

Foraminifera are an important component of the benthic deep-sea fauna and their distribution and occurrence is mainly controlled by the availability of food and the oxygen content in the water. Most deep-sea foraminifera depend on organic matter as food source which was produced in the photic zone of the oceans and has sunk to the sea floor. Because the flux of organic matter decreases with water depths, the availability of food is higher at bathyal depths than in the abyssal environment. Thus, food is generally the limiting factor for abyssal foraminifera. The flux of organic matter also varies throughout the year due to the seasonality in the primary production. This is especially present at temperate zones where furthermore the deposition of fresh phytodetritus at the sea floor can be observed, a result of strong spring productivity. Fresh phytodetritus is only temporarily available to foraminifera, but can strongly influence the distribution and abundances of foraminiferal species. However, investigations are limited and knowledge about the role of foraminifera in the remineralization process of phytodetritus in deep-sea sediments is very scarce.

For this reason, we performed *in-situ* feeding experiments on foraminifera in the Northeast Pacific (3985 m) as well as in the Arabian Sea at the Indian Margin (540 m). To simulate a phytodetritus sedimentation event, algal material was injected onto a defined sediment area directly at the sea floor to allow feeding by foraminifera for four days. Prior the experiment, algae were labeled with stable isotopes (^{13}C, ^{15}N) to allow the tracking of food and the estimation of uptake rates for the foraminifera. In addition, the assemblages of living foraminifera at the two deep-sea sites were investigated on species composition, distribution and abundances.

The assemblage of living foraminifera as well as their reaction towards the presence of phytodetritus varied strong between the two deep-sea sites, and can be related to the very different environmental conditions and the adaptation of foraminifera. The investigation site in the abyssal North Pacific is characterized by low flux of organic matter and oxic conditions. The foraminiferal assemblage is very diverse, and is dominated by soft-walled and agglutinated species. The very quick response which is comparable in magnitude to other abyssal sites shows their ability to immediately utilize available food in an environment of food limitation. This suggests that foraminifera are important to short-term carbon cycling in this environment. A very different picture of foraminiferal response to phytodetritus was obtained from the experiment in the oxygen minimum zone in the Arabian Sea. The assemblage of foraminifera at this site of almost anoxic and very eutroph conditions is characterized by a low species diversity due to the dominance of few calcareous species which show very high population densities. The response to the phytodetritus was very high in comparison to earlier investigations in eutroph environments and varied strong between the different foraminiferal species. The high population densities and uptake as well as the absence of macrofauna at this water depth suggest that foraminifera play a very important role in deep-sea carbon cycling under almost anoxic conditions.

ZUSAMMENFASSUNG

Foraminiferen sind ein wichtiger Bestandteil der benthischen Tiefseefauna und ihre Verteilung ist besonders abhängig vom Nahrungsangebot und Sauerstoffgehalt. Der Hauptteil der Nahrung von Tiefseeforaminiferen besteht aus organischem Material, welches in den lichtdurchfluteten Ozeanbereichen durch Primärproduktion gebildet wurde und auf den Meeresboden herabgesunken ist. Durch die Abnahme des Flusses an organischem Material mit Tiefe ist die Nahrungszufuhr in den bathyalen Meerestiefen größer als im abyssalen Bereich. Somit kann die Nahrungsverfügbarkeit für abyssale Foraminiferengesellschaften zum limitierenden Faktoren werden. Aufgrund jahreszeitlich bedingter Schwankungen in der Oberflächenprimärproduktion ist auch der Fluss an organischem Material in der Tiefsee stark saisonal geprägt, besonders in den gemäßigten Breiten, wo es zu bestimmten Zeitpunkten zudem zum Auftreten von frischem Phytodetritus am Meeresboden kommen kann. Solch ein zeitlich begrenztes Ereignis folgt meist dem Frühlingsproduktivitätsmaximum und kann die Verteilungs- und Populationsmuster von Tiefseeforaminiferen beeinflussen. Jedoch ist der derzeitige Wissensstand über die Rolle von Foraminiferen bei der Umsetzung von frischem Phytodetritus in Tiefseesedimenten und ihre generelle Rolle im Kohlenstoffkreislauf der Tiefsee sehr begrenzt.

Aus diesem Grund wurden zwei Fraßexperimente mit Foraminiferen im bathyalen Arabischen Meer (540 m) und im abyssalen Nordpazifik (3985 m) *in-situ* durchgeführt. Zur Simulation der impulsartigen Ablagerung von Phytodetritus wurde Algenmaterial für eine Dauer von vier Tagen auf eine definierte Sedimentoberfläche ausgebracht und somit den im Sediment lebenden Foraminiferen zum Fraß angeboten. Die vorangegangene Markierung des Algenmaterials mit stabilen Isotopen (^{13}C, ^{15}N) erlaubt die Verfolgung der Nahrung und die Berechnung von Aufnahmeraten für Foraminiferen. Außerdem wurden die Foraminiferengesellschaften auf ihre Zusammensetzung, vertikale Verteilgung und auf die Häufigkeiten der Arten untersucht.

Die Lebendvergesellschaftungen der Foraminiferen sowie deren Reaktion auf das Vorhandensein von Nahrung weisen große Unterschiede zwischen den beiden untersuchten Tiefseegebieten auf, welche sich auf die sehr andersartigen Umweltbedingen und Anpassungen der Foraminiferen zurückführen lassen. Die Station im abyssalen Nordpazifik zeichnet sich durch eine geringe Nahrungszufuhr und oxische Bedingungen aus. Die Foraminiferenfauna ist sehr artenreich, und wird von kleinen weichschaligen und agglutinierten Arten dominiert, wohingegen Kalkschaler kaum eine Rolle spielen. Die rasche Aufnahme des Phytodetritus, welche im Vergleich zu anderen Meeresgebieten gering war, weist auf die Anpassung der Foraminiferen an Nahrungsknappheit sowie ihre Fähigkeit, potentielle Nahrungsquellen sofortig zu nutzen. Daher sind Foraminiferen in diesem Tiefseehabitat wichtig im kurzzeitigen Kohlenstoffumsatz, zudem ihre Aufnahme an Phytodetritus höher ist die Aufnahme der Makrofauna. Im Gegensatz dazu ist das Untersuchungsgebiet innerhalb der Sauerstoffminimumzone des Arabischen Meeres durch sehr starken Sauerstoffmangel und hohe Nahrungszufuhr gekennzeichnet. Die Foraminiferenvergesellschaftung ist gekennzeichnet durch eine geringe Diversität und die sehr große Häufigkeit weniger kalkschaliger Arten. Die Aufnahme von Phytodetritus war sehr hoch im Vergleich zu anderen Experimenten und zeigte sehr starke Unterschiede zwischen den Arten. Die hohe Populationsdichte und Nahrungsaufnahme sowie die Abwesenheit der Makrofauna in dieser Wassertiefe weisen darauf hin, dass Foraminiferen eine sehr wichtige Rollen bei den Umsetzungsprozessen von organischem Material unter fast anoxischen Bedingungen spielen.

INTRODUCTION

1 Benthic foraminifera

Foraminifera are amoeboid protists (Eukaryotes, Rhizaria) characterized by the formation of granuloreticulose pseudopods which can be stretched outside their test through the aperture (mouth opening) where they branch net-like and allow the foraminifer to come in contact with its surrounding. Pseudopods are essential for foraminiferal respiration, food acquisition (particle collection, catch of prey), movement, anchoring on substrate, and also test construction. To protect their cytoplasmic body, most foraminifera build a test, of either calcium carbonate ("calcareous", Fig. 1), cemented mineral grains ("agglutinated"), or of organic material ("organic-walled"). Lately, also "naked" foraminifera without any test have been identified (Pawlowski et al., 1999a). In comparison to other single-celled groups, foraminifera display a high diversity in shape and size, ranging from few micrometers up to several millimeters.

Because they are present since the Pre-Cambrian (Pawlowski et al., 2003) and the great preservation potential of their robust tests, for paleontologists, foraminifera are very important tools in biostratigraphy and paleoceanography. The number of studies dealing with fossil foraminifera exceeds studies on recent foraminifera. Yet, a detailed knowledge of the biology, ecology and physiology of recent foraminiferal species is essential to allow their use for the reconstruction of past climates, oceanographic settings and environmental conditions.

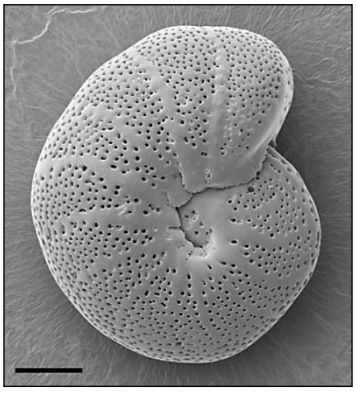


Figure 1 Scanning electron microscope picture of the calcareous foraminifer *Melonis barleeanum* (lateral view, bar = 100 µm).

The overwhelming majority of recent foraminifera species is found to live in contact with substrate (= benthic forms) whereas only 40-50 morphospecies are found to exhibit a planktonic mode of life. Estimates of the diversity of benthic species in modern oceans based on morphological and ecological characteristics range between 3000 to 4000 species (Murray, 2007). Most benthic species are found in the marine areas though some species also occur in brackish and fresh water (Pawlowski et al., 1999b), and simple forms even in the terrestrial soil (Meisterfeld et al., 2001). In marine environments, foraminifera are an important element of the benthic fauna, and populate any imaginable habitat – from salt marshes and shelf areas down to the abyssal trenches to the world's deepest point, the Challenger Deep (Akimoto et al., 2001). Benefiting from their diverse physiological adaptations, they are also found in all climatic regions and in extreme environments such as hypersaline lagoons (e.g. Murray, 1970), hydrothermal vents (e.g. Molina-Cruz and Ayala-

López, 1988), or methane seeps (e.g. Heinz et al., 2005). Within the deep sea, the world's largest ecosystem as it covers 70% of the earth's surface (Gage and Tyler, 1991), foraminifera are found to be abundant inhabitants of the sediment. Here, they can account for up to 50% or more of the eukaryotic biomass (Gooday et al., 1992).

2 Foraminiferal assemblages of marine environments

The distribution of benthic foraminifera in marine sediments is controlled by their environment. The most important abiotic influences are oxygen, temperature, substrate, and salinity, but foraminifera are also exposed to biological factors such as food supply, predation, and competition for resources and space (Murray, 2006). All environments are dynamic and are under the influence of disturbance which is produced by physical factors (waves, tides, currents, storms) and by organism activity (e.g. burrowing, locomotion, feeding). The impact of disturbance can vary greatly between environments and can become an important feature of the environment. So are, for example, coastal environments under the strong impact of wave action, while this factor is not of importance in the deep sea. The characteristic combination of the influencing abiotic and biotic for each environment yields in foraminiferal assemblages which can highly vary in the composition of species but also number of individuals and species per area between each other (Fig. 2). Because foraminifera can hence be associated with certain environmental conditions, they are suitable as indicators for facies (e.g. productivity, water depth) and hence play an important role in reconstruction of past environments and climates.

Benthic foraminifera have different demands and different tolerance to the changes of environmental factors (e.g. Armstrong and Brasier, 2005). So are most species adapted to normal marine salinities (35 PSU), where highest diversity of species is found (Ziegler, 1983). Environments of lower salinity (such as brackish lagoons or salt marshes) are inhabited only by few species and are often dominated by agglutinated foraminifera such as *Jadammina*, *Trochammina*, or *Miliammina* (e.g. Gehrels and van der Plassche, 1999). Another important factor on the distribution of benthic foraminifera is the water temperature since species are adapted to a certain range of temperature which must also meet the temperature range of successful reproduction. The dominance of agglutinated foraminifera in cold waters and the greater presence of calcareous species in warm waters also results from the rate calcium carbonate production which increases with water temperature (Ziegler, 1983). Larger foraminifera are found limited to warm waters though they also require oligotrophic conditions as most of them host photosynthetic endosymbionts. Environmental factor not only influence processes but interfere with another which also acts on the occurrence of foraminifera.

The interaction of light, temperature, substrate, water movement, and food availability affect dependence of foraminifera with water depth and result in strong changes in diversity and species composition with increasing water depth (Murray, 2006). Therefore, different foraminiferal faunas can be distinguished: fauna of marginal marine environments, fauna of the inner and outer shelf, fauna of the continental slope as well as the deep-sea fauna. Marginal marine environments (0-50 m water depth) are characterized by a generally high organic productivity and a relatively high environmental variability (especially in temperature and salinity). They include the intertidal zones, estuaries and lagoons, as well as the inner continental shelf (clastic shelf, coral reefs, sea grass meadows). And whereas the warm and oligotrophic waters of coral reefs are highly populated with larger foraminifera and thick-walled porcellaneous species (e.g. Langer and Lipps, 2003), assemblages of the intertidal region with strong fluctuations in water covering and temperature are extremely low in diversity and often dominated by the calcareous taxa *Ammonia*, *Elphidium,* or *Hayensina* (e.g. Alve and Murray, 2001). The dominance of miliolids, rotaliids, and larger foraminifera at the shallower shelf is in strong contrast to the deeper shelf areas. The very high productivity at the middle shelf to upper slope (50-600 m) is reflected in low species diversity with a strong dominance of the buliminacean, a group of usually eutroph foraminiferal species (e.g. *Bolivina*, *Uvigerina*, *Bulimina*, *Globobulimina*). With increasing water depth and declining productivity, species number increases and calcareous forms are now represented by the taxa *Epistominella*, *Melonis*, *Cassidulina*, or *Oridorsalis* (e.g. de Stigter et al., 1998).

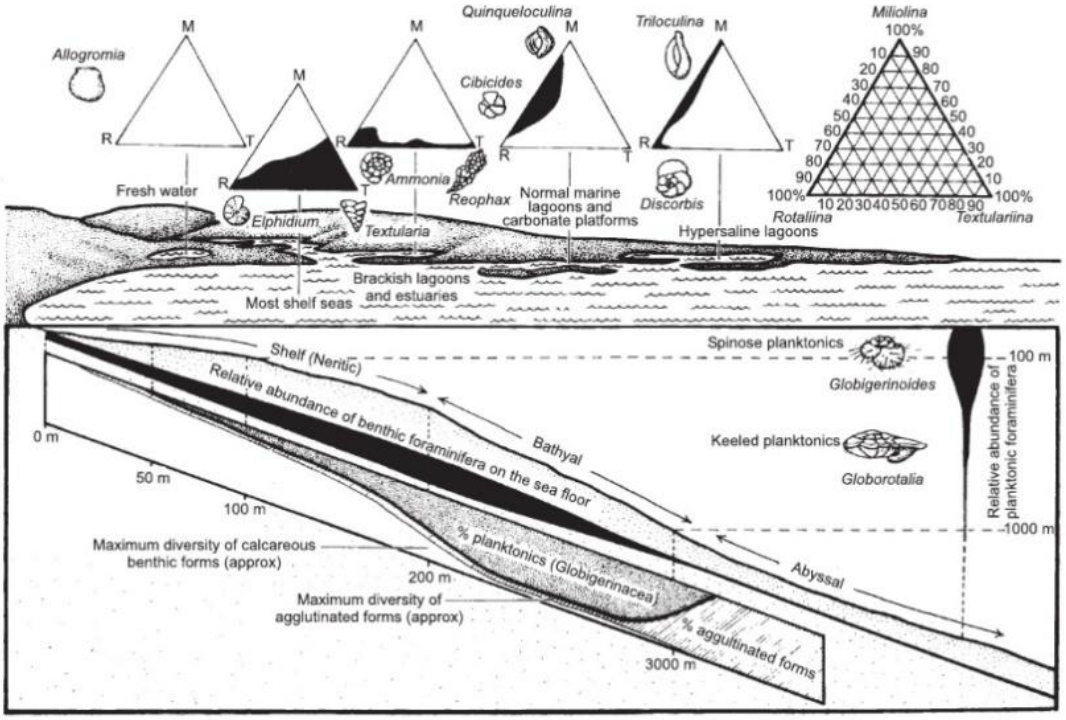


Figure 2 Distribution of benthic foraminifera in marine environments. From Armstrong and Brasier (2005).

Below the continental slope (> 2000 m), agglutinated species gain more and more importance in the assemblage composition and these deep-sea assemblages are in strong contrast to shelf communities (Fig. 2). The presence of calcareous foraminifera in the deep sea is strongly limited due to changes in water chemistry. At shallower water depths, the water is saturated with calcite which is used by calcareous and porcellaneous foraminifera to build up their tests. At about 3500-5000 m, depending on the oceanic basin and water masses, the calcite compensation depth (CCD) marks the depth, where calcite solution and supply are equal. Underneath water is not saturated with calcium carbonate anymore and calcite structures dissolve. Hence, recent foraminiferal assemblages found below the CCD are dominated by calcite-free forms: agglutinated, soft-walled, and allogromiid foraminifera (e.g. Bernstein et al., 1978). Assemblages at abyssal depths are often characterized by the presence of larger tubular agglutinated species, simple monothalameous forms, and komokiaceans (e.g. Schroeder et al., 1989; Gooday et al., 1997; Gooday et al., 2001; Nozawa et al., 2006)

The deep sea is a relatively stable environment of constant darkness, low temperatures and high pressure. But there are environmental influences that are variable with space and time such as turbidites, currents, which can highly affect the benthic organisms in deep-sea sediments. For deep-sea foraminifera, two factors have been found to be the most important regulators of the occurrence and distribution of benthic foraminifera: food availability and oxygen concentration.

3 Food availability in the deep sea

Most deep-sea foraminifera feed on organic matter originating from primary producers in the upper water column. The majority of the marine primary production is carried out by phytoplankton which are free-floating microscopic organisms performing photosynthesis such as diatoms, cyanobacteria or dinoflagellates. Being photoautotroph organisms, phytoplankton fixes dissolved carbon dioxide from the water and transforms it into organic carbon by using energy in form of light. Hence, phytoplankton only performs photosynthesis in the sun-lit surface waters, mainly at 10-100 m water depth. Below the photic zone, photosynthesis is impossible and the only primary production that takes place is chemosynthesis by bacteria. Because chemical compounds are needed for the bacterial turnover, chemosynthesis is highly distributed in areas of high organic biomass or output of inorganic compounds, e.g. whale carcasses on the sea floor (e.g. Bennett et al., 1994), hydrothermal vents (Karl et al., 1980), or cold seeps (e.g. Kennicutt et al., 1989). Because chemosynthesis in the deep sea is only of important on a local scale, it's important to the global marine productivity is very little. Hence, most benthic deep-sea organisms depend on organic matter produced in the photic surface waters as food source.

The main part of the phytoplankton biomass is remineralized and degraded by bacteria and other planktonic organisms (zooplankton) in the upper water column. Unconsumed remains (phytodetritus) sink through the water column and continue being degraded by biological processes in the bathypelagic zone. With increasing water depths, less and less organic material is present and only a split of what has been once produced in the photic zone arrives at the sea floor in the deep sea (Fig. 3). Gage and Tyler (1991) estimated that only 1-3% of surface production reaches abyssal depths. Thus, the flux of organic matter to the sea floor depends on the water depth and food limitation becomes of more importance within increasing depth.

In order to perform photosynthesis, environmental conditions must be adequate for phytoplankton, including a minimum light intensity and duration, nutrients (phosphate, nitrate, trace elements) and water temperature. Because these abiotic factors change throughout the year, primary production does not occur on a constant level throughout the year but shows seasonal differences in magnitude. As a result, the flux of organic matter to the sea floor in waters at temperate latitudes is also subject to seasonality, generally being highest after the productivity maximum in spring. Seasonal variation in the organic flux towards sea floor is present in all marine regions but the intensity, length and temporal occurrence differs largely between different oceanographic settings (Lampitt and Antia, 1997). In spite of such periodic and seasonal high fluxes of organic material, the availability of particulate food in the deep-sea remains a significant limiting factor for much of the year (Gage and Tyler, 1991).

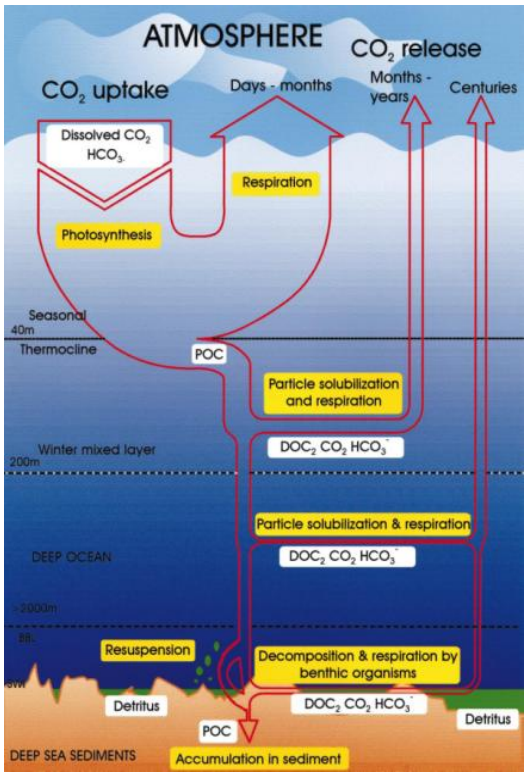


Figure 3 Scheme of the flux of carbon through the water column to deep-sea sediments in the North Atlantic. From Turley (2000).

A phenomenon in areas of highly seasonal primary production is the deposition of fresh phytodetritus at the sea floor. The greenish color of these deposits (Fig. 4) indicates very short transit time of phytoplankton remains through water column without being entirely degraded on its way and still displaying intact chloroplasts. The high settling speed of up to 100 meters per day (Suess, 1980; Gage and Tyler, 1991) is caused by the clustering of phytoplankton cells and the formation of aggregates often including also other components (called marine snow). Composition of fresh phytodetritus varies between geographic regions and can include a wide variety of planktonic species such as diatoms, dinoflagellates, cyanobacteria, small chlorophytes, coccolithophorids, or silicoflagellates (Billett et al., 1983; Lochte and Turley, 1988; Thiel et al.,

1988). The presence of fresh phytodetritus deposits on the deep-sea floor has been observed in the temperate North Atlantic (Billett et al., 1983; Thiel et al., 1988), as well as in the equatorial and North Pacific (Beaulieu and Smith, 1998). That the occurrence of fresh phytodetritus exhibits a seasonal signal and that the sinking carbon from surface waters can create a periodic food source for deep-sea benthos was first shown by Billett et al. (1983) and Lampitt (1985).

Earlier it was suspected that organisms in the deep sea live in an environment with steadily uniform conditions and that they would also not be influenced by temporal variations in environmental conditions in comparison to assemblages at shallower depths. A first evidence that the seasonal signal in the organic flux is reflected in the deep-sea benthos was provided by Smith and Baldwin (1984) who found the benthic oxygen consumption to increase after highest flux of organic matter arriving at the abyssal sea floor. Graf (1989) observed that the maximum primary production in spring is followed with a certain lag by increased densities of deep-sea organisms in summer whereas during winter and low surface productivity, numbers decline again to pre-summer conditions. He was the first to use the phrase “bentho-pelagic coupling” to describe the linked changes in deep-sea organisms to processes in surface waters.

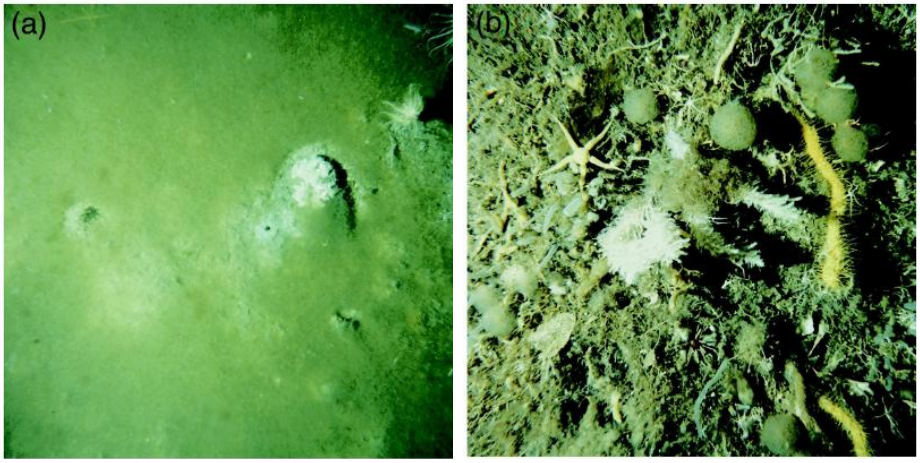


Figure 4 A-B Underwater photographs of sediment from the Antarctic shelf covered with greenish colored phytodetritus to different degrees: A) extremely high and thick cover of 87%, and B) lower cover of 3%. From Gutt et al. (1998).

4 Response of deep-sea foraminifera to organic matter

The proof that also deep-sea foraminifera are affected by the bentho-pelagic coupling was first given by Gooday (1988) when he observed an increase in foraminiferal numbers after phytodetritus deposition in the deep North Atlantic. Later, Loubere (1991) statistically tested the influence of environmental variables on deep-sea foraminiferal assemblages in the deep equatorial Pacific and found only surface ocean productivity to demonstrate a clear influence. The relationship between foraminiferal assemblage composition and the productivity was later also identified for the eastern Pacific, the Atlantic and Indic (Fariduddin and Loubere, 1997; Loubere, 1998; Loubere and Fariduddin, 1999) as well as for the higher latitudes (e.g. Schmiedl et al., 1997).

But not only the numerical appearance of deep-sea species was found to be controlled by the flux of organic matter, it also became apparent that their depth distribution within the sediment and test morphology was related to the flux of organic matter as well (Corliss, 1985; Corliss and Chen, 1988). Because morphotypes of foraminifera (e.g. cylindrical, spherical) varied between levels of productivity, species could be associated with a certain degree of organic flux. Also test morphologies were found to be linked to certain sediment depths. So were tapered forms found deeper in the sediment while trochospiral-shaped taxa were likely to occur at the sediment surface. Authors also defined different microhabitat preferences (epifaunal, shallow-infaunal, deep-infaunal) and put them in relation to particular test morphologies at certain sediment depths. Based on these observations, Jorissen et al. (1995) formulated the TROX model (Fig. 5) where they linked microhabitats of deep-sea foraminifera to the food quantity arriving at the sea floor and the inversely-related oxygen content (see Box 1). Field studies of recent foraminiferal assemblages (e.g. Schmiedl et al., 2000; Heinz and Hemleben, 2006) and laboratory experiments (e.g. Heinz et al., 2001; 2002; Geslin et al., 2004) later provided support for this theory and underlined that the flux of organic matter and oxygen are the most important controlling factors on the distribution and occurrence of benthic foraminifera in deep-sea sediments.

As shown before, fresh phytodetritus on the sea floor can affect deep-sea foraminifera. Unfortunately, the deposition of this food source occurs pulse-like and only for a restricted period of time. In order to study the immediate impact of phytodetritus on deep-sea foraminifera, investigation in the deep ocean at a particular time and place would be required. But as deep-sea research is bound to research vessels with special equipment, limited ship time and other logistic constraints, it is impossible to wait for such an event. Therefore, field observations involving freshly settled phytodetritus are rare and based on fortuitous observations (Fig. 6) rather than on targeted actions and new strategies were needed and developed.

Box 1. The TROX model

When organic material sinks to the sea floor, it becomes available as food source to heterotrophic consumers as food source (e.g. foraminifera). The remineralization of these organic compounds is associated with respiratory processes by the fauna and eventually leads to the decline of oxygen in the sediment if no new supply of the gas is provided. Therefore, the flux of organic matter to the sea floor is not only essential for food supply to foraminifera but can also indirectly have influence on oxygen conditions. In 1995, Jorissen et al. postulated the conceptual TROX model (TROX = Trophic-Oxygen-Microhabitat-Reaction) which links habitat selection by benthic foraminifera in the sediment column to oxygen concentration in the pore water and flux of organic matter (Fig. 5).

Under oligotrophic conditions, the vertical distribution of foraminifera within the sediment is limited by the low food supply. Though sufficient oxygen is present deeper in the sediment, food is only available in the upper sediment layer, causing foraminifera to stay close to the sediment surface. Thus, the distribution of foraminifera is controlled by food availability within the sediment.

In eutrophic environments, the flux of organic matter to the sea floor is high and sufficient food is available at the sediment surface but also within the sediment. Here, the ecosystem is not food-limited but a critical oxygen level determines how deep foraminifera are found alive within the sediment. As respiration and oxygen consumption are high, the sediment becomes depleted in oxygen in deeper depths. As a consequence, anaerobic conditions are present and reach even up to the sediment surface. Foraminifera are only found near the sediment surface where oxygen supply is possible due to gas exchanges with the sea water. Here, the occurrence of foraminifera is controlled by oxygen availability.

Where the flux of organic matter is sufficient to provide food also deeper in the sediment and the sediment is oxygenated, benthic foraminifera are found deep throughout the sediment column. In addition, the foraminiferal fauna in these mesotrophic environments is also more diverse as it provides space and food for a large number of individuals.

Using the TROX model as basis, Van der Zwaan et al. (1999) postulated the TROX-2 model. This concept states that the density and depth distribution of benthic foraminifera is effected by redox gradients (Mn, NO_3, SO_4) and competition for food whereupon both are regulated by the flux of organic matter.

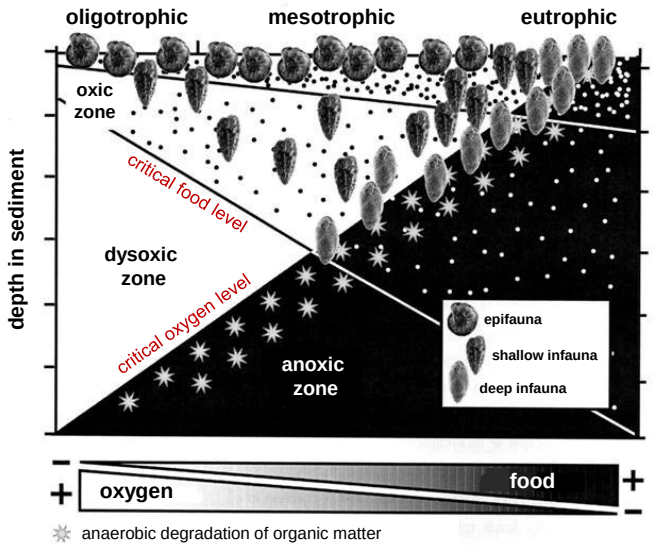


Figure 5 The TROX model. Modified after Jorissen et al. (1995).

Benefiting from advances in technology, sampling and photographing of the sea floor during a cruise in 1986 for the BIOTRANS Program in the abyssal Northeast Atlantic (4800 m) discovered freshly deposited phytodetritus for the first time (Thiel et al., 1988). After few days of observations, population density of certain foraminifera species had drastically increased in the presence of phytodetritus and showed the ability of the foraminiferal community to rapidly respond to a fresh food source (Gooday, 1988). Being able to study sediment with phytodetritus present provided an excellent opportunity to study the effect of this shortly-limited food source to the sediment community. Subsequent field observations in the same area revealed a specific assemblage of opportunistic species of foraminifera such as *Epistominella exigua* or *Alabaminella weddellensis* who exploit phytodetritus by showing faster growth and reproduction with resulting higher abundances and biomass (Lambshead and Gooday, 1990; Gooday, 1993; Smart and Gooday, 1997) in its presence. These field studies showed that the abundance and distribution of some foraminiferal species is directly linked to deposition of labile organic matter and follows the "phytodetrital signal" in the deep sea (Gooday and Hughes, 2002).

Figure 6 Different foraminifera species collected at the Indian Margin at 540 m depth. The greenish colored cytoplasm, visible through the calcareous tests. indicates the ingestion of fresh phytodetritus by these specimens.

Long-term observation at two sites in the deep Pacific (Drazen et al., 1998; Kitazato et al., 2000) found seasonal changes in foraminiferal populations following phytodetritus deposition characterized by short response times (weeks) and reproduction of opportunistic species. Becoming aware that seasonal phytodetritus deposition is highly affecting deep-sea foraminifera and that fresh phytodetritus can represent an important food source, experimental studies were subsequently launched to study the importance of fresh phytodetritus as food source for the benthic fauna and to identify determinants of organic matter remineralization rate in deep-sea environments. The addition of phytodetritus to foraminifera under laboratory conditions not only revealed very rapid ingestion of phytodetritus, as well as elevated individual numbers and reproduction and change of microhabitats (Heinz et al., 2002; Nomaki et al., 2005a; Koho et al., 2008), they also gave proof that deep-sea foraminifera are able to adapt their metabolic rates to the flux of organic matter (Linke, 1992). Observations of different responses by species towards phytodetritus presence during experiments (e.g. by Gooday, 1993) were later related to the quality of the food and feeding preference by Nomaki et al. (2005a). Other experiments on deep-sea foraminifera observed preferences for certain algal types (Heinz et al., 2002) or for specific components (fatty acids) of phytodetritus (Suhr et al., 2003). In the review by Gooday et al. (2008), a description of the different types of feeding by deep-sea foraminifera such as herbivory,

deposit feeding, suspension feeding, bacterivory or bearing of stercomata (pellets of waste material) are described.

Nevertheless, these experimental and field observations demonstrate the ability of benthic foraminifera to quickly react to phytodetritus which is of advantage in an environment where food input is temporally limited and competition with other sediment-inhabiting and phytodetritus feeding organisms (e.g. meiofauna, bacteria) is strong. Today we have a good idea on what kind of organisms inhabit deep-sea sediments but the exact structure of the benthic fauna is often not known as well as the role of species or groups in the trophic web. From carbon and nitrogen isotope analysis by Nomaki et al. (2008) we know that foraminifera are an important linkage in the deep-sea food web between the lowest and higher trophic levels being consumers but also prey for larger benthic organisms (Fig. 7). First field observations showed that deep-sea foraminifera can show higher uptake of phytodetritus than other benthic groups (e.g. Pfannkuche, 1993) and it was stressed that they are important to cycling of organic matter.

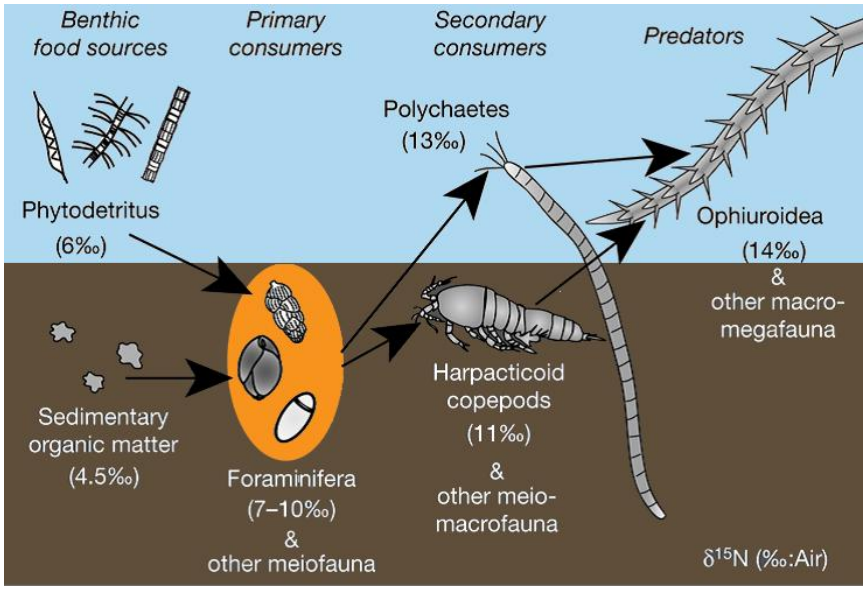


Figure 7 Structure of the benthic food web in sediments at the bathyal Sagami Bay, suggested by carbon and nitrogen isotopic compositions. Modified after Nomaki et al. (2008).

A modern and very direct approach to investigate and understand trophic processes and interaction at the sea floor triggered by the presence of phytodetritus is to directly follow the pathway of the food source through the benthic trophic web to the consumers in form of tracers. A great advantage of this method is the quantitative estimation of uptake, which allows comparison between sites and also between benthic groups as well as the assessment of the role of benthic foraminifera in the trophic web of the deep sea.

5 Isotope labeling experiments

Isotope labeling is a suitable method to directly track the pathway of a specific atom from the food source (phytoplankton) to the consumer (foraminifer). Labeling" the food is realized by replacing a specific stable isotope with another stable isotope of the same element. The concentration of the substitute should be very high in the labeled food source in comparison to its natural concentration. After labeling, the food is presented to the foraminiferal assemblage to be ingested. After a defined time span, foraminifera are extracted and the isotopic composition of the foraminiferal cytoplasm is measured. Increases above the pre-experimental isotope ratio are interpreted as ingestion of the labeled food source.

The most commonly used stable isotope is ^{13}C but also ^{15}N has just recently been discovered to be an adequate tracer (e.g. Hunter et al., 2012, Enge et al., unpublished). Under natural conditions, each of the two stable isotopes (^{13}C, ^{15}N) makes up 1% or less in living organisms. They are substituted for their lighter isotopes, ^{12}C and ^{14}N which are present in organic biomass to at least 99%. These relative abundances of the isotope pairs are also found in marine phytoplankton (Fry and Sherr, 1984) as well as in benthic foraminifera though the carbon ratio can slightly differ between species and habitats (Nomaki et al., 2005b; Nomaki et al., 2006; Sweetman et al., 2009; Enge et al., 2011). Food sources used in isotope labeling experiments on foraminifera are phytoplankton species common in the area of investigation, and which are cultivable under laboratory conditions. Prior the feeding experiment, algae are cultured in a medium which has been enriched in $NaH^{13}CO_3$. During the growth process, algal cells incorporate the heavier isotope ^{13}C and gradually increase their $^{13}C/^{12}C$ ratio. The final algal mass which is offered to the foraminifera during the incubation period shows an unnaturally high content of ^{13}C in comparison to the algae's natural composition. After the incubation, the cytoplasm of the foraminifer is extracted and analyzed for its TOC content and composition of stable carbon isotopes via mass spectroscopy. If the $^{13}C/^{12}C$ ratio of the foraminiferal cytoplasm is larger than the ratio prior the experiment, the labeled algae has been successfully ingested. The calculation of the percentage of ^{13}C in the foraminiferal cytoplasm does not only show the positive uptake of the labeled food source but also allows the estimation of the amount of phytodetritus ingested which is a major advantage to observational studies.

By applying the method of isotope labeling, the response of deep-sea foraminifera to a simulated phytodetritus deposition can be experimentally investigated. In order to do so, the labeled algal mass (phytodetritus) is placed onto the sediment surface for a defined period of time to allow feeding by foraminifera. The execution of the experiments can be performed in two ways: directly in the deep-sea on the sea floor under natural conditions (*in-situ*) or outside the natural habitat of the foraminifera (*ex-situ*).

Ex-situ experiments are usually carried on board of a research vessel. Sediment cores are taken at the desired water depth, brought up to the ship and stored under stable and controlled laboratory conditions before adding the ^{13}C-labeled algae. The advantages of this approach are the easy access to the experimental unit, the possibility to manipulate environmental factors (temperature, oxygen-supply, salinity, etc.) and the independence from special deep-sea devices (see *in-situ* experiments) which are costly and limited in number. The disadvantage of this method is that the experiments are carried under conditions of unnaturally low pressure to the foraminifera. Deep-sea organisms are adapted to pressures hundred times larger than at the earth's surface and it cannot be excluded that decompression which occurs during the transport through the water column and on board the research vessel, puts high stress on the foraminifera. Results from *ex-situ* experiments might not represent the behavior they would show at the sea floor and hence demonstrate lower uptake. Isotope labeling experiments performed by Woulds et al. (2007) in the Arabian Sea at 140 m and 300 m showed higher uptake by foraminifera under *in-situ* conditions than under *ex-situ* conditions. Therefore it is very important to be careful when comparing results obtained under different experimental conditions.

Performing isotope labeling experiments directly at the sea floor (*in-situ*) is thought to result in more accurate observations closest to natural conditions. Unfortunately, the realization of such experimental studies in the deep sea is associated with many constraints (logistics, costs, weather conditions, need of submersible or ROV), so that the first publication about a feeding experiment on foraminifera in the deep-sea was not released until 1999 by Levin et al. (1999). Thus it is not surprising that the number of *in-situ* isotope labeling experiments performed so far (not only on foraminifera) is very low. To this day, *in-situ* experiments including foraminifera have only been performed at seven different deep-sea sites (Fig. 8), including the two experiments presented in this thesis.

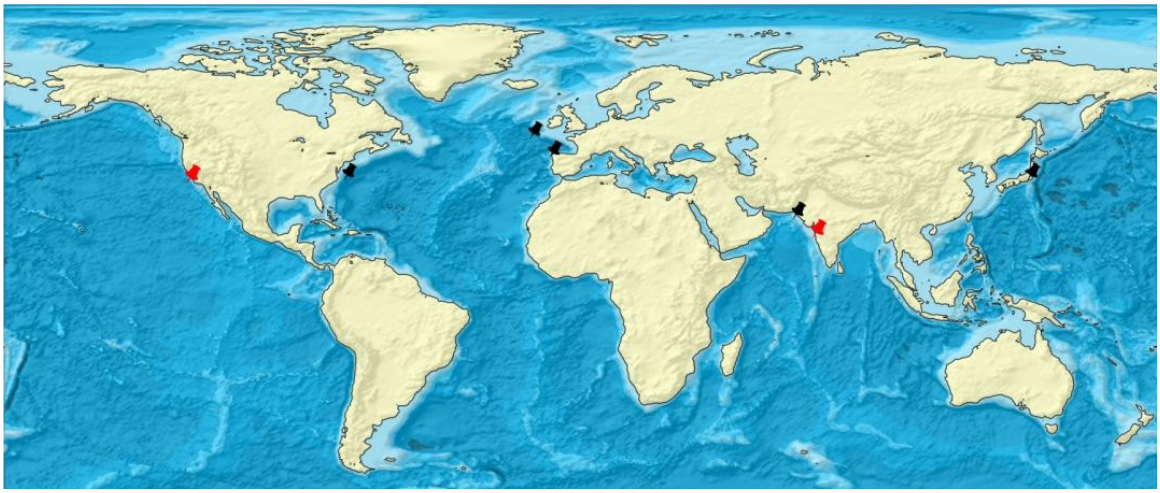


Figure 8 Location of isotope labeling experiments on foraminifera performed *in-situ*. Black symbols mark studies in the North Atlantic (Levin et al., 1999; Moodley et al., 2002; Witte et al., 2003b), in Sagami Bay in the Northwest Pacific (Kitazato et al., 2003; Nomaki et al., 2005b; 2006; 2009; 2011), and in the Arabian Sea (Woulds et al., 2007; Andersson et al., 2008). Red symbols show locality of studies presented in this thesis (Enge et al., 2011;2012; Enge et al., unpublished).

To enable the deposition of a defined algal mass onto a defined area of enclosed sea floor in the deep sea, special devices (Fig. 9) have been developed and have come in use during the last decades. So far, four different devices for *in-situ* experiments have been developed and applied: Plexiglas box (Levin et al., 1999), benthic chamber landers (Moodley et al., 2002; Witte et al., 2003b; Woulds et al., 2007; Andersson et al., 2008), incubation or culture cores (Kitazato et al., 2003; Nomaki et al., 2005b; 2006; 2009; 2011), and the Oceanlab spreader system (Enge et al., 2011; Enge et al., unpublished). The last three are built up of a casing of different size, material, and shape, onto which a box is connected containing the labeled algal mass. After the deployment of the devices at the undisturbed sea floor by a submersible or ROV, the manipulator arm of the later pushes a plunger or syringe on the algal-containing box to release the algal mass within the casing on the enclosed sediment. In the study by Levin et al. (1999) the algal mass was released from a shaker device into the box by the submersible itself. Detailed information on the devices and functioning can be obtained from the relevant publication. After the incubation period, sediment from inside the enclosed area is recovered by taking push cores. The subsequent processing of the sediment cores usually includes the horizontical slicing of the sediment cores, sieving and washing of the sediment samples, the extraction of foraminifera from the sediment, the identification of living specimens, the decalcification of the tests, and at last the isotopic analysis of the foraminiferal cytoplasm.

Figure 9 Devices used in the deep sea to perform *in-situ* feeding experiments: the Oceanlab spreader system (left), incubation or culturing cores (middle), and benthic chamber lander (right). Pictures are property of JAMSTEC (left, middle) and MBARI (right).

6 Findings from previous deep-sea *in-situ* feeding experiments

Previous *in-situ* feeding experiments using isotopic labeling were performed in very different marine environments such as abyssal plains, oxygen minimum zone sediments, eutrophic basins, and continental margins. So far, the response of foraminifera to phytodetritus under natural conditions was studied Eastern and Western North Atlantic, in Sagami Bay (Japan) and in the Arabian Sea at the Pakistan Margin. Investigations were performed at water depths from 140 to 4800 m and at sites of very different fluxes of organic matter to the sea floor or oxygen concentrations in the pore water. In addition, the focus was very variable between the investigations. On the one hand foraminifera were treated as group within the benthic community and compared to other groups (e.g. macrofauna, bacteria). Whereas other studies explicitly concentrated on foraminifera and put strong emphasis on ecological questions such as feeding preferences or diet. In order to give a few insights into the studies, the main outcomes of these experiments are provided below.

North Atlantic. The experiments conducted at the Carolina Margin (Levin et al., 1999) and at two sites in the Northeast Atlantic (Moodley et al., 2002; Witte et al., 2003b) were pioneering studies in the field of *in-situ* feeding experiments in the deep sea. The first sign of the importance of foraminifera to carbon cycling in abyssal depths was given by the study of Witte et al. (2003b). At 4800 m depth, foraminifera demonstrated the greatest response to phytodetritus deposition after three weeks of phytodetritus incubation in comparison to all other benthic groups although their biomass was smaller than that of the bacterial or macrofaunal biomass at this site. While feeding by foraminifera was low in the first days of the experiment (Fig. 10), the uptake after 23 days of phytodetritus presence was twice as high as the bacterial uptake and four times higher than the response by the macrofauna. The delayed response by the all groups was attributed to be a characteristic of deep-sea benthic organisms. This is in contrast to the study by Moodley et al. (2002) carried out in the abyssal Atlantic northwest of Spain (2170 m). Here, foraminifera were found to be rapid consumers of fresh phytodetritus and were responsible together with bacteria for 50% of the total community uptake within 35 hours after deposition. And although foraminifera only represented about 1% of the total biomass of the benthic fauna in both studies, 6-17% of the processed carbon (including respiration) were assigned to foraminiferal uptake, suggesting that foraminifera might be important in deep-sea carbon cycling. In a third study at the east coast of North America on the continental margin (850 m), larger agglutinated foraminifera exhibited high affinity to fresh phytodetritus and demonstrated rapid uptake (Levin et al., 1999). After 1 to 1.5 days, foraminifera had demonstrated the second highest uptake of all investigated benthic groups (e.g. annelids, bivalves, holothurians) which showed their importance to the short-term cycling at this site as well. While the first two North Atlantic studies were comparing the

entire foraminiferal assemblage to other benthic groups, Levin et al. (1999) were the first to consider the response of individual species (e.g. *Bathysiphon rufum*).

Sagami Bay. The Sagami Bay is a semi-enclosed bay located in the Western Pacific in the south of the Japanese Islands (Fig. 7) and characterized by high flux of organic matter to the sea floor (Kitazato et al., 2006). The spring phytoplankton bloom generally occurs from Mid-February to May, followed by phytodetritus deposition at the sea floor some weeks later (Kitazato et al., 2003). The *in-situ* experiments were run at the permanent station OBB2 at 1450 m water depth and were all conducted by scientists from the Japanese Agency for Marine-Earth Science and Technology (JAMSTEC). Whereas the experiments in the North Atlantic mainly focused on the comparison of uptake between different groups of benthic organisms, the studies performed in Sagami Bay dealt only with the response of foraminifera to phytodetritus, especially at species level. The conducted studies (Nomaki et al., 2005b; Nomaki et al., 2006; Nomaki et al., 2009) provided first knowledge on foraminiferal uptake rates in an eutrophic bathyal environment, on the influence of seasonality in the flux of organic matter on the foraminiferal feeding behavior as well as on species-specific reactions towards phytodetritus deposition. Not only was the focus on single species of foraminifera, but also on the influence of different food types on the feeding response. In the study by Nomaki et al. (2006), the authors were able to discriminate between selective phytophageous species such *Uvigerina akitaensis*, *Bolivina spissa,* or *Bolivina pacifica*, species that preferred sedimentary organic material and species that only feed on phytodetritus at times of high phytodetritus input and on sedimentary organic matter if phytodetritus is absent (Fig. 11).

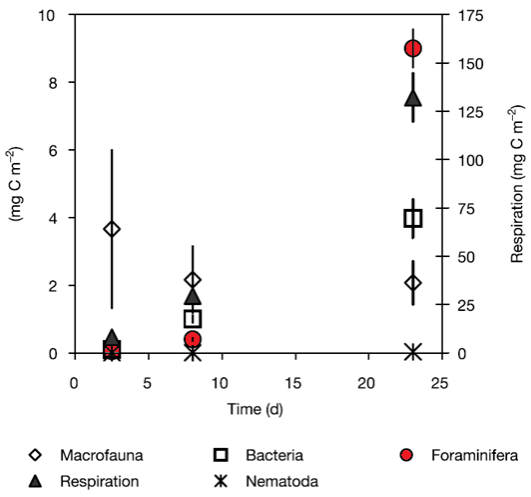


Figure 10 Pathways of ^{13}C-labeled phytodetritus with time in foraminifera (red circle) and other sediment-inhabiting faunal groups in the abyssal North Atlantic. Modified, from Witte et al. (2003a).

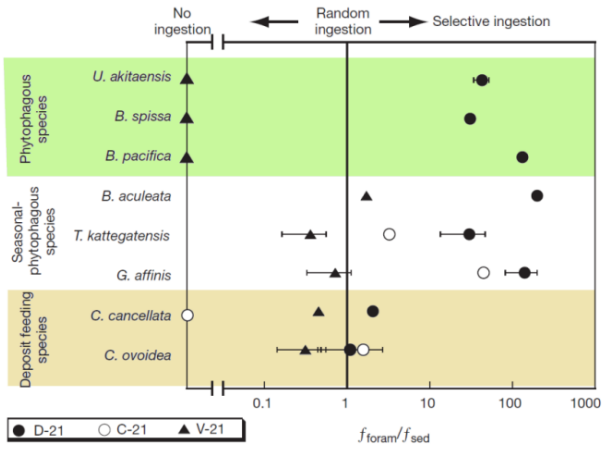


Figure 11 Categorization of benthic foraminifera according to their feeding types. Results of an *in-situ* feeding experiment carried out at Sagami Bay with three different ^{13}C-labeled food sources: *Dunaliella tertiolecta* (D; unicellular green algae), *Chaetoceros sociale* (C; diatom), and *Vibrio alginolyticus* (V; bacterium). Modified after Nomaki et al. (2006).

In another experiment, foraminifera not only ingested particulate food in form of phytodetritus but also consumed dissolved organic carbon (in form of glucose) which can serve as additional food source (Nomaki et al., 2011). The intense investigation on foraminifera in Sagami Bay is important to understand the trophic structure of the benthic community in eutrophic environments and shows that foraminifera play a large role in the early cycling of organic matter at the bathyal sea floor (Kitazato et al., 2003; Kitazato et al., 2006).

Arabian Sea. In the Arabian Sea, a stable oxygen-depleted water mass is present at mid water depth (200-1100 m), resulting from high organic matter flux and slow vertical mixing of water masses due to high stratification. This "oxygen minimum zone" (OMZ) is a natural phenomenon and relatively stable in the Arabian Sea though its vertical expansion can differ throughout time. Where the OMZ water mass impinges on the continental margin, the benthic community is exposed to dysoxic and anoxic conditions, leading to a species composition in the foraminiferal assemblage very different to oxygenated sediments at the same water depths in a different region. During a cruise near the Pakistan Margin in 2003 before and after the summer monsoon, a series of ex-situ and *in-situ* isotope labeling experiments was performed by Woulds et al. (2007) and Andersson et al. (2008) along a depth transect covering the slope area influenced by OMZ waters (140-1850 m). The feeding experiments focused on the influence of oxygen on the cycling of organic matter by benthic organisms (macrofauna, bacteria, foraminifera). Abundances and uptake of phytodetritus by foraminifera showed strong variation between the investigated depths, both being highest at the shallowest investigated site at 140 m. Foraminifera dominated the faunal uptake of organic matter in the hypoxic sediments at 300 m as well as at the deepest sites (1200-1850 m) by 70-100%, and showed an increase in uptake with longer incubation time (Woulds et al., 2007). These experiments show that foraminifera are significant contributors on the short-term cycling of freshly deposited phytodetritus at continental margins. Woulds et al. (2007) propose the dominance of uptake of organic material by foraminifera if oxygen concentrations within a certain threshold range (5.0 – 6.7 µmol/l) and underline the strong control of oxygen on the processing of organic matter by benthic organisms. The studies by Woulds et al. (2007) and Andersson et al. (2008) mark the start of *in-situ* experiments which particularly focus on the influence of oxygen on phytodetritus uptake. Yet, focus of both studies was on the response of the entire foraminiferal group. Single species were not separately studies except for *Uvigerina* ex gr. *U. semiornata* which demonstrated outstanding high uptake in comparison to other species.

FOCUS OF INCLUDED RESEARCH PAPERS

Previous feeding experiments have demonstrated that the response of deep-sea foraminifera to phytodetritus can vary in response time and magnitude. Studies have illustrated that these small single-celled eukaryotes are able to react quickly to food presence and that they can compete with other (larger) benthic organisms for such limited resource. Species-specific feeding preferences were discovered in Sagami Bay and it was shown that foraminifera are able to cope with low oxygen concentration better than other groups. Yet, it remains unknown if such strong species-specific preferences in feeding also prevail in abyssal environments. Similarly, the study by Woulds et al. (2007) demonstrated high activity of foraminifera in oxygen-depleted environments, but it remains unknown how foraminifera react to food under (near-) anoxic conditions? There are still too few studies to draw general conclusions and important general questions remain, such as whether or not there is a relationship between water depth and the foraminiferal response and whether or not factors other than oxygen or temperature influence uptake rates?

In a bid to answer some of these questions, two *in-situ* experiments have been performed in very different deep-sea environments. The deep sea is not a homogenous habitat by showing high variation in topographic features (seamounts, plains, vents), biological and abiotic influences (e.g. temperature, water currents, oxygen content, flux of organic matter, competition). And because these environmental factors also highly influence the distribution and occurrence of benthic foraminifera, more studies are needed at different localities to cover the variability of these factors. This thesis presents the analysis and interpretation of isotope labeling experiments from two deep-sea sites (North Pacific, Arabian Sea). While the investigated site in the Northeast Pacific represents a true abyssal environment (~4000 m, food-limited, oxygenated), foraminifera at the Indian Margin in the Arabian Sea at 540 m depth are exposed to high flux of organic matter but almost anoxic conditions. So far, no other experiments on foraminifera have been performed in these areas and knowledge about their role in carbon cycling in these deep-sea sediments is missing.

In order to interpret the results of these feeding experiments on foraminifera, it is essential to know the composition of the foraminiferal fauna and about the importance of single species to the community. Since data on living foraminifera for both sites was insufficient or lacking, the focus of this thesis was also on the investigation of foraminiferal assemblages in the abyssal Northeast Pacific and in the OMZ sediments of the Indian Margin. The obtained faunal data of the Pacific assemblage were further analyzed towards assemblage structure (e.g. diversity, dominance), the distribution of species within the sediment (microhabitat preferences), and the influence of the sampling period on the community structure (spring, fall comparison). Information on abyssal

foraminiferal assemblages are still very limited and restricted to few sites wherefore results for the North Pacific provide new data especially on soft-walled foraminifera. These small and inconspicuous forms have been often overlook in previous deep-sea studies (due to their small size), but appear to be very important components in deep-sea environments as observed during latest investigations (Gooday et al., 2004).

Publication 1, Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific presents the results of an *in-situ* feeding experiment on foraminifera, carried out 200 km off the coast of California at *Station M* at 3985 m depth. At this long-term observation site, processes involved in the bentho-pelagic coupling in the North Pacific are studied since more than two decades. So far, knowledge about the impact of foraminifera on the remineralization processes in deep-sea sediments and how they react to sudden food availability is scarce. In the area of *Station M*, the flux of organic matter to the sea floor is low and deposition of phytodetritus can occur in summer following the spring primary production maximum (Beaulieu and Smith, 1998). That foraminifera at *Station M* are able to respond to such pulses of organic matter within weeks was observed by Drazen et al. (1998). By artificial addition of phytodetritus directly onto the sea floor, the short-term response (4 days) of deep-sea foraminifera was investigated under natural conditions with additional focus on species level and the vertical distribution of species within the sediment. So far, only the response of the macrofauna to labeled phytodetritus has been investigated at *Station M* (Sweetman and Witte, 2008), and no *in-situ* feeding experiment involving foraminifera has been performed in the abyssal Pacific. In our feeding experiment we offered ^{13}C-labeled *Thalassiosira weissflogii* (diatoms) as food source to foraminifera in excess (~3 g/m^2) to simulate a typical phytodetritus deposition event following the primary productivity maximum in spring. Benefiting from high sensitivity of isotope measurements at JAMSTEC (Japan), we were able to analyze single species that were present in sufficient individual numbers and biomass and pooled the remaining species in groups in order to estimate the uptake of the entire foraminiferal assemblage. Stable carbon isotope analysis and carbon content measurements revealed large differences in uptake of fresh phytodetritus not only among foraminiferal groups and species, but also between different sediments depths. In general, the total uptake by the foraminiferal community was highest at the sediment surface at 0-1 cm and decreased with increasing sediment depth. This observation is similar to other deep-sea sites and might derive from the observed abundance peak of living foraminifera at the sediment surface, the low mixing of labeled algae into the sediment because of the short incubation time of four days or the preference of deep-infaunal species for more degraded organic material. Foraminiferal species demonstrated considerable differences in their uptake of phytodetritus, ranging from high uptake (e.g. *Saccorhiza ramosa*, *Adercotryma glomerata*) to low or no responses as it was observed for the numerically dominating soft-walled Saccamminids. The overall uptake was dominated by agglutinated (60%) and calcareous species (40%). The variation in foraminiferal uptake of the fresh phytodetritus suggests species-specific

feeding preferences and diets (e.g. bacteria, older degraded organic material) which have been assumed to cause species-specific differences in bathyal Sagami Bay (Nomaki et al., 2005b). It is also possible that the generally slower metabolic rates of deep-sea organisms are causing delayed response to phytodetritus by certain foraminiferal species because they are adapted to low input of organic matter. The total uptake of 0.82 mg C/m^2 observed during the four days (accounting for 0.03% of the added phytodetritus mass) is low but in the range of estimated uptake by foraminifera in the abyssal North Atlantic (Moodley et al., 2002; Witte et al., 2003b). The rapid response within four days shows the ability of foraminifera to utilize a limited food source of high quality if present, which is advantageous in an environment of high food competition. That foraminifera are an important faunal element in short-term mineralization of organic matter at this abyssal site can be assumed because the macrofauna at *Station M* demonstrates a lower response to phytodetritus deposition (Sweetman and Witte, 2008) when compared to the foraminiferal uptake. In summary, the study not only estimated the uptake by the foraminiferal community in a deep-sea setting but also provides species-specific foraminiferal uptake rates for abyssal species which have not been included in other experiments before.

Publication 2, Diversity and microhabitats of living benthic foraminifera in the abyssal Northeast Pacific focuses on the assemblage structure of recent foraminifera at 3985 m depth at the long-term observation site *Station M*, a true abyssal environment whose benthic fauna is under the influence of water surface-near initiated processes (e.g. primary production). The only previous study on foraminifera in this area focused on the assemblage response to food availability (Drazen et al., 1998), and information on the structure of the foraminiferal community is lacking. The aim of this study was the identification of patterns in the species numerical and relative abundance, species diversity, and microhabitat preferences. Finally, a comparison of the assemblage structure to deep-sea assemblage at other North Pacific sites was performed to learn more about the patterns of occurrence in relation to environmental conditions. Sediment cores collected at *Station M* in September 2007 and May 2009 were analyzed for the abundance of living foraminifera larger than 63 µm in the upper 5 cm of sediment. Due to methodological constraints during samplings two different approaches were used to determine foraminifera as alive at the time of sampling: staining with Rose Bengal and cytoplasm visibility. In total, the assemblage yielded 87 species of living foraminifera for both samplings and live specimens were found down to 5 cm depth in the sediment. Estimated abundances of 300 ind./10 cm^3 are relatively high for an abyssal setting and mainly result from the numerically dominating group of monothalamous soft-walled Saccamminids. These simple and small foraminifera have often been overlooked or excluded in former studies, although they have been found to be common and abundant inhabitants of deep-sea sediments (e.g. Gooday et al., 2001). Similar to other abyssal sites is also the high number of agglutinated species and the low abundance and low diversity of calcareous foraminifera. Their presence in low quantity indicates that the calcite compensation depth is deeper than 3985 m in this area but that the lysocline is close to the investigated site.

Identification of all foraminifera on species level was not possible which reflects the presence of new species which have not been found before. With regard to the vertical occurrence of foraminifera within the sediment, species were not uniformly distributed within the sediment column, but showed preferences for certain depths (microhabitats). Most species were found at the water-sediment interface and therefore demonstrated an epifaunal habitat such as *Adercotryma glomerata*, whereas other species were common in deeper sediment layer such as *Praeglobobulimina pacifica* whose average living depth was 3 cm. The broad vertical distribution and the relatively high species diversity reflect mesotrophic conditions where food input is high but does not cause oxygen depletion in the upper sediment. Comparing the assemblage structure of foraminiferal between studies conducted in the North Pacific to *Station M*, the highest similarity is found with the assemblage at the Hess Rise in the central abyssal Pacific. Foraminiferal assemblages located closer to our site but at shallower water depth were statistically more different. This shows that depth-related differences in abiotic and biotic conditions (e.g. flux of organic matter) are affecting the distribution of species of foraminifera more than geographical distance. In summary, the first taxonomic study on living foraminifera in the abyssal Northeast Pacific revealed an assemblage whose diversity estimates, species composition and species microhabitat preferences reflect the abyssal setting.

Publication 3, Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin is based on an *in-situ* isotope labeling experiment which was performed at the continental margin in the eastern Arabian Sea at 540 m depth. Foraminifera in these sediments are exposed to eutrophic conditions and strong oxygen depletion as the site is located in the core region of the OMZ. The aim of the study was the investigation of the feeding behavior of foraminifera under near-anoxic conditions (0.02-0.05 ml O_2/l) and their impact on phytodetritus processing after a pulsed settling event. In this experiment, the food source *Thalassiosira weissflogii* (diatoms) was not only labeled with ^{13}C, but simultaneously with ^{15}N to test whether this stable isotope can be also used as tracer in feeding experiments with foraminifera. The algal mass applied to the sea floor (650 mg C/m^2, 120 mg N/m^2) for four days simulated a phytodetritus deposition event of natural magnitude. Faunal investigations of the assemblage in the upper centimeter of sediment revealed high abundances of living foraminifera (~4000 ind./10 cm^3) and an outstanding dominance of calcareous species (99.5%) in the >125 µm size fraction. The focus of this study was put on the nine most dominant species and their response to phytodetritus, because they accounted together for 94% of the total number of living foraminifera. Analyses of the carbon and nitrogen stable isotope ratio and resulting high labeling with ^{13}C and ^{15}N evidenced that all investigated species were feeding on phytodetritus within four days. *Uvigerina schwageri* showed an outstanding high response (40% of total uptake) while the most abundant two species *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. demonstrated low ingestion of algal material. The observed strong interspecific differences in phytodetritus uptake suggest specific adaptation and feeding preferences, though it cannot be

excluded that also the individual biomass and the numerical appearance of species are influencing parameters. Results of the experiment show that foraminifera are able to rapidly utilize high amounts of organic material under anoxic conditions showing that they are well-adapted to food in excess. After four days, foraminifera had taken up 101 mg C/m^2 (16% of the total added carbon), exceeding by far all previous uptake rates on phytodetritus in deep-sea sediments obtained from *in-situ* experiments (Fig. 11). We assume that adaptations of foraminifera to oxygen depletion and high food input have yielded in the high uptake. The foraminiferal assemblage at this station is dominated by few specialists who prefer eutrophic conditions often associated with low oxygen concentration. Their ability to perform denitrification (e.g. Risgaard-Petersen et al., 2006) resulting in tolerance to low oxygen concentrations and the absence of macrofauna (Hunter et al., 2012) may have contributed to their proliferation in this hostile environment as well. In summary, we provided the first species-specific carbon and nitrogen uptake rates for foraminifera in near-anoxic sediments and were able to identify ^{15}N as suitable tracer in feeding experiments with foraminifera in addition to the commonly used ^{13}C. The observed enormous number of living foraminifera and their rapid and high phytodetritus uptake give strong evidence that they play a major role in short-term carbon cycling in almost anoxic sediments at the Indian Margin.

CONCLUSIONS AND OUTLOOK

Structure of foraminiferal assemblages

Prior the investigations in the abyssal Northeast Pacific and at the Indian Margin in the Arabian Sea no information was given about the detailed population structure and species distribution of recent benthic foraminifera in these areas. The different environmental conditions of these two sites are very well reflected in the foraminiferal assemblages who are in strong contrast to another. A diverse assemblage of relatively low abundance of ~300 ind./10 cm^3 and dominated by soft-walled and agglutinated species was found at the North Pacific site (3985 m), characterized by oxic and oligotroph conditions. On the contrary, the almost oxygen-depleted sediment at the Indian Margin (540 m) with high flux of organic matter is an extreme environment which is populated by few highly adapted species of calcareous foraminifera (low diversity) that occur due to low competition in extreme high population density (~4000 ind./10 cm^3). The information gained from these two sites could be useful for the application on fossil assemblages of benthic foraminifera to reconstruct past environments and possible changes (e.g. increase of food flux, or oxygen depletion). The detailed analysis of the soft-walled morphospecies at the North Pacific site provides new data for this often overlooked group of foraminifera in form of distribution, ecology and morphology. The dominance of the soft-walled foraminifera underline their importance to the abyssal benthic community and neglecting them will result in the underestimation of the foraminiferal diversity in deep-sea sediments.

Importance of foraminifera to carbon cycle modeling

The two labeling experiments provided new knowledge about the feeding ecology of benthic foraminifera and their role in carbon cycling in very different deep-sea environments. The uptake estimates of phytodetritus for both foraminiferal assemblages allow the comparison to other locations and different organisms groups. The identification of species that are important for each particular deep-sea environment can be of interest for application in paleoceanography or -ecology. So might be *Uvigerina schwageri* an indicator species for high organic flux and almost anoxic conditions.

The uptake of phytodetritus by the foraminifera in the abyssal North Pacific was in high contrast to the reaction of foraminifera at the Indian Margin, both reflecting the adaptation of foraminifera to the particular environmental conditions. Foraminifera in the deep Pacific reacted to the presence of phytodetritus very fast (advantageous in an environment of food limitation and high food competition), but at a low level (adaption to low food flux). As the study by Sweetman and

Witte (2008) showed a lower macrofaunal response, foraminifera seem to be important contributors to the carbon cycling at this abyssal site. At the Indian Margin few foraminiferal species showed a very high phytodetritus uptake which might be an adaptation to the constant high organic influx. Being able to ingest high amounts of food very fast, tolerating the extremely low oxygen concentrations and experiencing no competition and predation by the macrofauna, indicates that benthic foraminifera must play a major role in these oxygen-depleted sediments at the Indian Margin.

The applied method of isotope labeling allowed the estimation of phytodetritus uptake and hence the direct comparison of uptake rates obtained by other deep-sea experiments. A list of the estimated uptake rates of phytodetritus by foraminifera from previous experiments (*in-situ* and *ex-situ*) can be found in Tab. 1. The uptake of the abyssal Pacific assemblage was similar in magnitude and within the response time of assemblages in the deep North Atlantic (Moodley et al., 2002; Witte et al., 2003b), very likely demonstrating the typical response of abyssal foraminifera (Fig. 12). The estimated uptake of the Indian Margin foraminifera exceeds all other observed responses to phytodetritus during *in-situ* feeding experiments (Fig. 12). The main differences to all of these studies are the extreme low oxygen concentrations (0.02-0.05 ml/l), the very high population density of living foraminifera (~4000 ind./10 cm^3) and the absence of the macrofauna which cannot cope with the extreme low oxygen concentrations (Hunter et al., 2012). Being adapted to these extreme oxygen conditions is a big advantage for foraminifera at this site**,** and having no competition/predation might be the reasons for the extreme uptake rates.

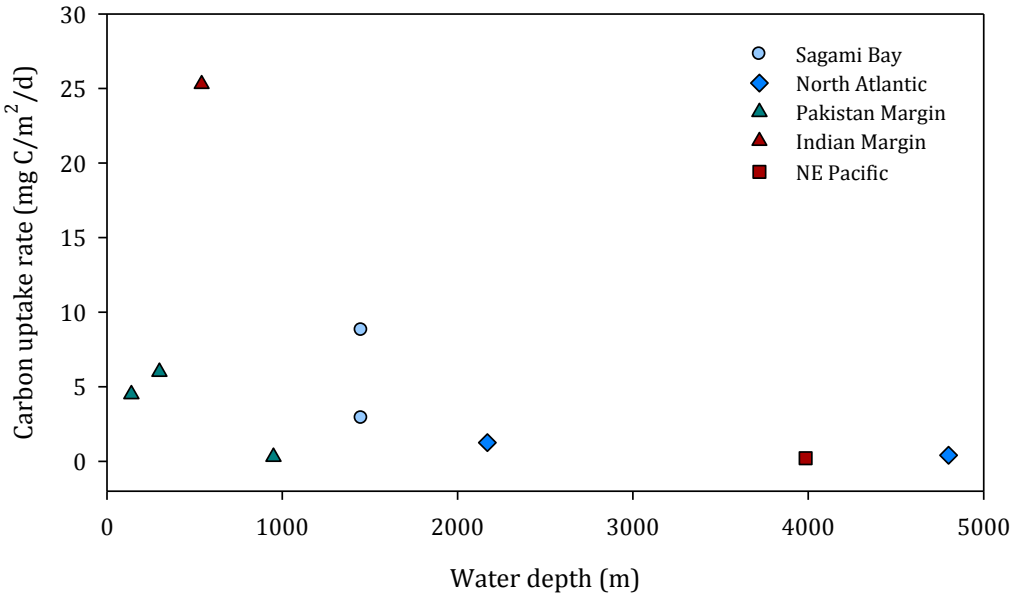


Figure 12 Comparison of uptake rates of organic carbon by benthic foraminifera during *in-situ* feeding experiments using ^{13}C-labeled phytodetritus as food source. The red symbols mark the studies which are object of this thesis and were carried out within the oxygen minimum zone in the Arabian Sea (triangle) and in the abyssal Northeast Pacific (star). Data from previous studies derive from: North Atlantic (Moodley et al., 2002; Witte et al., 2003b), Sagami Bay (Nomaki et al., 2005b; Nomaki et al., 2006), and Pakistan Margin (Woulds et al., 2007).

Table 1 List of *in-situ* and *ex-situ* feeding experiments using ^{13}C-labeled food sources to investigate carbon cycling in marine sediments. Investigations concentrated on benthic foraminifera (F), macrofauna (Ma), meiofauna (Me), bacteria (B), or on the total benthic fauna (Fa). Experiments were performed in the Pacific (Pa), Atlantic (At), Arabian Sea (AS) and in the Mediterranean Sea (Me). Mesh size given refer to size classes of benthic foraminifera. The given uptake and uptake rates are related to foraminifera if in a mixed experiment with other groups.

Location	Bathymetric depth (m)	Experiment set-up	Investigated organisms	Mesh size (µm)	Incubation time	Sediment depth (cm)	Carbon uptake (mg C/m²)	Carbon uptake rate (mg C/m²/d)	References
Sagami Bay (NW Pa)	1445	*in-situ*	**F**	63	2h, 2d, 4d, 6d	0 - 3	($\delta^{13}C$)	-	Kitazato et al. (2003)
	1449	*in-situ*	**F**	63	2d, 6d, 11d	0 - 3	2.0 - 31.0	1.0 – 2.9	Nomaki et al. (2005)
	1450	*in-situ*	**F**	63	2d, 21d	0 - 5	($\delta^{13}C$, f)	8.8	Nomaki et al. (2006)
	1453	*in-situ*	**F**	63	2d, 4d, 6d	0 - 5	fatty acids (FA)	-	Nomaki et al. (2009)
	1453	*in-situ*	**F**	125	9d	0-15	($\Delta\delta^{13}C$, f)	-	Nomaki et al. (2011)
Station M (NE Pa)	3985	*in-situ*	**F**	63	4d	0 - 3	0.82	0.2	Enge et al. (2011)
	4062	*in-situ*	Ma	-	1.5d	0 - 10	0.08	0.1	Sweetman and Witte (2008b)
Carolina Margin (NW At)	850	*in-situ*	Ma (**F**)	300	1d, 1.5d, 3mo, 14mo	0 - 15	($\delta^{13}C$)	-	Levin et al. (1999)
	850	*in-situ*	Ma	-	1.5d	0 - 15	($\delta^{13}C$)	-	Blair et al. (1996)
PAP (NE At)	4800	*in-situ*	**F**, Ma, Me, B	30	2.5d, 8d, 23d	0 - 1	0 - 9	0.4	Witte et al. (2003b)
	~4825	*in-situ*	Ma	-	2.5d, 8d, 23d	0 - 10	($\delta^{13}C$)	-	Aberle and Witte (2003)
NW Spain (N At)	2170	*in-situ*	**F**, B	300	35h	0 - 5	1.82	1.25	Moodley et al. (2002)
	2170	*ex-situ*	Fa (**F**), B	63	1d	0 - 1	0.12	0.12	Moodley et al. (2005)
Nazaré Canyon (N At)	~ 3500	*in-situ*	Me	-	1d, 7d, 14d	0 - 2	0.02 – 0.06	0.004 – 0.02	Ingels et al. (2011)
North Sea (NE At)	intertidal	*in-situ*	Ma, Me, B	-	4.5h, 58h, 134h	0 - 7	($\Delta\delta^{13}C$)	-	Middelburg et al. (2000)
	intertidal	*in-situ, ex-situ*	Ma	-	12h, 30h, 32h, 132h	0 - 16	($\Delta\delta^{13}C$)	-	Kamp and Witte (2005)
	intertidal	*ex-situ*	**F**, B	63	3h, 6h, 12h, 53h	0 - 15	($\Delta\delta^{13}C$)	-	Moodley et al. (2000)
	intertidal	*ex-situ*	Fa (**F**), B	63	1d	0 - 1	16.4	16.4	Moodley et al. (2005)
	37	*ex-situ*	Fa (**F**), B	63	1d	0 - 1	4.9	4.9	Moodley et al. (2005)
Norwegian fjord (NE At)	~ 690	*ex-situ*	**F**	250	2d, 7d, 14d	0 - 6	0 - 0.03	0.002	Sweetman et al. (2009)
	~ 690	*ex-situ*	Ma	-	2d, 7d, 14d	0 - 10	0.04 - 0.7	0.05	Sweetman and Witte (2008a)
	1265	*in-situ*	B, Ma	-	1.5d, 3d	0 - 10	3 - 21	2 - 7	Witte et al. (2003a)
Pakistan Margin (Ar)	140 - 1850	*in-situ, ex-situ*	**F**, Ma, Me, B	150 - 300	2d, 5d	0-20	0.6 – 26.3	0.2 – 7.0	Woulds et al. (2007), Andersson et al. (2008)
Indian Margin (Ar)	540	*in-situ*	**F**	125	4d	0 - 1	101	25.3	Enge et al. (unpublished)
	540-1100	*in-situ*	Ma	-	4d, 7d	0 - 10	0.3 – 5.5	0.05 – 1.4	Hunter et al. (2012)
Cretan Sea (E Me)	1540	*in-situ*	B	-	1.5d	0 – 8	($\Delta\delta^{13}CO_2$, FA)	6 - 47	Bühring et al. (2006)
N Aegean Sea (Me), E Me	102-3859	*ex-situ*	Fa (**F**), B	63	1d	0 - 1	0 – 0.6	0.6	Moodley et al. (2005)

Hence, oxygen not only controls the presence of species but can also indirectly influence the uptake of phytodetritus by foraminifera and other benthic organisms (Woulds et al., 2007). This would partly explain the lower uptake in the OMZ core at the Pakistan Margin (300 m) at higher oxygen concentration (0.11 ml/l), yet with macrofauna presence and foraminiferal abundances of 335 ind./10 cm^3.

But oxygen might not be the only cause for the different reaction of foraminifera between deep-sea sites. Witte et al. (2003b) proposed water temperature to exert an influence which was later investigated by Moodley et al. (2005) by performing a series of *ex-situ* ^{13}C-labeling experiments along a depth gradient (intertidal to 3895 m) covering areas of low and higher water temperature in the Mediterranean Sea. The response to phytodetritus was higher at shallow and deep-sea sites at warmer temperatures (14-18°C) than at shallow and deep-sea areas of lower temperature (4°C).

In summary, the (depth-related) flux of organic matter, the presence of competitors or predators (oxygen controlled) as well as temperature seem to be important influences on the uptake of phytodetritus of deep-sea foraminifera. But further studies like the experimental approach of Woulds et al. (2007) and Andersson et al. (2008) are necessary with feeding experiments being conducted along a depth transect covering different water temperatures, oxygen and food conditions, allowing the investigation of possible combinations of these two major influences.

Suggestions for future isotope labeling experiments

Future feeding experiments using isotopically labeled phytodetritus in order to simulate food pulses and to study the response of foraminifera should be taken the following considerations into account:

- *Using a mixture of phytoplankton species*.
  Offering a broader food spectrum could reflect a more natural food composition rather than a single species (Witte et al., 2003b). Alternatively, offering several food types (e.g. typical phytoplankton species of the region) in separate approaches like it was done by Nomaki et al. (2006; 2011) could provide insight on foraminifer's diets.

- *Increase of incubation time with labeled phytodetritus to weeks or months*.
  This approach is needed to see who is involved in long-term carbon cycling after the initial response. Deep-sea organisms might need to activate their metabolism after long time of starvation or encystment which might apply for species which did not show feeding within few days but are abundantly distributed, such as soft-walled saccamminids (Enge et al., 2011). That

foraminifera can delay their response was shown by Witte et al. (2003b). In the only long-term study Levin et al. (1999) showed that labeling can be obtained even after 14 months.

- *Uptake measurements on species level.*
  Previous studies in Sagami Bay and included in this thesis have shown that the variation in phytodetritus uptake is high between species. For understanding processes in the trophic food web it is essential to know about main contributors in the carbon cycling to be able to draw ecological conclusions.

- *Use of ^{15}N as marker*.
  Nitrogen in form of its stable isotope ^{15}N has shown in the Arabian Sea experiment to be a useful marker to follow the pathway of food to foraminifera, and could be also considered in future experiments next to the commonly used marker ^{13}C. The observed uptake of nitrogen from particulate organic matter (phytodetritus) gives insight on where foraminifera obtain the essential but limited nutrient which they need for biomass build-up (e.g. amino acids, nucleic acids). Knowledge about the nitrogen cycle in deep-sea sediment and the role foraminifera play within is scarce.

- *Performing experiments at lower latitudes*.
  So far, isotope labeling experiments on foraminifera have been solely performed in the northern hemisphere at temperate or warm climates. But foraminifera are also an important element of the benthic fauna in the southern hemisphere and in Arctic or Antarctic deep sea (e.g. Wollenburg and Mackensen, 1998; Cornelius and Gooday, 2004). Though the diets of foraminiferal species in cold habitats have been in focus of few studies (Suhr et al., 2003; Suhr et al., 2008), their role in the trophic food web is largely unknown, and studies on the relationship between food supply and foraminifera are limited to few investigations (e.g. Wollenburg and Kuhnt, 2000).

REFERENCES

Aberle, N., Witte, U., 2003. Deep-sea macrofauna exposed to a simulated sedimentation event in the abyssal NE Atlantic: *in situ* pulse-chase experiments using ^{13}C-labelled phytodetritus. Marine Ecology-Progress Series 251, 37-47.

Akimoto, K., Hattori, M., Uematsu, K., Kato, C., 2001. The deepest living foraminifera, Challenger Deep, Mariana Trench. Marine Micropaleontology 42 (1-2), 95-97.

Alve, E., Murray, J.W., 2001. Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England. Journal of Foraminiferal Research 31 (1), 12-24.

Andersson, J.H., Woulds, C., Schwartz, M., Cowie, G.L., Levin, L.A., Soetaert, K., Middelburg, J.J., 2008. Short-term fate of phytodetritus in sediments across the Arabian Sea Oxygen Minimum Zone. Biogeosciences 5, 43-53.

Armstrong, H.A., Brasier, M.D., 2005. Microfossils, 2nd edition. Blackwill Publishing, Oxford, 304 pp.

Beaulieu, S.E., Smith, K.L. Jr, 1998. Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition. Deep-Sea Research II 45 (4-5), 781-815.

Bennett, B.A., Smith, C.R., Glaser, B., Maybaum, H.L., 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Marine Ecology-Progress Series 108, 205-223.

Bernstein, B.B., Hessler, R.R., Smith, R., Jumars, P.A., 1978. Spatial dispersion of benthic foraminifera in the abyssal central north Pacific. Limnology and Oceanography 23(3), 401-416.

Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytodetritus to the deep-sea benthos. Nature 302 (5908), 520-522.

Blair, N.E., Levin, L.A., DeMaster, D.J., Plaia, G., 1996. The short-term fate of fresh algal carbon in continental slope sediments. Limnology and Oceanography 41 (6), 1208-1219.

Bühring, S.I., Lampadariou, N., Moodley, L., Tselepides, A., Witte, U., 2006. Benthic microbial and whole-community responses to different amounts of ^{13}C-enriched algae: *In situ* experiments in the deep Cretan Sea (Eastern Mediterranean). Limnology and Oceanography 51 (1), 157-165.

Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. Nature 314 (6010), 435-438.

Corliss, B.H., Chen, C., 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. Geology 16 (8), 716-719.

Cornelius, N., Gooday, A.J., 2004. 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. Deep-Sea Research II 51 (14-16), 1571-1602.

de Stigter, H.C., Jorissen, F.J., Van der Zwaan, G.J., 1998. Bathymetric distribution and microhabitat partitioning of live (Rose Bengal stained) benthic foraminifera along a shelf to bathyal transect in the southern Adriatic Sea. Journal of Foraminiferal Research 28 (1), 40-65.

Drazen, J.C., Baldwin, R.J., Smith, K.L. Jr, 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II 45 (4-5), 893-913.

Enge, A.J., Kucera, M., Heinz, P., (2012). Diversity and microhabitat preferences of benthic foraminifera in the abyssal Northeast Pacific. Marine Micropaleontology 96-97, 84-104.

Enge, A.J., Nomaki, H., Ogawa, N.O., Witte, U., Moeseneder, M.M., Lavik, G., Ohkouchi, N., Kitazato, H., Kucera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Marine Ecology-Progress Series 438, 129-142.

Enge, A.J., Witte, U., Kucera, M., Heinz, P., (unpublished). Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin.

Fariduddin, M., Loubere, P., 1997. The surface ocean productivity response of deeper water benthic foraminifera in the Atlantic Ocean. Marine Micropaleontology 32 (3-4), 289-310.

Fry, B., Sherr, E.B., 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and fresh-water ecosystems. Contributions in Marine Science 27, 13-47.

Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: A natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, 504 pp.

Gehrels, W.R., van der Plassche, O., 1999. The use of *Jadammina macrescens* (Brady) and *Balticammina pseudomacrescens* Brönninmann, Lutze und Whittaker (Protozoa: Foraminiferaida) as sea-level indicators. Palaeogeography Palaeoclimatology Palaeoecology 149 (1-4), 89-101.

Geslin, E., Heinz, P., Jorissen, F., Hemleben, C., 2004. Migratory responses of deep-sea benthic foraminifera to variable oxygen conditions: laboratory investigations. Marine Micropaleontology 53 (3-4), 227-243.

Gooday, A.J., 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep-sea. Nature 332 (6159), 70-73.

Gooday, A.J., 1993. Deep-sea benthic foraminiferal species which exploit phytodetritus: Characteristic features and controls on distribution. Marine Micropaleontology 22 (3), 187-205.

Gooday, A.J., Hori, S., Todo, Y., Okamoto, T., Kitazato, H., Sabbatini, A., 2004. Soft-walled, monothalamous benthic forainiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. Deep-Sea Research I 51 (1), 33-53.

Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. Marine Micropaleontology 46 (1-2), 83-110.

Gooday, A.J., Kitazato, H., Hori, S., Toyofuku, T., 2001. Monothalamous soft-shelled foraminifera at an abyssal site in the north Pacific: a preliminary report. Journal of Oceanography 57, 377-384.

Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., 1992. The role of benthic foraminifera in deep-sea food webs and carbon cycling, in: Rowe, G.T., Pariente, V. (Eds.), Deep-Sea Food Chains and the Global Carbon Cycle, Kluwer Adacemic Publishers, Dordrecht, pp. 63-91.

Gooday, A.J., Nomaki, H., Kitazato, H., 2008. Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity, in: Austin, W.E.N., James, R.H. (Eds.), Biogeochemical Controls on Palaeoceanographic Environmental Proxies, Geological Society, London, Special Publications, London, pp. 97-119.

Gooday, A.J., Shires, R., Jones, A.R., 1997. Large, deep-sea agglutinated foraminifera: Two differing kinds of organization and their possible ecological significance. Journal of Foraminiferal Research 27 (4), 278-291.

Graf, G., 1989. Benthic pelagic coupling in a deep-sea community. Nature 341 (6241), 437-439.

Gutt, J., Starmans, A., Dieckmann, G., 1998. Phytodetritus deposited on the Antarctic shelf and upper slope: its relevance for the benthic system. Journal of Marine Systems 17, 435-444.

Heinz, P., Hemleben, C., 2006. Foraminiferal response to the Northeast Monsoon in the western and southern Arabian Sea. Marine Micropaleontology 58 (2), 103-113.

Heinz, P., Hemleben, C., Kitazato, H., 2002. Time-response of cultured deep-sea benthic foraminifera to different algal diets. Deep-Sea Research I 49 (3), 517-537.

Heinz, P., Kitazato, H., Schmiedl, G., Hemleben, C., 2001. Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions. Journal of Foraminiferal Research 31 (3), 210-227.

Heinz, P., Sommer, S., Pfannkuche, O., Hemleben, C., 2005. Living benthic foraminifera in sediments influenced by gas hydrates at the Cascadia convergent margin, NE Pacific. Marine Ecology-Progress Series 304, 77-89.

Hunter, W.R., Levin, L.A., Kitazato, H., Witte, U., 2012. Macrobenthic assemblage structure and organismal stoichiometry control faunal processing of particulate organic carbon and nitrogen in oxygen minimum zone sediments. Biogeosciences 9 (3), 993-1006.

Ingels, J., Billett, D.S.M., Van Gaever, S., Vanreusel , A., 2011. An insight into the feeding ecology of deep-sea canyon nematodes - Results from field observations and the first *in-situ* ^{13}C feeding experiment in the Nazaré Canyon. Journal of Experimental Marine Biology and Ecology 396, 185-193.

Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Marine Micropaleontology 26 (1-4), 3-15.

Kamp, A., Witte, U., 2005. Processing of C-13-labelled phytoplankton in a fine-grained sandy-shelf sediment (North Sea): relative importance of different macrofauna species. Marine Ecology-Progress Series 297, 61-70.

Karl, D.M., Wirsen, C.O., Jannasch, H.W., 1980. Deep-sea primary production at the Galapagos hydrothermal vents. Science 207, 1345-1347.

Kennicutt, M.C., Brooks, J.M., Macko, S.A., Bidigare, R.R., McDonald, S.J., Adkison, D., 1989. An upper slope "cold" seep community: Northern California. Limnology and Oceanography 34 (3), 635-640.

Kitazato, H., Nomaki, H., Heinz, P., Nakatsuka, T., 2003. The role of benthic foraminifera in deep-sea food webs at the sediment-water interface: Results from *in situ* feeding experiments in Sagami Bay. Frontier Research on Earth Evolution 1, 227-232.

Kitazato, H., Oguri, K., Soh, W., Nomaki, H., Shimanaga, M., Nakatsuka, T., Glud, R.N., Middelboe, M., Wenzhofer, F., Heinz, P., 2006. Dynamic Sedimentary Processes at Active Ocean Margins: Results from *in situ* measurements and experiments in Sagami Bay, Japan. Frontier Research on Earth Evolution 2, 1-3.

Kitazato, H., Shirayama, Y., Nakatsuka, T., Fujiwara, S., Shimanaga, M., Kato, Y., Okada, Y., Kanda, J., Yamaoka, A., Masuzawa, T., Suzuki, K., 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from "Project Sagami 1996-1999". Marine Micropaleontology 40 (3), 135-149.

Koho, K.A., Langezaal, A.M., van Lith, Y.A., Duijnstee, I.A.P., Van der Zwaan, G.J., 2008. The influence of a simulated diatom bloom on deep-sea benthic foraminifera and the activity of bacteria: A mesocosm study. Deep-Sea Research I 55 (5), 696-719.

Lambshead, P.J.D., Gooday, A.J., 1990. The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic - the assemblage response. Deep-Sea Research A 37 (8), 1263-1283.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Research A 32 (8), 885-897.

Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep seas: regional characteristics and temporal variability. Deep Sea Research I 44 (8), 1377-1403.

Langer, M.R., Lipps, J.H., 2003. Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. Coral Reefs 22 (2), 143-154.

Levin, L.A., Blair, N.E., Martin, C.M., DeMaster, D.J., Plaia, G., Thomas, C.J., 1999. Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *in situ* experiments using ^{13}C-labeled diatoms. Marine Ecology-Progress Series 182, 37-54.

Linke, P., 1992. Metabolic adaptations of deep-sea benthic foraminifera to seasonally varying food input. Marine Ecology-Progress Series 81, 51-63.

Lochte, K., Turley, C.M., 1988. Bacteria and cyanobacteria associated with phytodetritus in the deep sea. Nature 333 (6168), 67-69.

Loubere, P., 1991. Deep-sea benthic foraminiferal assemblage response to a surface ocean productivity gradient: a test. Paleoceanography 6 (2), 193-204.

Loubere, P., 1998. The impact of seasonality on the benthos as reflected in the assemblages of deep-sea foraminifera. Deep-Sea Research I 45 (2-3), 409-432.

Loubere, P., Fariduddin, M., 1999. Benthic foraminifera and the flux of organic carbon to the seabed, in: Sen Gupta, B. (Ed.), Modern foraminifera, Kluwer Academic Publishers, Great Britain, pp. 181-199.

Meisterfeld, R., Holzmann, M., Pawlowski, J., 2001. Morphological and Molecular Characterization of a New Terrestrial Allogromiid Species: *Edaphoallogromia australica* gen. et spec. nov. (Foraminifera) from Northern Queensland (Australia). Protist 152, 185-192.

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos carbon: An *in situ* ^{13}C-labeling study. Limnology and Oceanography 45 (6), 1224-1234.

Molina-Cruz, A., Ayala-López, A., 1988. Influence of the hydrothermal vents on the distribution of benthic foraminifera from the Guaymas Basin, Mexico. Geo-Marine Letters 8, 49-56.

Moodley, L., Boschker, H.T.S., Middelburg, J.J., Pel, R., Herman, P.M.J., de Deckere, E., Heip, C.H.R., 2000. Ecological significance of benthic foraminifera: ^{13}C-labelling experiments. Marine Ecology-Progress Series 202, 289-295.

Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M.J., Heip, C.H.R., 2002. Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Marine Ecology-Progress Series 236, 23-29.

Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., Heip, C.H.R., 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. Journal of Marine Research 63 (2), 457-469.

Murray, J.W., 1970. The foraminifera of the hypersaline Abu Dhabi Lagoon, Persian Gulf. Lethaia 3 (1), 51-68.

Murray, J.W., 2006. Ecology and applications of benthic foraminifera. Cambridge University Press, Cambridge, 426 pp.

Murray, J.W., 2007. Biodiversity of living benthic foraminifera: How many species are there? Marine Micropaleontology 64 (3-4), 163-167.

Nomaki, H., Heinz, P., Hemleben, C., Kitazato, H., 2005a. Behavior and response of deep-sea benthic foraminifera to freshly supplied organic matter: A laboratory feeding experiment in microcosm environments. Journal of Foraminiferal Research 35 (2), 103-113.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005b. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: *In situ* tracer experiments. Limnology and Oceanography 50 (1), 134-146.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N.O., Kogure, K., Ikemoto, E., Kitazato, H., 2006. Different ingestion patterns of ^{13}C-labeled bacteria and algae by deep-sea benthic foraminifera. Marine Ecology-Progress Series 310, 95-108.

Nomaki, H., Ogawa, N.O., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., Kitazato, H., 2008. Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence. Marine Ecology-Progress Series 357, 153-164.

Nomaki, H., Ogawa, N.O., Takano, Y., Suga, H., Ohkouchi, N., Kitazato, H., 2011. Differing utilization of glucose and algal particulate organic matter by deep-sea benthic organisms of Sagami Bay, Japan. Marine Ecology-Progress Series 431, 11-24.

Nomaki, H., Ohkouchi, N., Heinz, P., Suga, H., Chikaraishi, Y., Ogawa, N.O., Matsumoto, K., Kitazato, H., 2009. Degradation of algal lipids by deep-sea benthic foraminifera: An *in situ* tracer experiment. Deep-Sea Research I 56 (9), 1488-1503.

Nozawa, F., Kitazato, H., Tsuchiya, M., Gooday, A.J., 2006. 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. Deep-Sea Research I 53 (8), 1406-1422.

Pawlowski, J., Bolivar, I., Fahrni, J., de Vargas, C., Bowser, S.S., 1999a. Naked foraminiferans revealed. Nature 399 (6731), 27-27.

Pawlowski, J., Bolivar, I., Fahrni, J.F., de Vargas, C., Bowser, S.S., 1999b. Molecular evidence that *Reticulomyxa filosa* is a freshwater naked Foraminifer. Journal of Eukaryotic Microbiology 46 (6), 612-617.

Pawlowski, J., Holzmann, M., Berney, C., Fahrni, J., Gooday, A.J., Cedhagen, T., Habura, A., Bowser, S.S., 2003. The evolution of early Foraminifera. Proceedings of the National Academy of Sciences of the United States of America 100 (20), 11494-11498.

Pfannkuche, O., 1993. Benthic response to the sedimentation of particulate organic matter at the Biotrans Station, 47-Degrees-N, 20-Degrees-W. Deep-Sea Research II 40 (1-2), 135-149.

Risgaard-Petersen, N., Langezaal, A.M., Ingvardsen, S., Schmid, M.C., Jetten, M.S.M., Op den Camp, H.J.M., Derksen, J.W.M., Pina-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., van der Zwaan, G.J., 2006. Evidence for complete denitrification in a benthic foraminifer. Nature 443 (7107), 93-96.

Schmiedl, G., de Bovee, F., Buscail, R., Charriere, B., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. Marine Micropaleontology 40 (3), 167-188.

Schmiedl, G., Mackensen, A., Muller, P.J., 1997. Recent benthic foraminifera from the eastern South Atlantic Ocean: Dependence on food supply and water masses. Marine Micropaleontology 32 (3-4), 249-287.

Schönfeld, J., 2012. History and development of methods in recent benthic foraminiferal studies. Journal of Micropalaeontology 31, 53-72.

Schroeder, C.J., Medioli, F.S., Scott, D.B., 1989. Fragile abyssal foraminifera (including new Komokiacea) from the Nares Abyssal Plain. Micropaleontology 35 (1), 10-48.

Smart, C.W., Gooday, A.J., 1997. Recent benthic foraminifera in the abyssal northeast Atlantic ocean: relation to phytodetrital inputs. Journal of Foraminiferal Research 27 (2), 85-92.

Smith, K.L. Jr, Baldwin, R.J., 1984. Seasonal fluctuations in deep-sea sediment community oxygen consumption: central and eastern North Pacific. Nature 307 (624-626).

Suess, E., 1980. Particulate organic carbon flux in the oceans - surface productivity and oxygen utilization. Nature 288, 260-263.

Suhr, S.B., Alexander, S.P., Gooday, A.J., Pond, D.W., Bowser, S.S., 2008. Trophic modes of large Antarctic Foraminifera: roles of carnivory, omnivory, and detritivory. Marine Ecology-Progress Series 371, 155-164.

Suhr, S.B., Pond, D.W., Gooday, A.J., Smith, C.R., 2003. Selective feeding by benthic foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty acid biomarker analysis. Marine Ecology-Progress Series 262, 153-162.

Sweetman, A.K., Sommer, S., Pfannkuche, O., Witte, U., 2009. Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord. Journal of Foraminiferal Research 39 (1), 15-22.

Sweetman, A.K., Witte, U., 2008a. Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. Deep-Sea Research I 55 (11), 1503-1514.

Sweetman, A.K., Witte, U., 2008b. Response of an abyssal macrofaunal community to a phytodetrital pulse. Marine Ecology-Progress Series 355, 73-84.

Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A.J., Hemleben, C., Mantoura, R.F.C., Turley, C.M., Patching, J.W., Riemann, F., 1988. Phytodetritus on the deep-sea floor in a central oceanic region of the northeast Atlantic. Biological Oceanography 6 (2), 203-239.

Turley, C.M., 2000. Bacteria in the cold deep-sea benthic boundary layer and sediment-water interface of the NE Atlantic. FEMS Microbiology Ecology 33, 89-99.

Turley, C.M., Lochte, K., 1990. Microbial response to the input of fresh detritus to the deep-sea bed. Global and Planetary Change 89 (1-2), 3-23.

Witte, U., Aberle, N., Sand, M., Wenzhofer, F., 2003a. Rapid response of a deep-sea benthic community to POM enrichment: an in situ experimental study. Marine Ecology-Progress Series 251, 27-36.

Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.R., Jorgensen, B.B., Pfannkuche, O., 2003b. *In situ* experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424 (6950), 763-766.

Wollenburg, J.E., Kuhnt, W., 2000. The response of benthic foraminifers to carbon flux and primary production in the Arctic Ocean. Marine Micropaleontology 40 (3), 189-231.

Wollenburg, J.E., Mackensen, A., 1998. Living benthic foraminifers from the central Arctic Ocean: faunal composition, standing stock and diversity. Marine Micropaleontology 34 (3-4), 153-185.

Woulds, C., Cowie, G.L., Levin, L.A., Andersson, J.H., Middelburg, J.J., Vandewiele, S., Lamont, P.A., Larkin, K.E., Gooday, A.J., Schumacher, S., Whitcraft, C., Jeffreys, R.M., Schwartz, M., 2007.

Oxygen as a control on seafloor biological communities and their roles in sedimentary carbon cycling. Limnology and Oceanography 52 (4), 1698-1709.

Ziegler, B., 1983. Einführung in die Paläobiologie Teil 2, Spezielle Paläontologie, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 409 pp.

ACKNOWLEDGMENTS

Coming so far would have not been possible without the help of many people and I am very grateful for all their support on a professional and private basis.

First of all I want to thank my first supervisor PD Dr. Petra Heinz. For giving me the possibility to work on such an interesting topic and to get to know many other scientists from this field. Always having an open ear if questions or need for discussion were arising. And I also want to thank her for supporting me in the participation in conferences, workshops and cruises.

I also want to thank Prof. Dr. Michal Kucera, my second supervisor who I am thankful for his time he spent with me reviewing my work. Gave me great input on how to look at my results and to learn to ask the right questions.

I want to thank both of them for evaluation my PhD thesis and Prof. Dr. Herve Bocherens and Prof. Dr. Angelika Brandt for being members of the defense committee.

I'm also thankful to Dr. Hartmut Schulz and Margret Bayer for helping with the SEM and during our cruises where I could benefit from their long-term experience. Also many thanks to the rest of the working group "Mikropal". For sharing free exercise lessons in the mountains during group retreats and very enjoyable Christmas parties at the hut. Especially I want to thank my "Hiwis" Anne Bayer, Ralf Leidig and most of all Marie Zahnert for their help and picking foraminifera in endless hours.

Also many thanks go to colleagues from other international research institutes for fruitful corporations.

I cannot give enough thanks to my family, especially to my parents. Never questioning my career choice and supporting me in every way is more than I could have asked for. Thank you so much.

And at last I want to thank my friends for their comfort, trust, open ears and help during the last years. Couldn't wish for better ones.

Publication 1

Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific

Vol. 438: 129–142, 2011
doi: 10.3354/meps09298

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 5

OPEN ACCESS

Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific

Annekatrin J. Enge[1,*], Hidetaka Nomaki[2], Nanako O. Ogawa[2], Ursula Witte[3], Markus M. Moeseneder[3,4], Gaute Lavik[5], Naohiko Ohkouchi[2], Hiroshi Kitazato[2], Michal Kučera[1], Petra Heinz[1]

[1]Department for Geosciences, University of Tübingen, Hölderlinstrasse 12, 72074 Tübingen, Germany
[2]Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka, 237-0061, Japan
[3]Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, UK
[4]National Oceanography Centre, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK
[5]Max Planck Institute for Marine Microbiology, Celsiusstrasse 1, 28359 Bremen, Germany

ABSTRACT: Foraminifera are an important faunal element of the abyssal ecosystem and largely depend on deposited particulate organic matter from the photic zone to sustain their metabolism for growth and reproduction. However, their role in the carbon cycle in deep-sea sediments is insufficiently studied. We investigated benthic foraminifera at Station M (4000 m depth) in the Northeast Pacific and assessed the response of individual species to a simulated phytodetritus pulse during an *in situ* feeding experiment. Sediments were incubated for 4 d with ^{13}C-labeled diatoms (*Thalassiosira weissflogii*) applied to the sediment surface. The living foraminiferal community (>0.063 mm) of the upper 3 cm contained >100 species and was strongly dominated by a few taxa of soft-walled saccamminids. Population density of the entire living foraminiferal community was highest at the sediment surface (mean ± SD = 279 ± 72 ind. 10 cm^{-3} in background and ^{13}C-incubated cores) and decreased gradually with depth. Large differences were observed in the uptake of the algal material among species and between depth levels. During the experiment, 0.82 mg C m^{-2} were ingested, mainly by calcareous (~60%) and agglutinated (~40%) foraminifera. Uptake was highest at the sediment surface and 3 to 5 times less in deeper sediment horizons. Despite clear signs of vitality and a strong representation in the foraminiferal community, none of the soft-walled species showed a noticeable response to the offered algal material. We conclude that soft-walled foraminifera may not be important to the short-term phytodetrital matter cycling at the abyssal sea floor.

KEY WORDS: Deep sea · North Pacific · *In situ* feeding experiment · δ^{13}C · Isotopic labeling · Benthic foraminifera · Carbon remineralization · Soft-walled saccamminid

INTRODUCTION

In the deep sea, foraminifera are an important component of the benthic community and can account for 50% or more of the eukaryotic biomass (Gooday et al. 1992). Altenbach (1992) estimated that 6 to 10% of the total flux of organic matter to the sediment surface in the deep sea is ingested by benthic foraminifera. In the deeper regions of the oceans (>1000 m depth), the biomass of benthic foraminifera is posi-

*Email: annekatrin.enge@uni-tuebingen.de

tively correlated with the flux of organic matter (Altenbach 1992, Altenbach & Struck 2001). Mainly controlled by oxygen concentration and food availability, individual foraminiferal species have adapted to different environmental conditions and display specific microhabitat preferences within the sediment (Corliss & Emerson 1990, Jorissen et al. 1995). Differences in the amount and delivery pattern of phytodetritus have a direct impact on benthic foraminifera (Gooday & Lambshead 1989, Lambshead & Gooday 1990) in controlling their abundance and the distribution of species (Thiel et al. 1988, Gooday 1993).

Feeding experiments using isotopically-labeled food (e.g. with ^{13}C) and tracking the ingested tracer by changes in the isotopic composition of the cytoplasm have become an effective tool to study *in situ* phytodetrital carbon uptake by these organisms (Blair et al. 1996). Such approaches have been successfully operated in foraminifera within different habitats: the intertidal flat in the southern North Sea (Moodley et al. 2000), a fjord in Norway (Sweetman et al. 2009), the bathyal region of the Northwest Pacific (Nomaki et al. 2005b, 2006, 2009, 2011), and the abyssal North Atlantic (Moodley et al. 2002, Witte et al. 2003b). These studies showed that benthic foraminifera within each particular habitat contributed to carbon cycling but with large differences in the degree of uptake. However, it remains unclear why such differences in carbon uptake occur, to what degree the results can be generalized to other regions, and how the ecological preferences of individual species affect the rate and pattern of carbon uptake in benthic foraminifera.

We aimed to investigate the contribution of foraminifera to carbon remineralization in the abyssal ocean. Results will give more information about the role of foraminifera within the global marine carbon cycle, also in comparison to other benthic organisms and different marine habitats. We chose Station M (Stn M) in the abyssal Northeast Pacific to perform the *in situ* feeding experiment.

The extensive study of benthic and pelagic processes at Stn M over the last 2 decades by K. Smith and colleagues has created a complex picture of the system and the influencing factors, worth for designing a model for deep-sea processes (Smith et al. 2006) and helpful in interpreting the abiotic influence on the foraminiferal assemblage. The role of benthic organisms in carbon cycling at this abyssal site has been investigated, though predominately on macrofauna (e.g. Sweetman & Witte 2008a,b). Drazen et al. (1998) reported a positive long-term response of the foraminiferal density towards food availability at Stn M, but considered only specimens >300 µm in size and investigated the numerical change of foraminifera as a taxon rather than measuring uptake or looking at single species. In comparison, we explored the role of benthic foraminifera >63 µm and concentrated on specific rates of species. Thus, a very different assemblage was examined, as we also included soft-walled species as an important part of the investigated fauna.

Observations on population densities in the central North Pacific (Hessler & Jumars 1974, Bernstein et al. 1978, Snider et al. 1984) and in the Northeast Pacific at Stn M (Drazen et al. 1998) have shown the numerical importance of benthic foraminifera among the sediment-inhabiting fauna in this region, indicating their important contribution to carbon cycling here. Especially monothalamous soft-walled foraminifera are important components of deep-sea sediments (Gooday 1994), in particular in oligotrophic areas and below the carbonate compensation depth with an assumed diet of refractory organic material and bacteria (Gooday et al. 2008). Despite their numerical significance, the taxonomy, ecology, and role of monothalamous soft-walled foraminifera in deep-sea sediments remain mostly unknown and require further study. This will be the first time that soft-walled foraminifera are included in a feeding experiment using isotopic labeling. We investigated and compared species-specific ingestion rates of benthic foraminifera, focusing on single morphotypes of soft-walled species because of their numerical dominance in the foraminiferal fauna. High measurement sensitivity allowed us to achieve the first species-level analysis of a soft-walled fauna from the abyssal plain.

The marine diatom *Thalassiosira weissflogii* was chosen as a potential food source in our experiment. This species is a cosmopolitan bloom-forming taxon which has been previously used in a series of deep-sea feeding experiments, and the genus is commonly found in detrital aggregates at the investigation site, Stn M (Beaulieu & Smith 1998).

MATERIALS AND METHODS

Study site

The feeding experiment was carried out at Stn M (34° 50′ N, 123° 00′ W) in the abyssal Northeast Pacific in September 2007. This site is located 220 km west off Point Conception, California, USA (Fig. 1), at the base of the Monterey Deep-Sea Fan and has

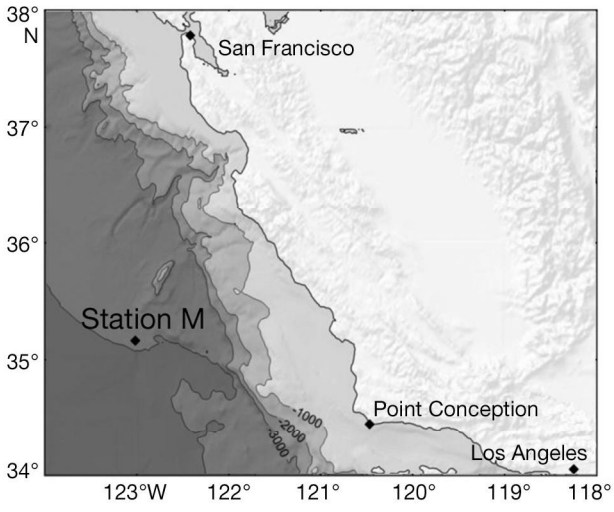


Fig. 1. 'Station M' off California, USA, site of the *in situ* feeding experiment

been described in detail by Smith & Druffel (1998). The sea floor at Stn M shows little topographical relief (<100 m over 1600 km^2), has silty-clayey sediments (Smith & Druffel 1998), and dissolved oxygen is present in the pore water to ~3 cm sediment depth (Reimers 1987).

Phytoplankton primary production along the coast of California occurs from spring to fall (Smith & Druffel 1998), with a net production range of 200 to 1200 mg C m^{-2} d^{-1} (Ruhl & Smith 2004, Smith et al. 2008). The export of photosynthetically derived organic matter and the abyssal particulate organic carbon (POC) flux at Stn M are correlated (Smith et al. 2008) and exhibit both intra- and inter-annual variability (Smith et al. 1994, 2001, 2006, Smith & Druffel 1998). The POC flux measured at 3000 m depth from 1998 to 2006 ranged between 0 and 70 mg C m^{-2} d^{-1}, with a mean of ~10 mg C m^{-2} d^{-1} (Smith et al. 2008, 2009). Hence, phytodetritus is available to benthic organisms only during a limited period of time.

Preparation of ^{13}C-labeled algae

The diatom *Thalassiosira weissflogii* was cultured at 15°C (16 h light:8 h dark) in artificial seawater (Grasshoff et al. 1999) amended with f/2 medium (CCMP) and ^{13}C-bicarbonate (99 atom% ^{13}C-enriched $NaHCO_3$, Cambridge Isotope Laboratories). Algae were harvested by centrifugation (1400 *g*, 15 min) and washed 3 times with sterile-filtered (0.2 µm) seawater to remove excess $NaH^{13}CO_3$ and any dissolved organic ^{13}C exuded by the diatoms. The harvest was quick-frozen in liquid nitrogen to avoid cell rupture and stored at –80°C until freeze-drying. The dried algae contained 53.45 atom% ^{13}C (measured on a Flash EA 1112 Series Elemental Analyzer connected via a Conflo III to a Delta^{Plus} Advantage isotope ratio mass spectrometer, Thermo Finnigan).

Experimental setup

The *in situ* feeding experiment was carried out during the 'PULSE 53' cruise of the RV 'Western Flyer' at 3953 m depth with 2 Oceanlab spreader systems (290 mm inner diameter). The plexiglass tubes of the spreaders were deployed at the sea floor and pushed into the sediment by the remotely operated vehicle ROV 'Tiburon' until standing firmly upright. Each spreader lid held a container with a suspension of 215 mg of ^{13}C-labeled freeze-dried *Thalassiosira weissflogii*, which was applied to the enclosed sediment surface by pushing a plunger that subsequently releases the algae. The lids of the spreaders were removed after the algal material had entirely deposited on the sediment surface. The added algal biomass corresponds to about a quarter of the annual POC flux at Stn M (e.g. Smith et al. 2008, 2009) and can be considered as a realistic simulation of a rapidly sinking bloom event. Incubation of sediments with labeled algae lasted 4 d. The sufficient amount of food and the open system with continuous water exchange guaranteed a set up very similar to natural conditions. After the incubation period, 1 push core (plexiglass tube, 70 mm internal diameter) from each of the 2 spreader devices and 2 additional push cores from the surrounding sediment were recovered by the ROV. Sediment cores were immediately sliced (0–1, 1–2, 2–3 cm) on board the research vessel and kept frozen at –20°C. We concentrated on the oxygenated upper 3 cm of sediment, as foraminiferal assemblages of abyssal sediments are dominated by epifaunal and shallow infaunal species (Corliss & Emerson 1990, Gooday 1994).

Sample preparation

In the laboratory (University of Tübingen), sediment samples were thawed and washed over a mesh (63 µm) with artificial seawater of 34 to 35 psu (23.4 g NaCl, 4.0 g $MgSO_4 \times 7\ H_2O$, 0.8 g KCl, 0.26 g $CaCl_2$, and distilled water up to 1 l final volume). After sieving, residues were frozen at –20°C until further pro-

cessing. Separation of living and dead specimens was based on visual assessment of cytoplasm presence (Moodley et al. 2002, Nomaki et al. 2005b, 2006, Sweetman et al. 2009) and the degree to which it filled the test. Foraminifera were wet-picked under cooled conditions and identified to species level if possible. We had to adjust the counting method for several types of agglutinated groups: (1) counts of fragments of multi-chambered specimens (*Reophax, Hormosinella*) were normalized to complete specimens by dividing fragment counts by the maximum number of chambers observed in intact tests of each species, (2) fragments of tubular-shaped species (e.g. *Rhabdammina*, *Saccorhiza*) were converted to individual counts by dividing the number of fragments by 3 (Kurbjeweit et al. 2000). All individuals of species that could not be analyzed separately because of insufficient biomass were pooled into 1 taxonomic group and are referred to as 'other.' In agglutinated foraminifera, multiple species were grouped together based on their general morphology, related to possible habitat adaptations. The group 'tubular' agglutinates includes specimens of the taxon Astrorhizida (except Saccamminidae), while members of the taxa Lituolida, Trochamminida, and Textularida were pooled under 'non-tubular' agglutinated.

Before processing material for isotopic analysis, glassware and silver cups were combusted (450°C, 5 h), and picking tools were cleaned with a mixture of dichloromethane and methane (1:1, v:v) to be organic free. All foraminifera were carefully brushed to remove organic matter on the outside of the test, washed twice in filtered artificial seawater, and then transferred into silver cups (each filled with 30 µl of filtered seawater). Subsequently, the filled cups were dried at 50°C for several hours before adding 20 µl hydrochloric acid (6.25%) to remove all calcium carbonate in the samples. To completely dry the samples, heating and acidification were repeated once more, and samples were kept at 50°C for 3 d.

Measurements of the total organic carbon (TOC) content and the ratio of the carbon isotopes (^{13}C:^{12}C) of the foraminiferal cytoplasm were realized at the Japanese Agency for Marine-Earth Science and Technology (JAMSTEC) and at the Max Planck Institute (MPI) for Marine Microbiology in Bremen, Germany. At JAMSTEC, acidified samples in silver capsules were further wrapped with a tin capsule before elemental analyzer/isotopic ratio mass spectrometer (EA/IRMS) analysis. Both capsules were pre-cleaned by a methanol:dichloromethane (1:1, v:v) solution. The required minimum amount of TOC for reliable isotopic measurements was either 700 ng (JAMSTEC; Ogawa et al. 2010) or 10 µg (MPI). To obtain species-level analysis, we pooled individuals of 1 species or group from both cores of identical treatment (^{13}C-incubation or background) at the same sediment depth. Therefore, no replicates were measured and not all species or groups were analyzed at each depth level.

Calculation of carbon uptake

The carbon isotope ratio (^{13}C:^{12}C) of foraminiferal cytoplasm was measured against the international Vienna Pee Dee Belemnite standard (VPDB) and is expressed as the difference between sample and standard in the δ-notation: $\delta^{13}C$ (‰) = $[(^{13}C{:}^{12}C_{sample})/(^{13}C{:}^{12}C_{VPDB}) - 1] \times 10^3$. Specific uptake of labeled ^{13}C by foraminifera was calculated as excess (above background) and is expressed in the Δ-notation: $\Delta\delta^{13}C$ (‰) = $\delta^{13}C_{sample} - \delta^{13}C_{background}$. Carbon uptake was calculated as the product of the excess atom% ^{13}C and the carbon content of the cytoplasm in the sample, divided by the atom% ^{13}C of the labeled algae: C-uptake (µg C) = $[(\text{atom\% } ^{13}C_{sample} - \text{atom\% } ^{13}C_{background}) / 53.45 \text{ atom\%}] \times (TOC_{sample})$ (Sweetman & Witte 2008a,b, Sweetman et al. 2009).

The natural $\delta^{13}C$ variation was calculated for every foraminiferal species from the mean background $\delta^{13}C$ value by addition and subtraction of the standard deviation (SD). The resultant species-specific range was then used to separate significant enrichment from natural $\delta^{13}C$ variation in species, i.e. calculated $\Delta\delta^{13}C$ values within the range were excluded from further uptake estimation. Error terms stated in combination with calculated data (e.g. on foraminiferal abundance, TOC content) are SD.

RESULTS

Abundance and biomass of living foraminifera

Highest numbers of living foraminifera were found at the sediment surface (279 ± 72 ind. 10 cm^{-3}), and abundances declined with sediment depth. Altogether, >100 species were identified, and the assemblage was highly dominated by a few taxa. Soft-walled foraminifera were the most abundant group at all 3 sediment depths (Table 1) and contributed up to 71% of the specimens in the deeper layers. These foraminifera (Saccamminidae, Astrorhizida) are monothalamous saccamminids with variable external morphology. The taxonomic classification of this group of

agglutinated foraminifera remains uncertain because of lack of characters and poor taxonomic knowledge. So we divided them into *Saccamminid* sp. 1 to 4 on the basis of the shape and length of the 'neck' and the composition of the outer wall (smooth and shiny, coarse, or coarse with small particles sticking to the wall). This group will hereafter be referred to as 'soft-walled' and will be handled separately from the remaining agglutinated species. Agglutinated foraminifera other than the monothalamous saccamminids were also present at all depths and showed the highest diversity (68 taxa). Calcareous foraminifera with 45 taxa showed an abundance maximum in the top cm and a minimum at 1–2 cm depth. Their total population density corresponds to only 10% of the total foraminiferal assemblage (10 to 34 ind. 10 cm^{-3}).

In general, agglutinated foraminifera contributed most to the foraminiferal biomass at 0–2 cm depth (Table 1), whereas calcareous and soft-walled foraminifera showed less but comparatively similar contribution to the overall biomass. Abundance and biomass of the living foraminiferal populations did not differ between ^{13}C-incubated and background sediments (paired *t*-tests, n = 4, p > 0.05) (Fig. 2A,B).

In total, 2 types of monothalamous saccamminids, 6 calcareous and 8 agglutinated species occurred in sufficient numbers and biomass to allow species-specific isotope analyses.

Table 1. Foraminiferal numbers and biomass at Station M in background (core nos. 1 & 2) and incubated sediment cores (core nos. 3 & 4). TOC: total organic carbon

Depth (cm)	Core no.	Abundance (n 10 cm^{-2})			Biomass (µg TOC 10 cm^{-2})		
		Agglutinated	Calcareous	Soft-walled	Agglutinated	Calcareous	Soft-walled
0–1	1	72	19	103	10	5	6
	2	118	36	152	20	11	8
	3	112	31	112	20	10	6
	4	168	52	144	36	9	7
1–2	1	30	8	116	5	2	8
	2	42	18	119	8	9	8
	3	94	11	149	20	3	8
	4	63	5	81	13	2	6
2–3	1	27	17	165	3	9	11
	2	14	19	99	2	9	7
	3	35	13	92	8	5	5
	4	44	12	78	9	3	4

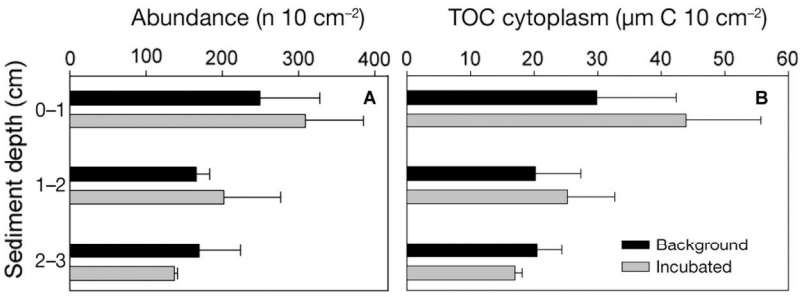


Fig. 2. (A) abundance (n 10 cm^{-2}) and (B) biomass (µg total organic carbon, TOC, 10 cm^{-2}) of living foraminifera from background and ^{13}C-incubated sediments (mean + SD, 2 cores each)

Organic carbon content in foraminiferal cytoplasm

Carbon content for 1 individual was obtained by dividing measured total TOC content of pooled individuals (Table 2) through the number of measured specimens. Mean TOC content of 1 foraminifer ranged between 0.04 and 52.01 µg (Table 2). Soft-walled and calcareous foraminifera had a mean TOC content of 0.07 ± 0.02 and 0.20 ± 0.19 µg ind.$^{-1}$, respectively (from both sediment treatments). Agglutinated foraminifera showed a higher mean TOC (1.62 ± 8.52 µg). The largest difference in the TOC content per individual between sediment levels was found in the group 'other tubular agglutinated' in the ^{13}C-incubated sediment (Table 2). TOC content did not differ significantly between foraminiferal cytoplasm from ^{13}C-incubated and background sediment (paired *t*-test for all species/groups and depths: $t = -0.44$, $p = 0.66$, $n = 16$). Of 16 single species/groups tested, only *Cribrostomoides subglobosum* showed a significant difference between the 2 core types (paired *t*-test: $t = -275.37$, $p = 0.02$) with higher TOC content in the ^{13}C-incubated cores.

Natural isotopic signatures

The isotopic signatures of benthic foraminifera from background sediment exhibited a mean $\delta^{13}C$ of −19.5 ± 2.9‰ (Fig. 3, Table 2) and were slightly heavier than the $\delta^{13}C$ of sedimentary TOC with an average of −22.2‰ (U. Witte et al. unpublished data). The group 'other calcareous' displayed the overall lightest (−23.2‰, at 0–1 cm) and heaviest value (−7.1‰, at 1–2 cm). Differences in the

Table 2. Total organic carbon content (TOC) content, isotopic signatures and carbon uptake of foraminifera from background and incubated sediments. n: number of individuals; n for tubular agglutinated specimens (marked with ⋆) represents number of fragments. Single TOC values represent measurement of pooled samples divided by n. Bkgr. & inc. TOC: mean TOC ± SD, combined from background (bkgr.) and incubated (inc.) sediments across 0 to 3 cm depth. Missing background $\delta^{13}C$ signatures were substituted as follows: *C. subglobosum* (1–2 cm): mean of values from 0–1 and 2–3 cm; *Saccorhiza ramosa* (0–1, 2–3 cm): same value as for 1–2 cm; *I. tumidula* (0–1 cm): averaged from all other calcareous signatures at 0–1 cm; *C. cancellata* (0–1 cm): averaged from the values presented by Nomaki et al. (2006). ⋆⋆: excess ($\Delta\delta^{13}C$) which does not exceed natural background variation (see 'Materials and methods'). nd: no data

	Depth	Background sediment			^{13}C-incubated sediment			Bkgr. & inc. TOC (µg per ind.)	$\Delta\delta^{13}C$ (‰)	C uptake (µg C m^{-2})
		n	TOC (µg per ind.)	$\delta^{13}C$ (‰)	n	TOC (µg per ind.)	$\delta^{13}C$ (‰)			
Soft-walled taxa										
Saccamminid sp. 3	0–1 cm	263	0.06	–21.6	443	0.08	–17.8	0.08 ± 0.01	3.8	0.07
	1–2 cm	176	0.10	–20.6	174	0.09	–19.6		1.0	0.05
	2–3 cm	49	0.08	–21.0	133	0.09	–19.1		1.9	0.08
Saccamminid sp. 4	0–1 cm	453	0.04	–20.9	520	0.04	–16.5	0.05 ± 0.01	4.4	0.58
	1–2 cm	546	0.04	–19.1	526	0.06	–20.2		–1.1 ⋆⋆	nd
	2–3 cm	726	0.04	–19.2	357	0.07	–18.8		0.5 ⋆⋆	nd
Other soft-walled	0–1 cm	90	0.08	–19.2	102	0.12	–27.1	0.07 ± 0.03	–7.9 ⋆⋆	nd
	1–2 cm	72	0.07	–18.7	92	0.06	–17.9		0.8	0.01
	2–3 cm	92	0.06	–19.2	84	0.05	–17.4		1.8	0.02
Total soft-walled taxa	0–3 cm							0.07 ± 0.02		0.82
Calcareous taxa										
Epistominella pusilla	0–1 cm	37	0.06	–17.8	83	0.05	145	0.07 ± 0.02	162.8	1.89
	1–2 cm	15	0.10	–18.7	nd	nd	nd		nd	nd
	2–3 cm	27	0.06	–20.0	10	0.09	–4.1		15.9	0.08
Globocassidulina subglobosa	0–1 cm	30	0.03	–15.9	70	0.08	–10.3	0.09 ± 0.04	5.6	0.08
	1–2 cm	14	0.14	–21.9	18	0.18	–12.9		9.0	0.05
	2–3 cm	13	0.09	–20.9	nd	nd	nd		nd	nd
Ioanella tumidula	0–1 cm	nd	nd	(–19.7)	25	0.06	–7.5	0.056	12.2	0.06
Melonis barleeanum	0–1 cm	13	0.21	–17.7	6	0.46	–17.0	0.37 ± 0.22	0.7	0.01
	1–2 cm	9	0.64	–17.9	13	0.18	–17.6		0.3	0.00
Other calcareous	0–1 cm	87	0.35	–23.2	86	0.72	1636.2	0.30 ± 0.22	1659.4	342.58
	1–2 cm	25	0.17	–7.1	12	0.17	nd		nd	nd
	2–3 cm	20	0.27	–19.7	25	0.13	nd		nd	nd
Total calcareous taxa	0–3 cm							0.20 ± 0.19		344.75
Agglutinated taxa										
Adercotryma glomerata	0–1 cm	70	0.07	–22.6	91	0.04	141.5	0.067 ± 0.03	164.0	1.57
	1–2 cm	16	0.11	–18.5	nd	nd	nd		nd	nd
	2–3 cm	16	0.09	–18.7	12	0.04	–9.6		9.1	0.03
Cribrostomoides subglobosum	0–1 cm	9	0.38	–19.0	44	0.16	225	0.25 ± 0.13	244.0	5.06
	1–2 cm	11	0.41	–19.5	40	0.19	nd		nd	nd
	2–3 cm	nd	nd	(–19.3)	15	0.13	–12.6		6.7	0.04
Cyclammina cancellata	0–1 cm	nd	nd	(–19.8)	1	52.01	–7.7	52.01	12.1	1.69
Hormosinella guttifera	0–1 cm	74	0.05	–18.0	99	0.06	8.7	0.11 ± 0.12	26.7	1.65
	1–2 cm	25	0.07	–16.7	27	0.06	39.0		55.7	0.84
	2–3 cm	15	0.34	–19.6	28	0.04	3.4		23.0	0.32
Trochammina globigeriniformis	0–1 cm	11	0.10	–16.9	35	0.14	2030	0.09 ± 0.03	2046.9	44.03
	1–2 cm	16	0.07	–18.5	30	0.05	nd		nd	nd
Trochammina inflata	0–1 cm	22	0.07	–18.9	43	0.04	5.3	0.06 ± 0.02	24.2	0.22
Other non-tubular agglutinated	0–1 cm	255	0.18	–21.5	383	0.14	485.8	0.14 ± 0.04	507.3	98.27
	1–2 cm	126	0.12	–21.7	145	0.18	202.5		224.2	30.44
	2–3 cm	108	0.17	–18.7	141	0.07	–11.7		7.0	0.22
Rhabdammina abyssorum⋆	0–1 cm	266	0.32	–21.4	443	0.30	23.2	0.29 ± 0.07	44.6	16.37
	1–2 cm	20	0.19	–20.0	198	0.33	–17.2		2.8	0.62
Saccorhiza ramosa⋆	0–1 cm	nd	nd	(–17.4)	4	4.38	–18.1	1.95 ± 1.69	–0.7 ⋆⋆	nd
	1–2 cm	4	0.90	–17.4	87	0.68	285.8		303.2	49.46
	2–3 cm	nd	nd	(–17.4)	10	1.85	813		830.4	158.71
Other tubular agglutinated⋆	0–1 cm	150	0.59	–20.3	173	0.73	292.8	1.04 ± 1.33	313.1	59.91
	1–2 cm	1	3.38	–16.5	nd	nd	nd		nd	nd
	2–3 cm	20	0.31	–18.0	42	0.19	–11.3		6.7	0.27
Total agglutinated taxa	0–3 cm							1.62 ± 8.52		469.71

natural $\delta^{13}C$ signature among sampling depths were largest within the group 'other calcareous,' *Globocassidulina subglobosa*, as well as for *Adercotryma glomerata* (Fig. 3). Mean natural $\delta^{13}C$ signatures of foraminifera did not differ significantly (3 paired *t*-tests, $p > 0.05$) between 0–1 (–20.0 ± 2.2‰), 1–2 (–18.1 ± 4.0‰) and 2–3 cm (–19.5 ± 0.9‰). No differences (3 paired *t*-tests, $p > 0.05$) were found between the 3 major taxonomic groups: soft-walled –20.0 ± 1.1‰, calcareous –18.4 ± 4.1‰, and agglutinated –19.2 ± 1.7‰.

^{13}C excess

Higher $\delta^{13}C$ in the cytoplasm of living foraminifera from incubated sediment compared to the background is attributed to the ingestion of ^{13}C-labeled algae material. The $\Delta\delta^{13}C$ values are positive for most of the species and indicate widespread ^{13}C enrichment (Table 2). Highest excess was observed for *Trochammina globigeriniformis* (2047‰), 'other calcareous' (1659‰), and *Saccorhiza ramosa* (830‰), while *Melonis barleeanum* showed lowest excess values (0.3–0.7‰). A trend of decreasing ^{13}C excess with increasing depth was found for *Epistominella pusilla*, *Adercotryma glomerata*, *Cribrostomoides subglobosum*, *Rhabdammina abyssorum*, 'other non-tubular,' and 'other tubular' agglutinated species (Fig. 4). In contrast, *Globocassidulina subglobosa*, *Hormosinella guttifera*, and *S. ramosa* showed higher ^{13}C excess within the sediment than at the sediment surface.

Labeled carbon uptake by foraminifera

Uptake of labeled carbon ^{13}C by benthic foraminifera was observed in all investigated sediment horizons and summed up to 815 µg C m^{-2} (added total for 0–3 cm, Table 2). The uptake rate was hence 0.2 mg C m^{-2} d^{-1} (standardized overall carbon uptake to the length of the experiment by assuming that uptake was linear). Uptake of ^{13}C was highest at the sediment surface with 574 µg C m^{-2} (sum for 0–1 cm depth) and lower within the sediment (82 µg C m^{-2} at 1–2 cm; 160 µg C m^{-2} at 2–3 cm). The 3 taxonomic groups showed enormous differences in uptake (Fig. 5). Agglutinated foraminifera contributed the most to the total uptake (0–3 cm; Fig. 6), whereas the soft-walled saccamminids did not appear to have incorporated any of the offered ^{13}C at any sediment depth. Uptake by calcareous foraminifera was res-

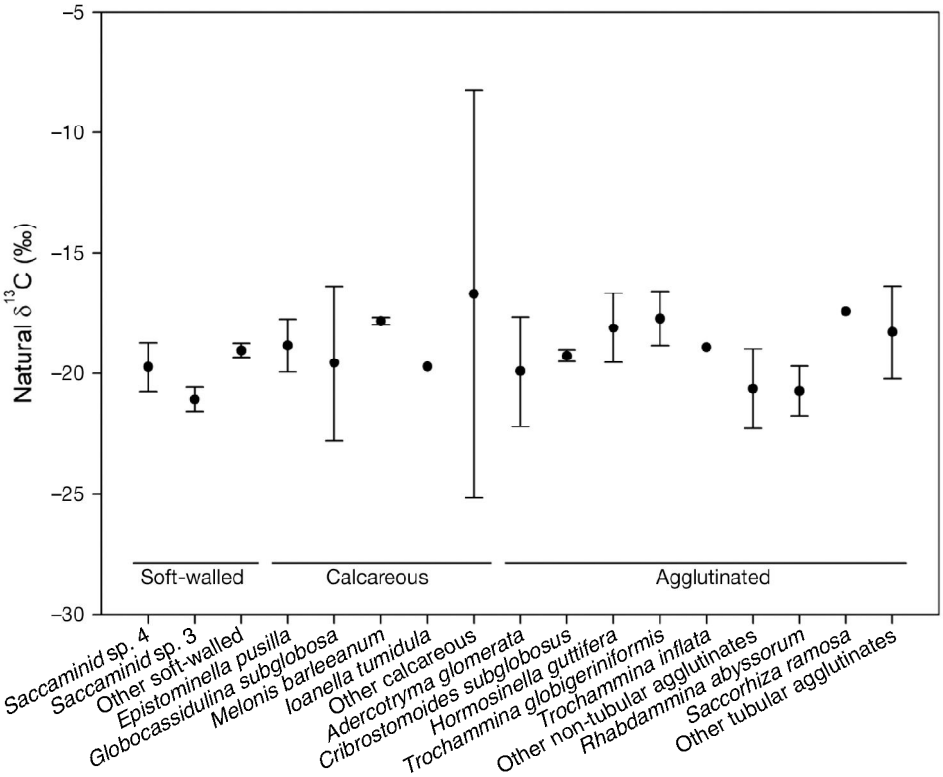


Fig. 3. Natural $\delta^{13}C$ signatures (‰) of the cytoplasm of foraminifera from background sediments. Means ± SD for each single species or group across the length of the sediment column (0 to 3 cm, see Table 2)

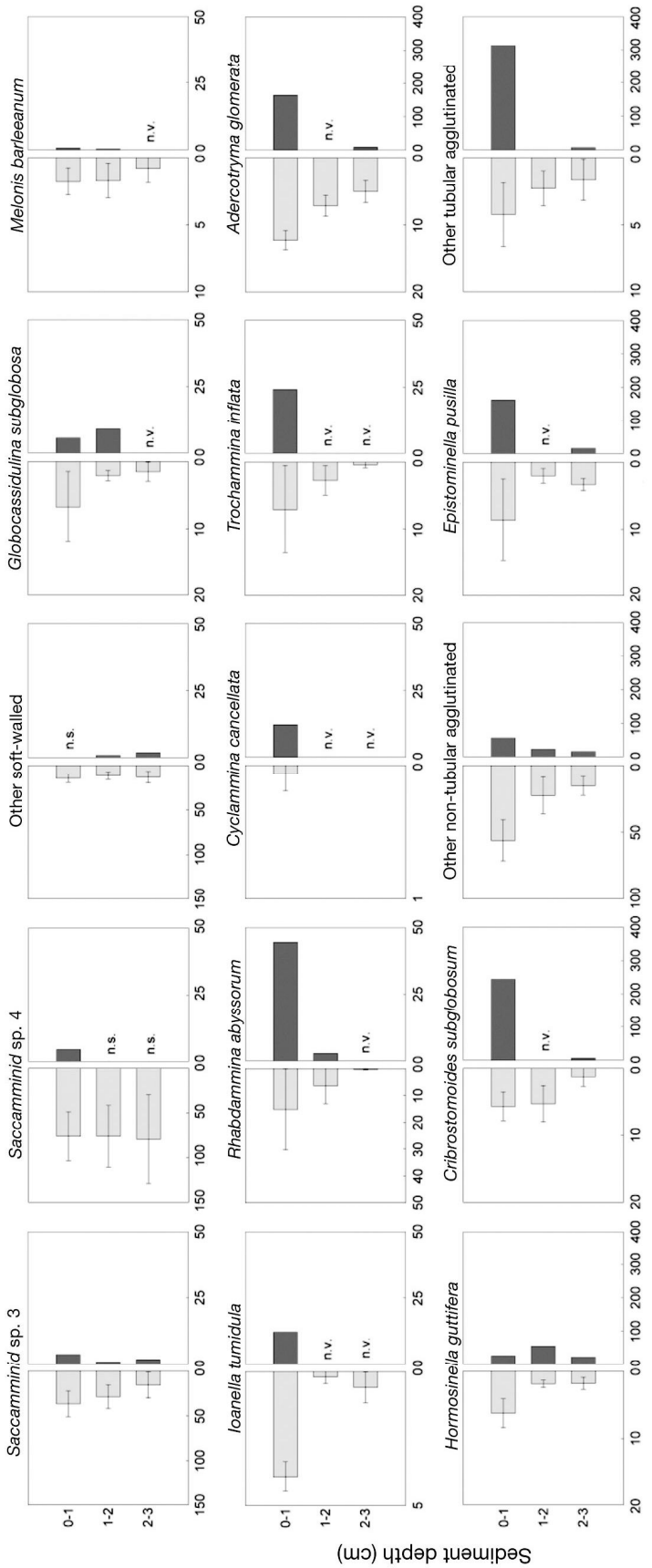


Fig. 4. Abundance (ind. 10 cm^{-2}, means ± SD, 4 cores) and $\Delta\delta^{13}C$ (‰) of single species and groups of foraminifera (several species pooled) at 3 depth levels (0–1, 1–2, 2–3 cm). nv: no value (failed isotopic measurements or insufficient carbon content). ns: $\Delta\delta^{13}C$ values below natural background variation. Note: scaling of the x-axis differs among species

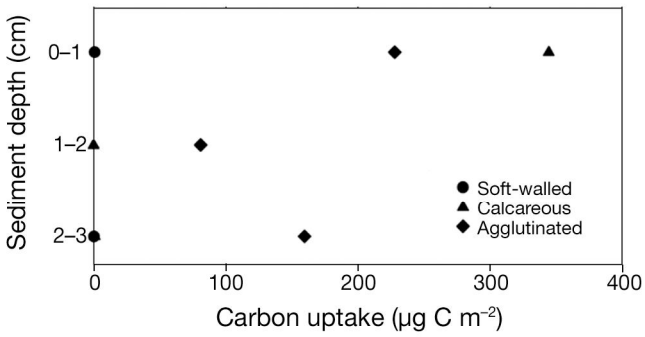


Fig. 5. Carbon uptake (µg C m^{-2}) by 3 foraminiferal groups at 3 depth levels (0–1, 1–2, 2–3 cm)

tricted to the sediment surface, but with the largest portion (60%) of all groups at this depth (Fig. 5). Deeper in the sediment, the uptake of ^{13}C was exclusively linked to agglutinated foraminifera. Especially the tubular *Saccorhiza ramosa* showed enormous potential with 61% and 99% of the overall foraminiferal carbon uptake at 1–2 cm and 2–3 cm (Table 2). Individual species showed a very diverse response to the application of phytodetritus in terms of magnitude and depth location of the carbon uptake (Table 2). Most of the species showed maximum uptake at 0–1 cm, and lower uptake deeper in the sediment. Highest carbon uptake (>50 µg C m^{-2}) was observed for *S. ramosa* (2–3 cm), 'other calcareous' (0–1 cm), 'other tubular' (0–1 cm), and 'other non-tubular' (0–1 cm) agglutinated species. *Cribrostomoides subglobosum*, *Rhabdammina abyssorum*, and *Trochammina globigeriniformis* displayed carbon uptake between 5 and 50 µg C m^{-2}. *Epistominella pusilla*, *Cyclammina cancellata*, *Adercotryma glomerata*, and *Hormosinella guttifera* between 1 and 5 µg C m^{-2}, whereas soft-walled species showed uptake ≤0.6 µg C m^{-2}. Among the calcareous group, only *E. pusilla* showed any noticeable uptake >1 µg C m^{-2}. *Trochammina inflata* was the only agglutinated species with a negligible response. Due to failed isotopic measurements, values are missing for *A. glomerata* (1–2 cm), *C. subglobosum* (1–2 cm), *T. globigeriniformis* (1–2 cm, 2–3 cm), and 'other calcareous' (1–2 cm, 2–3 cm). These 4 taxa together accounted for 16.1% and 7.6% of the total biomass of living foraminifera at 1–2 cm and 2–3 cm depth, respectively. Assuming that the isotopic analyses had therefore covered 83.9% (1–2 cm) and 92.4% (2–3 cm) of all possible feeders, we estimated the uptake to 100% from the proportion of biomass of the missing species on the total biomass. Hence, the potential foraminiferal uptake at Stn M would have been 98 µg C m^{-2} and 173 µg C m^{-2} at 1–2 cm and 2–3 cm depth, respectively.

DISCUSSION

Distribution of foraminifera

The foraminiferal community at Stn M is dominated by soft-walled and agglutinated species. The presence of calcareous species and the good preservation of their shells point to an abyssal setting above the carbon compensation depth. A large proportion of monothalamous foraminifera in the total community was also observed by Nozawa et al. (2006) in the abyssal equatorial Pacific. In our experiment, abundance and biomass of living foraminifera did not dif-

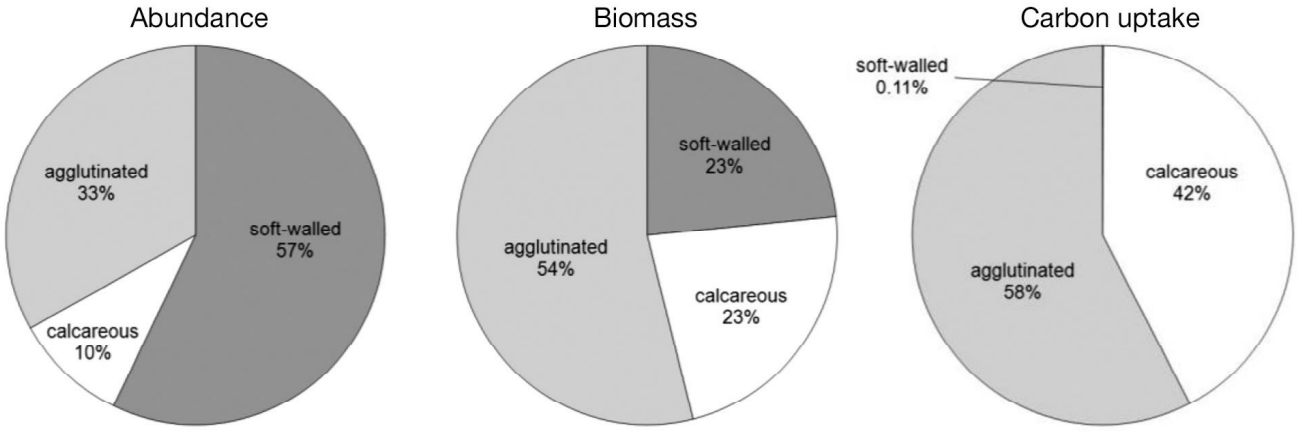


Fig. 6. Proportional contribution of the 3 foraminiferal groups to abundance, biomass (as total organic carbon, TOC), and carbon uptake

fer among the treated and untreated sediment cores (Table 1). As the push cores were taken only several meters apart from each other it can be expected that the foraminifera in all cores were influenced by similar biotic and abiotic conditions.

The number of living foraminifera may have been overestimated, especially for species with opaque tests (miliolids and agglutinated species), since such tests could not be opened for inspection to prevent cytoplasm loss. For isotopic analysis we only used specimens that had been identified as definitely living by visibility of cytoplasm. It cannot be excluded, however, that some of the analyzed foraminifera were inhabited by foreign organisms (Gooday 1984, Grimm et al. 2007).

Short-term response of the benthic community

After 4 d, the benthic foraminiferal community at Stn M had taken up 0.82 mg C m^{-2} (0–3 cm sediment depth). Similar rapid responses by bathyal and abyssal foraminifera within a few days to phytodetrital pulses were observed by Moodley et al. (2002) and Nomaki et al. (2005b). Linke et al. (1995) and Gross (2000) detected fresh food material in digestive vacuoles and a greenish coloring by ingested chloroplasts in deep-sea foraminifera during a microcosm experiment within 3 d after feeding. We expect from other feeding experiments (Levin et al. 1999, Witte et al. 2003b, Nomaki et al. 2005b, 2011, Sweetman et al. 2009) that a longer incubation with food would have translated into higher uptake. High labeling after a 4 d experiment, but an overall low uptake of ^{13}C by foraminifera, was observed by Witte et al. (2003b). A significant change by foraminifera was shown after 23 d, and Witte et al. (2003b) explained this belated response to phytodetritus as a characteristic of abyssal deep-sea communities. The delayed response by foraminifera in a bathyal Norwegian fjord was attributed to the dominance of deep-infaunal species with a preference for degraded material, as well as to the larger size of the foraminifera (Sweetman et al. 2009). A slower phytodetritus ingestion by larger individuals compared to smaller specimens was observed by Nomaki et al. (2011) in Sagami Bay.

During our 4 d feeding experiment at Stn M benthic foraminifera demonstrated a carbon uptake rate of 0.2 mg C m^{-2} d^{-1}. In the abyssal North Atlantic, Witte et al. (2003b) found uptake rates of 0.1 mg C m^{-2} d^{-1} (8 d incubation) or 0.4 mg C m^{-2} d^{-1} (23 d incubation). Carbon uptake rates by foraminifera at bathyal depths vary between 1.0 and 8.8 mg C m^{-2} d^{-1} (Moodley et al. 2002, Nomaki et al. 2005b, 2006) and are higher than that at Stn M. The flux of organic matter decreases with water depth. Also, foraminifera in shallower waters are adapted to more constant food supply. The lower response by the foraminifera at Stn M could be attributed to low metabolic rates caused by long periods of starvation. Also the foraminiferal biomass differed considerably between Stn M and the above-mentioned bathyal sites (Moodley et al. 2002, Nomaki et al. 2005b, 2006), being higher at bathyal depths. Differences in bottom water temperature (Moodley et al. 2005) or foraminiferal physiology (Nomaki et al. 2005b) may also be responsible for differences in the magnitude of uptake.

Uptake of labeled food during *in situ* feeding experiments at Stn M was higher for foraminifera (this study) than for the macrofauna (Sweetman & Witte 2008b), although macrofauna was present with larger biomass and abundance. However, shorter incubation might have resulted in the lower uptake by the macrofauna. In the Northeast Atlantic at 2170 m depth, foraminifera and bacteria showed the same rapid response to phytodetritus while the macrofauna was less engaged (Moodley et al. 2002). At 4800 m depth in the North Atlantic, Witte et al. (2003b) found the macrofauna to dominate the short-term carbon uptake, while foraminifera clearly demonstrated highest carbon ingestion after 23 d, exceeding the response by bacteria and the meiofauna (nematodes). During a 3 d feeding experiment in a Norwegian fjord, bacteria showed a higher carbon uptake than the macrofauna (Witte et al. 2003a).

Vertical differences in carbon uptake by benthic foraminifera

Benthic foraminifera at Stn M showed greater uptake of labeled algae at the sediment surface than deeper in the sediment (Fig. 5). The uptake of food by foraminifera depends on individual uptake rates as well as on the population density. The high standing stock of foraminifera at the sediment surface at Stn M (Fig. 2) may be associated with the high carbon uptake at in the surface layer (Fig. 4). Also, the microhabitat and food preferences are responsible for the different response times. Deep-infaunal foraminifera are not able to respond as fast as epifaunal species due to the distance to the food source. Rudnick (1989) also found delayed responses by sediment-dwelling meiobenthos in comparison to organisms at the sediment surface. Also, the preference for more degraded material, commonly present in deep-infaunal forami-

nifera (Kitazato & Ohga 1995), can cause a missing feeding signal in deeper sediment layers.

The changes of the $\delta^{13}C$ value in sediment make it possible to follow the path of the labeled algae within the sediment column. After 4 d, the algal material was mixed down to 2 cm depth (U. Witte et al. unpublished data), i.e. maximum phytodetritus penetration depth was as deep as the algal uptake by foraminifera. Highest uptake of carbon by foraminifera at the sediment level with the highest algal concentration was also observed by Nomaki et al. (2005b) at the bathyal Sagami Bay. The low response at 2–3 cm might be explained by the incomplete penetration of food into deeper sediment layers during the incubation time. Aberle & Witte (2003) found highest labeling down to 5 cm depth after 23 d. Hence, the incubation time in our experiment might have been too short for complete vertical transport of algal material. However, vertical mixing can be promoted by bioturbation by larger animals such as annelids within several days (Blair et al. 1996, Witte et al. 2003a). Nomaki et al. (2005b) found rapid mixing of added algae within 2 to 6 d down to 3 cm depth during their feeding experiments as a result of the activity and burrows of macrobenthic organisms. Macrofauna at Stn M is present down to 10 cm sediment depth (Sweetman & Witte 2008b), but bioturbation during our experiment might have occurred at a lower rate or been more limited to the surface layer. The aforementioned macrofaunal study points out that deep-dwelling polychaetes were not as abundant as surface-dwelling species at Stn M. Therefore, we conclude that short incubation time and a low bioturbation rate might have played a role in the missing penetration of phytodetritus to deeper sediment which then did not reach infaunal species such as *Melonis*.

In our cores with experimental food addition, biomass and abundance of foraminifera weakly increased in the 0–2 cm sediment horizon after 4 d, whereas at 2–3 cm depth, the trend of fewer foraminifera was found in the incubated sediment. This might suggest either reproduction induced by feeding or upward migration of species from deeper sediment layers. Nomaki et al. (2005a) observed migration by benthic foraminifera taking place only days after the food addition and concluded that reproduction and the following growth (increase of size and chamber number of the newly produced cells) require longer time periods. Laboratory experiments have shown that deep-sea foraminifera are able to move through the sediment at a speed of several millimeters per day (Hemleben & Kitazato 1995, Gross 2000). Therefore, migration from 2 or 3 cm depth towards the surface during our 4 d incubation could have been possible, especially by foraminifera with a feeding preference for fresh phytodetritus.

Carbon uptake by soft-walled foraminifera

Soft-walled foraminifera constituted >50% of all specimens and up to 23% of the foraminiferal biomass in Stn M sediments (Fig. 6). They showed noticeable similarities to monothalamous allogromiid species found by Gooday (2002) and Gooday et al. (2008). For the first time this group has been subject to an *in situ* feeding experiment using isotope labeling. Monitoring the response of soft-walled foraminifera towards phytodetritus by means of change in abundance has been carried out before. In the abyssal North Atlantic, several taxa of soft-walled Saccamminidae did not respond to phytodetritus at the sediment surface, whereas the majority of the benthic foraminifera increased in number (Gooday 1988). An important observation of our study was the lack of a short-term response of this dominating group to a nutrient-rich food source under *in situ* conditions, despite clear signs of vitality in form of intact tests and a high degree of test filling with cytoplasm. Although the biomass of soft-walled foraminifera at Stn M is similar to that of calcareous species, soft-walled foraminifera do not directly make use of freshly deposited phytodetritus as an energy source. On the one hand, this might be attributed to slow metabolism. Gooday et al. (2008) found monothalamous allogromiid species ingesting organic material at a slower rate than other foraminiferal species. If this also applied to the soft-walled group in our study, the lack of response might be due to the short duration of the experiment. On the other hand, soft-walled foraminifera might favor feeding strategies that do not include phytodetritus. Small monothalamous allogromiid species have been associated with bacterivory (Gooday 2002) and the ingestion of refractory organic material (Gooday et al. 2008). Bernhard & Bowser (1992) reported exclusive feeding of allogromiid foraminifera on bacterial films, while calcareous and agglutinated foraminifera did not feed on bacteria.

Carbon uptake by calcareous and agglutinated foraminifera

Single species of calcareous and agglutinated foraminifera at Stn M showed considerable differences in the uptake of phytodetritus in terms of mag-

nitude and variation with sediment depth. We assume that several factors are responsible for the observed differences.

Epifaunal or opportunistic species show fast reaction to phytodetritus (Gooday 1993). The uptake of phytodetritus by *Epistominella pusilla* in our experiment (Fig. 4) is in accordance with earlier observations that have identified this small species to be opportunistic (Gooday 1993, 1996, Gooday & Lambshead 1989, Lambshead & Gooday 1990, Gooday & Hughes 2002, Heinz & Hemleben 2003, 2006) and phytophagous (Gooday et al. 2008). The agglutinated species *Adercotryma glomerata* also demonstrated algal uptake. This species prefers the epifaunal habitat (Gooday 1993, Heinz et al. 2001, 2002), occurring in high abundances when phytodetritus is present (Thiel et al. 1988) and showing elevated growth and reproduction (Gooday & Hughes 2002). *Cribrostomoides subglobosum* showed elevated feeding rates in our experiment and may be an important species for the cycling of organic matter in the deep-sea. This species was previously found living on the sediment surface and within 0–3 cm sediment depth (Kaminski et al. 1988, Linke & Lutze 1993). It can react quickly to phytoplankton settlement on the sea floor (Altenbach 1992). *Saccorhiza ramosa* was the only species that showed highest isotope signals deeper in the sediment, not matching its abundance maximum at the sediment surface. The agglutinated, tubular test of this species is oriented perpendicular to the sediment surface with 40 to 70% of its length buried in the sediment (Altenbach et al. 1988). Given this position and the large size of this species (several millimeters), the observed uptake maximum at 2–3 cm depth could be explained by transport and storage of labeled food within the sediment-covered test portion. As only a few fragments of *Saccorhiza* were available for analysis, the isotopic data are possibly less representative.

Deep-sea foraminifera demonstrate a high variety of dietary preferences (reviewed by Gooday et al. 2008) and selective food choice (Nomaki et al. 2006), which might explain the lack of response towards the offered phytodetritus by several species during our experiment. Food quality can also be responsible for low or non-existing uptake. *Melonis barleeanum* with an infaunal microhabitat (Corliss 1985, 1991, Rosoff & Corliss 1992, Heinz et al. 2002) has an affinity for organic matter (e.g. Caralp 1989b, Loubere 1991, Schmiedl et al. 1997), and prefers degraded organic matter of lower nutritional value (Caralp 1989a, Fontanier et al. 2002, Sweetman et al. 2009). Nomaki et al. (2005b) observed shallow infaunal species to ingest ^{13}C-labeled food faster and more extensively than deep-infaunal species; the latter ingested more slowly and preferred more altered food in culture experiments (Kitazato & Ohga 1995). From their feeding experiments in a Norwegian fjord and in the North Atlantic, Witte et al. (2003b) and Sweetman et al. (2009) concluded that using fresh algae rather than more degraded organic matter and using a single algal species rather than a mixture might have caused the low uptake by benthic foraminifera.

Acknowledgements. We sincerely thank K. L. Smith Jr. and coworkers from MBARI and the officers and the crew of the RV 'Western Flyer' for making the realization of the experiments possible. We thank A. Gooday for help in identifying the soft-walled foraminifera. This research was supported by the Deutsche Forschungsgemeinschaft (DFG, project HE-2460/5-1) and the UK National Environmental Research Council (NERC NE/E006426/1).

LITERATURE CITED

Aberle N, Witte U (2003) Deep-sea macrofauna exposed to a simulated sedimentation event in the abyssal NE Atlantic: *in situ* pulse-chase experiments using ^{13}C-labelled phytodetritus. Mar Ecol Prog Ser 251:37–47

Altenbach AV (1992) Short-term processes and patterns in the foraminiferal response to organic flux rates. Mar Micropaleontol 19:119–129

Altenbach AV, Struck U (2001) On the coherence of organic carbon flux and benthic foraminiferal biomass. J Foraminifer Res 31:79–85

Altenbach AV, Unsoeld G, Walger E (1988) The hydrodynamic environment of *Saccorhiza ramosa* (Brady). Meyniana 40:119–132

Beaulieu SE, Smith KL Jr (1998) Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition. Deep-Sea Res II 45:781–815

Bernhard JM, Bowser SS (1992) Bacterial biofilms as a trophic resource for certain benthic foraminifera. Mar Ecol Prog Ser 83:263–272

Bernstein BB, Hessler RR, Smith R, Jumars PA (1978) Spatial dispersion of benthic foraminifera in the abyssal central north Pacific. Limnol Oceanogr 23:401–416

Blair N, Levin L, DeMaster D, Plaia G (1996) The short-term fate of fresh algal carbon in continental slope sediments. Limnol Oceanogr 41:1208–1219

Caralp MH (1989a) Abundance of *Bulimina exilis* and *Melonis barleeanum* — relationship to the quality of marine organic matter. Geo-Mar Lett 9:37–43

Caralp MH (1989b) Size and morphology of the benthic foraminifer *Melonis barleeanum* — relationships with marine organic matter. J Foraminifer Res 19:235–245

Corliss BH (1985) Microhabitats of benthic foraminifera within deep-sea sediments. Nature 314:435–438

Corliss BH (1991) Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. Mar Micropaleontol 17:195–236

Corliss BH, Emerson S (1990) Distribution of Rose Bengal

stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep-Sea Res A 37:381–400

Drazen JC, Baldwin RJ, Smith KL Jr (1998) Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Res II 45: 893–913

Fontanier C, Jorissen FJ, Licari L, Alexandre A, Anschutz P, Carbonel P (2002) Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. Deep-Sea Res I 49:751–785

Gooday AJ (1984) Records of deep-sea rhizopod tests inhabited by metazoans in the North-east Atlantic. Sarsia 69: 45–53

Gooday AJ (1988) A response by benthic foraminifera to the deposition of phytodetritus in the deep-sea. Nature 332: 70–73

Gooday AJ (1993) Deep-sea benthic foraminiferal species which exploit phytodetritus: characteristic features and controls on distribution. Mar Micropaleontol 22: 187–205

Gooday AJ (1994) The biology of deep-sea foraminifera — a review of some advances and their applications in paleoceanography. Palaios 9:14–31

Gooday AJ (1996) Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes. Deep-Sea Res I 43:1395–1421

Gooday AJ (2002) Organic-walled allogromiids: aspects of their occurence, diversity and ecology in marine habitats. J Foraminifer Res 32:384–399

Gooday AJ, Hughes JA (2002) Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. Mar Micropaleontol 46:83–110

Gooday AJ, Lambshead PJD (1989) Influence of seasonally deposited phytodetrtitus on benthic foraminferal populations in the bathyal northeast Atlantic — the species response. Mar Ecol Prog Ser 58:53–67

Gooday 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 Adacemic Publishers, Dordrecht, p 63–91

Gooday AJ, Nomaki H, Kitazato H (2008) Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity. In: Austin WEN, James RH (eds) Biogeochemical controls on palaeoceanographic environmental proxies, Vol 303. Geological Society, London, p 97–119

Grasshoff K, Kremling K, Ehrhardt M (1999) Methods of seawater analysis, 3rd edn. Wiley-VCH, Weinheim

Grimm GW, Stogerer K, Ertan KT, Kitazato H, Kucera M, Hemleben V, Hemleben C (2007) Diversity of rDNA in *Chilostomella*: molecular differentiation patterns and putative hermit types. Mar Micropaleontol 62:75–90

Gross O (2000) Influence of temperature, oxygen and food availability on the migrational activity of bathyal benthic foraminifera: evidence by microcosm experiments. Hydrobiologia 426:123–137

Heinz P, Hemleben C (2003) Regional and seasonal variations of recent benthic deep-sea foraminifera in the Arabian Sea. Deep-Sea Res I 50:435–447

Heinz P, Hemleben C (2006) Foraminiferal response to the Northeast Monsoon in the western and southern Arabian Sea. Marine Micropaleontol 58:103–113

Heinz P, Kitazato H, Schmiedl G, Hemleben C (2001) Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions. J Foraminifer Res 31:210–227

Heinz P, Hemleben C, Kitazato H (2002) Time-response of cultured deep-sea benthic foraminifera to different algal diets. Deep-Sea Res I 49:517–537

Hemleben C, Kitazato H (1995) Deep-sea foraminifera under long time observation in the laboratory. Deep-Sea Res I 42:827–832

Hessler RR, Jumars PA (1974) Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Res 21:185–209

Jorissen FJ, de Stigter HC, Widmark JGV (1995) A conceptual model explaining benthic foraminiferal microhabitats. Mar Micropaleontol 26:3–15

Kaminski MA, Grassle JF, Whitlatch RB (1988) Life history and recolonization among agglutinated foraminifera in the Panama Basin. Abh Geol B-A 41:229–243

Kitazato H, Ohga T (1995) Seasonal changes in deep-sea benthic foraminiferal populations: results of long-term observations at Sagami Bay, Japan. In: Sakai H, Nozaki Y (eds) Biogeochemical processes and ocean flux in the western Pacific. Terra Scientific Publishing Company (TERRAPUB), Tokyo, p 331–342

Kurbjeweit F, Schmiedl G, Schiebel R, Hemleben C, Pfannkuche O, Wallmann K, Schafer P (2000) Distribution, biomass and diversity of benthic foraminifera in relation to sediment geochemistry in the Arabian Sea. Deep-Sea Res II 47:2913–2955

Lambshead PJD, Gooday AJ (1990) The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic — the assemblage response. Deep-Sea Res A 37:1263–1283

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 ^{13}C-labeled diatoms. Mar Ecol Prog Ser 182: 37–54

Linke P, Lutze GF (1993) Microhabitat preferences of benthic foraminifera — a static concept or a dynamic adaptation to optimize food acquisition. Mar Micropaleontol 20: 215–234

Linke P, Altenbach AV, Graf G, Heeger T (1995) Response of deep-sea benthic foraminifera to a simulated sedimentation event. J Foraminiferal Res 25:75–82

Loubere P (1991) Deep-sea benthic foraminiferal assemblage response to a surface ocean productivity gradient: a test. Paleoceanography 6:193–204

Moodley L, Boschker HTS, Middelburg JJ, Pel R, Herman PMJ, de Deckere E, Heip CHR (2000) Ecological significance of benthic foraminifera: ^{13}C labelling experiments. Mar Ecol Prog Ser 202:289–295

Moodley L, Middelburg JJ, Boschker HTS, Duineveld GCA, Pel R, Herman PMJ, Heip CHR (2002) Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Mar Ecol Prog Ser 236: 23–29

Moodley L, Middelburg JJ, Soetaert K, Boschker HTS, Herman PMJ, Heip CHR (2005) Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. J Mar Res 63:457–469

Nomaki H, Heinz P, Hemleben C, Kitazato H (2005a) Behavior and response of deep-sea benthic foraminifera to freshly supplied organic matter: a laboratory feeding experiment in microcosm environments. J Foraminifer Res 35:103–113

Nomaki H, Heinz P, Nakatsuka T, Shimanaga M, Kitazato H (2005b) Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: in situ tracer experiments. Limnol Oceanogr 50:134–146

Nomaki H, Heinz P, Nakatsuka T, Shimanaga M and others (2006) Different ingestion patterns of ^{13}C-labeled bacteria and algae by deep-sea benthic foraminifera. Mar Ecol Prog Ser 310:95–108

Nomaki H, Ohkouchi N, Heinz P, Suga H and others (2009) Degradation of algal lipids by deep-sea benthic foraminifera: an *in situ* tracer experiment. Deep-Sea Res I 56: 1488–1503

Nomaki H, Ogawa NO, Takano Y, Suga H, Ohkouchi N, Kitazato H (2011) Differing utilization of glucose and algal particulate organic matter by deep-sea benthic organisms of Sagami Bay, Japan. Mar Ecol Prog Ser 431: 11–24

Nozawa F, Kitazato H, Tsuchiya M, Gooday AJ (2006) 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. Deep-Sea Res I 53:1406–1422

Ogawa NO, Nagata T, Kitazato H, Ohkouchi N (2010) Ultrasensitive elemental analyzer/isotope ratio mass spectrometer for stable nitrogen and carbon isotope analyses. In: Ohkouchi N, Tayasu I, Koba K (eds) Earth, life, and isotopes. Kyoto University Press, Kyoto, p 339–353

Reimers CE (1987) An *in situ* microprofiling instrument for measuring interfacial pore water gradients: methods and oxygen profiles from the north Pacific Ocean. Deep-Sea Res II 334:2019–2035

Rosoff DB, Corliss BH (1992) An analysis of recent deep-sea benthic foraminiferal morphotypes from the Norwegian and Greenland Seas. Palaeogeogr Palaeoclimatol Palaeoecol 91:13–20

Rudnick DT (1989) Time lags between the deposition and meiobenthic assimilation of phytodetritus. Mar Ecol Prog Ser 50:231–240

Ruhl HA, Smith KL Jr (2004) Shifts in deep-sea community structure linked to climate and food supply. Science 305: 513–515

Schmiedl G, Mackensen A, Muller PJ (1997) Recent benthic foraminifera from the eastern South Atlantic Ocean: dependence on food supply and water masses. Mar Micropaleontol 32:249–287

Smith KL Jr, Druffel ERM (1998) Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. Deep-Sea Res II 45:573–586

Smith KL Jr, Kaufmann RS, Baldwin RJ (1994) Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern north Pacific Ocean. Limnol Oceanogr 39:1101–1118

Smith KL Jr, Kaufmann R, Baldwin R, Carlucci A (2001) Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. Limnol Oceanogr 46:543–556

Smith KL Jr, Baldwin RJ, Ruhl HA, Kahru M, Mitchell BG, Kaufmann RS (2006) Climate effect on food supply to depths greater than 4,000 meters in the northeast Pacific. Limnol Oceanogr 51:166–176

Smith KL Jr, Ruhl H, Kaufmann R, Kahru M (2008) Tracing abyssal food supply back to upper-ocean processes over a 17-year time series in the northeast Pacific. Limnol Oceanogr 53:2655–2667

Smith KL Jr, Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufmann RS (2009) Climate, carbon cycling, and deep-ocean ecosystems. Proc Natl Acad Sci USA 106: 19211–19218

Snider LJ, Burnett BR, Hessler RR (1984) The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep-Sea Res A 31: 1225–1249

Sweetman AK, Witte U (2008a) Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. Deep-Sea Res I 55:1503–1514

Sweetman AK, Witte U (2008b) Response of an abyssal macrofaunal community to a phytodetrital pulse. Mar Ecol Prog Ser 355:73–84

Sweetman AK, Sommer S, Pfannkuche O, Witte U (2009) Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord. J Foraminifer Res 39:15–22

Thiel H, Pfannkuche O, Schriever G, Lochte K and others (1988) Phytodetritus on the deep-sea floor in a central oceanic region of the northeast Atlantic. Biol Oceanogr 6: 203–239

Witte U, Aberle N, Sand M, Wenzhofer F (2003a) Rapid response of a deep-sea benthic community to POM enrichment: an in situ experimental study. Mar Ecol Prog Ser 251:27–36

Witte U, Wenzhofer F, Sommer S, Boetius A and others (2003b) *In situ* experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424: 763–766

Editorial responsibility: Matthias Seaman, Oldendorf/Luhe, Germany

Submitted: March 7, 2011; Accepted: July 18, 2011
Proofs received from author(s): September 16, 2011

Publication 2

Diversity and microhabitats of living benthic foraminifera in the abyssal Northeast Pacific

Marine Micropaleontology 96–97 (2012) 84–104

Contents lists available at SciVerse ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Diversity and microhabitats of living benthic foraminifera in the abyssal Northeast Pacific

Annekatrin J. Enge [a,*], Michal Kucera [b], Petra Heinz [a]

[a] University of Tuebingen, Department for Geosciences, Hoelderlinstrasse 12, 72074 Tuebingen, Germany
[b] Marum—Centre for Marine Environmental Sciences, Leobener Strasse, 28359 Bremen, Germany

ARTICLE INFO

Article history:
Received 25 November 2011
Received in revised form 6 August 2012
Accepted 20 August 2012

Keywords:
Benthic foraminifera
Deep sea
North Pacific
Diversity
Vertical distribution
Soft-walled foraminifera

ABSTRACT

We investigated assemblages of living benthic foraminifera (>63 μm) from replicate samples at *Station M* in the abyssal Northeast Pacific. Push cores collected in September 2007 (StatM07) and May 2009 (StatM09) from 3953 m depth were examined for population densities, species composition, and vertical occurrence within the sediment. Analysis of rose Bengal-stained (StaM09) and cytoplasm bearing (StaM07) foraminifera revealed average total abundances in the top 1 cm of 284 ind./10 cm^3 (StaM07) and 365 ind./10 cm^3 (StaM09). At both sites monothalamous saccamminids were numerically abundant, at StM09 they dominated the 1–2 cm interval and at StaM07 they dominated at all depths. Calcareous taxa were numerically least abundant, while agglutinated foraminifera displayed the highest number of species. The occurrence of few abundant and many rare species resulted in diversity measures for StaM09 (H' 3.3, α 17.9) and StaM07 (H' 2.6, α 15.2). Numbers of individuals peaked at the sediment surface and declined with sediment depth; living specimens present down to 5 cm depth. The majority of species displayed an epifaunal or shallow-infaunal habitat. The observed vertical distribution patterns, species diversity, and assemblage composition are similar to other abyssal North Pacific assemblages and reflect the level of organic flux at *Station M*.

1. Introduction

The North Pacific has been subject to numerous studies dealing with recent benthic foraminifera. The first information on benthic foraminifera in the Western and central abyssal Pacific was provided by the findings from the Challenger Expedition of 1873–1876. The resulting Challenger report by Henry B. Brady in 1884 listed 875 foraminiferal species classified in 362 genera and detailed drawings of collected specimen are still the basis for identifying material in present-day (republished in 1994 by Jones with an updated taxonomy). Over a period of two decades in the early 1900s, Joseph A. Cushman produced very detailed and extensive descriptive studies on benthic foraminifera in the shallow and bathyal Northern Pacific which he summarized in Cushman (1927). Later, Smith (1973) found a sparsely represented, but diverse and mostly agglutinated foraminiferal fauna north of Hawaii at water depths between 76 and 7230 m. Several studies added further knowledge of benthic foraminifera in the deep central Pacific (Hessler and Jumars, 1974; Bernstein et al., 1978; Bernstein and Meador, 1979; Snider et al., 1984), so did Schroeder et al. (1988) who identified 61 species of agglutinated foraminifera in sediments at 5500–6100 m depth. Tendal and Hessler (1977) concentrated on the group of Komokiacea and found them to show main distribution in abyssal regions such as in the North Pacific. Whereas these pioneering studies helped establish the taxonomy of foraminifera from the deep-sea environment, they had paid little attention to the ecology, abundance, and habitats of the recorded species. In addition, due to their small size and low value for paleoceanography or biostratigraphy, soft-shelled foraminifera have been rarely studied in the past. Benefiting from improved methodological techniques and their enhanced recognition as an ecologically significant component of deep-sea foraminiferal assemblages, subsequent studies on benthic foraminifera in the North Pacific highlighted the importance of soft-shelled and organic-walled species from regions near the arctic circle (Gooday et al., 2001, 2004) as well as near the equator (Gooday et al., 2004; Nozawa et al., 2006; Radziejewska et al., 2006; Burmistrova et al., 2007; Ohkawara et al., 2009).

On the whole, the aforementioned studies have contributed to the knowledge of foraminiferal species richness and demonstrated the important contribution of this group to the abyssal North Pacific meiofauna (Snider et al., 1984) and macrofauna (Drazen et al., 1998; Smith et al., 2002). However, most of these deep-sea investigations were conducted either in the western, central, or equatorial region of the North Pacific. Investigations on benthic foraminiferal assemblages on the west coast of North America have been largely restricted to bathyal depths (e.g. by Mackensen and Douglas, 1989; Silva et al., 1996; Bernhard et al., 2001; Heinz et al., 2005; Sheperd et al., 2007). Studies conducted in the abyssal Northeast Pacific rather focused on the response of benthic foraminifera to variable food supply (Drazen et al., 1998; Enge et al., 2011), the presence of hard

* Corresponding author.
E-mail address: annekatrin.enge@uni-tuebingen.de (A.J. Enge).

0377-8398/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.marmicro.2012.08.004

substrate (Beaulieu, 2001), and to changes in carbon dioxide concentration in the water (Ricketts et al., 2009). The study of Bernhard (1992) gives information on population structure and depth zonation of benthic foraminifera at the California margin (624–3728 m) and provides distribution profiles for single species within the sediment for this area. However, detailed information on the abyssal foraminiferal community (>63 μm), species abundances and their depth distribution is still very scarce.

The present study aims to provide the first quantitative investigation of abyssal benthic foraminifera in the Northeast Pacific. Located at ~4000 m depth near the coast of California, the long term observation site *Station M* has been established two decades ago to investigate processes in the surface water and at the abyssal sea floor in the Northeast Pacific. To this end, sediment cores collected in September 2007 and May 2009 at this site were analyzed for absolute and relative abundance of living foraminiferal species (>63 μm) in the upper sediment column (0–5 cm). In addition to providing detailed data on the assemblage composition and diversity, we also assessed the degree of spatial heterogeneity between core assemblages from each sampling. In terms of ecological requirements of benthic foraminifera, the vertical distribution of foraminifera within the sediment was studied to determine the habitats of individual species within the sediment.

2. Materials and methods

2.1. Study site

The investigation site *Station M* is located in the Northeast Pacific (35°09′ N, 123°00′ W) at 3953 m water depth at a distance of 220 km from the central coast of California, U.S.A. (Fig. 1). This abyssal sampling site lies underneath the California Current that flows southward at the surface alongside the west coast of North America. Upwelling and rising temperatures in spring lead to increased biomass and plumes of phytoplankton of maximum extent. The yearly net primary production ranges between 200 and 1200 mg C/m^2/d (Smith et al., 2008). The export of photosynthetically derived organic matter and the abyssal particle organic carbon (POC) flux at *Station M* are correlated and exhibit both intra- and inter-annual variability (Smith et al., 1994; Smith and Druffel, 1998), resulting in a mean annual POC flux 50 m above sea floor of 2 g C/m^2/y (Smith et al., 2001). For further and detailed information, results of the 17-year-time-series (1990–2006) at *Station M* on primary production, fluxes to the sea floor (particulate organic matter, total, nitrogen, calcite, etc.), and detrital aggregate density on the sea floor are provided by Smith et al. (2008).

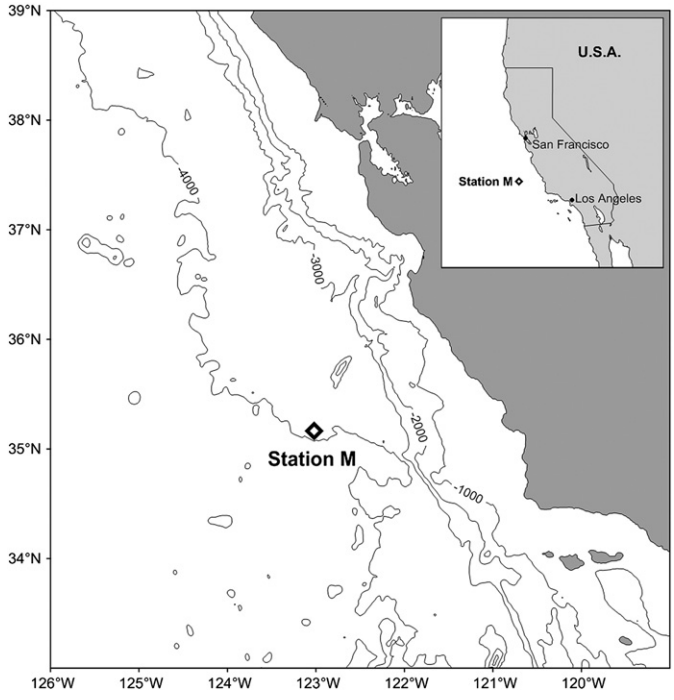


Fig. 1. Location of the sampling site *Station M* off the coast of California, U.S.A.

The sediment at *Station M* is composed of silty clay and the sea floor shows little topographic relief with <60 m relief over 770 km^2 (Smith et al., 1992). Mean current speeds of 2.2 cm/s were recorded at 2.5 m above bottom by Beaulieu and Baldwin (1998). Bottom water oxygen concentrations of 142–146 μmol/l (~3.5 ml/l) were measured at *Station M* (Smith et al., 1992) and oxygen has been detected in pore water down to ~3 cm sediment depth in the abyssal North Pacific (Reimers, 1987).

2.2. Sample acquisition

The foraminiferal community at *Station M* was investigated on sediment samples collected during two cruises with the research vessel Western Flyer: cruise "PULSE 54" in May 2009 (StaM09 sampling) and cruise "PULSE 53" in September 2007 (StaM07 sampling). At both sampling events, sediment cores (70 mm inner diameter) were pushed into the sediment close to each other (within 10 m distance) by a remotely operated vehicle. Four cores were taken in September 2007 and two cores in May 2009. The unequal number of replicates was due to time limitation during the May 2009 sampling. On board, the sediment of the recovered cores was immediately sliced (0–1, 1–2, 2–3, 3–5 cm) and kept refrigerated at 4 °C until further processing in the laboratory.

2.3. Sample preparation and identification of living/dead foraminifera

2.3.1. StaM09

The top samples (0–5 cm) of the two sediment cores obtained in May 2009 were soaked in a rose Bengal (rB) solution (1 g/l ethanol) for several days in the laboratory, washed, and then sieved with a 63 μm mesh. The dried residue was split with an Otto–Mikrosplitter into aliquots of which one (1/4 or 1/8) was counted entirely. Living specimens were identified by reddish-pink stained cytoplasm. For better identification, specimens were wetted with water and opaque tests of some porcellaneous and agglutinated species were broken for better recognition of cytoplasm coloration.

2.3.2. StaM07

Samples taken in September 2007 were part of a feeding experiment with ^{13}C-labeled algae. Hence, the here discussed data from the StaM07 samples are the same as the September 2007 samples in (Enge et al., 2011). In total, 4 cores were recovered in September: two cores from untreated sediments (A, B) and two cores from sediments incubated with ^{13}C-labeled algae for four days (C, D). Because the upper 3 cm of sediment were used for the analysis of foraminiferal cytoplasm for isotopic analysis, these samples could not be treated with rB or any other stain used in foraminiferal studies to discriminate living from dead foraminifera (Bernhard, 2000) as this could have affected the carbon isotope composition of the cytoplasm.

The samples 0–1 cm, 1–2 cm and 2–3 cm were washed over a 63 μm mesh with artificial seawater of 34–35 PSU (distilled water was added up to 1 liter final volume with 23.4 g NaCl, 4.0 g $MgSO_4 \times 7 H_2O$, 0.8 g KCl, 0.26 g $CaCl_2$). The elutriated samples were kept frozen at −20 °C until further processing. The separation of living and dead foraminifera was achieved by visual assessment of cytoplasm and the degree to which the test was filled with cytoplasm. The method of identifying live foraminifera without applying a staining method has been applied successfully in several other studies (e.g. Moodley et al., 2002; Witte et al., 2003; Nomaki et al., 2005) where isotopic analysis were later performed on foraminiferal cytoplasm. For better

Table 1
Abundance of living (Rose Bengal-stained) foraminifera from the four replicate cores of the StaM07 sampling at 3–5 cm depth (ind./10 cm³).

StaM07: 3–5 cm	Ind./10 cm³			
	Core A	Core B	Core C	Core D
Saccamminid sp. 1	0.5	5.2	1.0	4.2
Saccamminid sp. 2	–	3.1	1.0	–
Saccamminid sp. 3	2.6	5.2	2.1	3.1
Saccamminid sp. 4	–	1.0	8.3	1.0
Bolivina sp.	–	–	–	2.1
Bulimina cf. *pyrula*	–	7.3	2.1	–
Chilostomella oolina	–	–	2.1	–
Epistominella exigua	0.5	–	1.0	–
Epistominella pusilla	1.0	2.1	1.0	1.0
Fursenkoina pauciloculata	–	–	–	1.0
Globobulimina spp.	–	2.1	–	2.1
Globocassidulina subglobosa	1.0	3.1	–	–
Gyroidina sp. 1	–	1.0	–	–
Ioanella tumidula	–	1.0	–	–
Miliolid spp.	–	–	1.0	-
Oridorsalis umbonatus	–	1.0	–	–
Praeglobobulimina ovata	1.6	1.0	8.3	5.2
Pyrgo murrhina	–	1.0	–	–
Pyrgo sp. 1	–	3.1	1.0	–
Quinqueloculina weaveri	–	1.0	–	–
Spiroglutina asperula	0.5	–	–	–
Triloculina sp. 1	–	1.0	–	–
Uvigerina auberiana	0.5	1.0	–	–
Adercotryma glomeratum	–	1.0	–	–
Ammodiscus anguillae	0.5	1.0	–	2.1
Eratidus foliaceus recurvus	0.5	–	1.0	–
Evolutinella rotulata	–	1.0	–	–
Glomospira gordialis	–	–	1.0	–
Hormosinella guttifera	–	0.2	0.8	–
Karreriella bradyi	–	–	1.0	–
Lagenammina difflugiformis	–	2.1	2.1	–
Lagenammina tubulata	–	–	1.0	–
Reophax sp.	–	–	0.3	–
Saccammina sphaerica	0.5	–	–	–
Saccorhiza ramosa	1.3	–	–	–
Trochammina globigeriniformis	–	2.1	–	–
Trochammina cf. *inflata*	–	1.0	–	–
Total	11	49	37	22

recognition of the yellowish-whitish cytoplasm, foraminifera were picked in water.

The collected sediment samples of the depth interval 3–5 cm from the StaM07 sampling were treated the same way as the StaM09 samples by staining with rB. Because they were treated differently than the 0–3 cm samples of the same sediment cores, the obtained data will not be included in this work but absolute abundances are given in Table 1 for additional information.

2.4. Counting and documentation of foraminifera

All foraminifera were identified at species level if possible. The counting method had to be adjusted for several types of agglutinated foraminifera. Counts of fragments of multi-chambered elongate species such as *Reophax* spp. or *Hormosinella* spp. were normalized to complete specimens by dividing the fragment counts by the maximum number of chambers observed in intact tests of each species. Difficulties in quantification were also present for tubular forms (e.g. *Rhabdammina* spp., *Saccorhiza* spp.). As the tests of these foraminifera can break during sample treatment even if filled with cytoplasm, the number of fragments counted will not reflect the number of foraminifera. To give rough estimates on population density, three fragments of standardized size were converted into one single specimen (Kurbjeweit et al., 2000). This was necessary to obtain comparable results with other data sets used for regional comparison (see Section 4.6). Pictures of specimens were taken with a scanning electron microscope (model LEO 1450 VP) at the University of Tübingen for documentation and identification purposes.

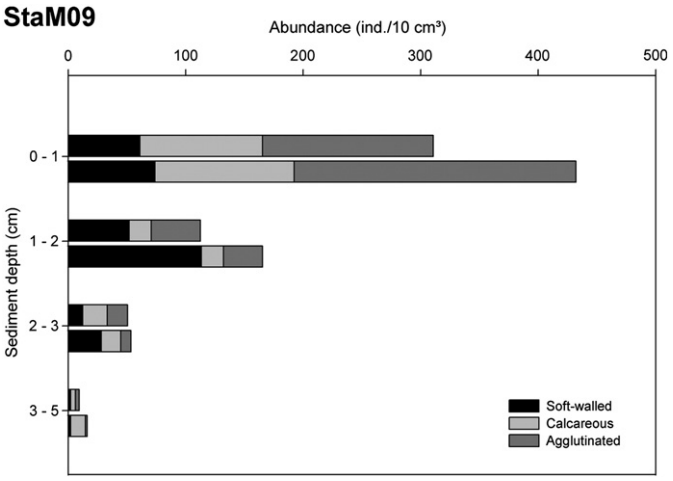


Fig. 2. Absolute abundances of living foraminifera (soft-walled, calcareous, agglutinated) in the upper 5 cm sediment (StaM09 sampling, 2 cores).

2.5. Statistical analyses

The observed number of species present in a sample was considered as species richness *S*. Species diversity was determined with the Shannon index H' (Shannon and Weaver, 1949) and Fisher's α (Fisher et al., 1943). Diversity was also illustrated graphically by means of rarefaction curves (Hurlbert, 1971). In order to compare the distribution of species among samples, the dominance *D* (Simpson, 1949) was calculated as well as the evenness *E* as $e^{H'/S}$ after Buzas and Gibson (1969). Furthermore, the average living depth (ALD_x) was estimated after Jorissen et al. (1995) with 5 cm (StaM09) and 3 cm (StaM07) as *x*, the deepest investigated depth. To investigate the community structure of the foraminiferal assemblage of StaM09 assemblages, a correspondence analysis was performed. For it, only species that accounted for 1% or more in both of the two replicate samples were included. Diversity calculations and multivariate analysis were realized on the basis of census counts and carried out with PAST 1.91 (Hammer et al., 2001).

Table 2
Absolute abundances of living foraminifera at *Station M* from Rose Bengal-stained samples collected in September 2009 (StaM09, 0–5 cm), and from unstained samples obtained in September 2007 (StaM07, 0–3 cm). Total numbers include soft-walled, calcareous and agglutinated foraminifera. The abundance of soft-walled specimens is additionally stated separately in parentheses. Numbers of living foraminifera from the Rose Bengal treated samples StaM07: 3–5 cm depth are found in Table 1.

		0–1 cm (ind./10 cm³)	1–2 cm (ind./10 cm³)	2–3 cm (ind./10 cm³)	3–5 cm (ind./20 cm³)	0–3 cm (ind./30 cm³)	0–5 cm (ind./50 cm³)
StaM09	A	309 (61)	109 (50)	49 (14)	19 (4)	466 (124)	485 (129)
	B	420 (75)	167 (116)	54 (28)	34 (6)	642 (220)	676 (451)
StaM07	A	194 (104)	153 (117)	209 (165)	–	556 (386)	–
	B	304 (150)	176 (116)	131 (98)	–	611 (364)	–
	C	256 (112)	254 (148)	140 (91)	–	650 (351)	–
	D	380 (143)	147 (81)	133 (77)	–	660 (301)	–

3. Results

3.1. StaM09

3.1.1. Abundances

The total number of living foraminifera in the upper 5 cm sediment from the 2 cores taken in May 2009 is shown in Table 2. Mean abundance was found to be 581 ± 135 ind./50 cm^3 (errors given within the text are standard deviations). Both cores demonstrated a maximum abundance (365 ± 79 ind./10 cm^3) at 0–1 cm depth and a clear decrease of foraminiferal numbers with sediment depth (Fig. 2). Lowest total foraminiferal numbers (13 ± 6 ind./10 cm^3) were found in the deepest investigated depth interval (3–5 cm). In total, 63% of the living specimens were found in the uppermost cm, while 24% were found at 1–2 cm depth and 9% and 5% at 2–3 and 3–5 cm depth, respectively.

The calcareous/agglutinated assemblage (excluding monothalamous saccamminids) at 0–5 cm was present with an average standing stock of 404 ± 67 ind./50 cm^3. The majority of specimens (73%) occurred in the topmost cm with 297 ± 69 ind./10 cm^3. A clear decline of calcareous and agglutinated species was observed with increasing depth (Table 2).

3.1.2. Assemblage composition

The assemblage for StaM09 at 0–5 cm sediment depth was represented by calcareous and agglutinated species (see Plates 1–3). Within the group of agglutinates, monothalamous soft-walled saccamminids (Astrorhizida) (Pl. 1, Figs. 1–5) were highly abundant. Therefore, *Saccamminid* sp. 1–5, *Saccamminid* "silver" and *Saccamminid* spp. were handled separately from the remaining "typical" agglutinated species, and will from now on be referred to as "soft-walled" foraminifera throughout the article. Komokiacea were found and documented as present in the sediment samples at *Station M*, but were not included in the following analyses because their fragile tests were heavily fragmented. StaM09 samples were numerically dominated by agglutinated specimens (41%) while soft-walled and calcareous foraminifera made up 29% and 30% of the entire population density (Fig. 3). The group of agglutinated foraminifera was not only most abundant, but also represented by the highest number of species with 46 identified taxa (60% of all taxa found). A total of 32 calcareous taxa (35%) were found while soft-walled individuals were identified with 4 morphotypes (5%). Abundances of single species for both replicate cores are given in Table 3. More than half of the population density (52%) belonged to the 7 most dominant species *Saccamminid* sp. 4, *Epistominella pusilla*, *Trochammina globigeriniformis*, *Globocassidulina subglobosa*, *Rhabdammina abyssorum*, *Reophax helenae*, *Reophax bilocularis*, *Praeglobobulimina ovata*, and *Hormosinella guttifera*. In total, *Saccamminid* sp. 4 was the most abundant species by making up 27% of the total abundance and clearly dominating the upper 3 cm sediment.

With regard to the vertical distribution of foraminifera within the sediment, the highest numbers of individuals and taxa were found in the topmost cm with 53 species. The fauna at 0–1 cm was dominated by *Saccamminid* sp. 4 (15%), *E. pusilla* (9%), *T. globigeriniformis* (7%) and *G. subglobosa* (6%). With increasing sediment depth, species richness declined steadily from an average of 53 species (0–1 cm, both cores taken together) to 20 species (1–2 cm), 14 species (2–3 cm) and 6 species (3–5 cm). *P. ovata* was the most abundant species at 3–5 cm depth (41%). No significant differences were found between the two replicate cores of StaM09 for total species abundances (paired *t*-test: $t = -1.69$, $p = 0.11$) nor for relative abundances (paired *t*-test, $t = 0.30$, $p = 0.76$).

3.1.3. Diversity

Diversity measurements were based on counts of all morphospecies irrespective of their degree of taxonomic identification. Taxa of lumped individuals, whose identification was not possible due to damage of test parts important for identification, were not included into diversity analyses. Species richness was similar between the two replicates with 53 morphospecies; the mean diversity was 3.3 for H' and 17.9 for Fisher's α (Table 4). The allocation of specimens to species was also similar for both replicates, resulting in a similar shape of rarefaction curves (Fig. 4). Mean dominance D was 0.1 and mean evenness E was 0.4 (Table 4).

The calcareous/agglutinated assemblage of the two replicates demonstrated lower dominance and higher diversity (H', α) than the total assemblage which included soft-walled foraminifera (Table 4). In the uppermost cm, the diversity of the total assemblage was 3.4 and 19.0 for H' and α in both replicates (Table 3).

3.1.4. Habitat depth of species

In terms of the vertical distribution within the upper 5 cm of the sediment, individual species of foraminifera showed considerable variation in their total occurrence as well as their preferred living depth (Table 3). Species like *Adercotryma glomeratum*, *H. guttifera* or *T. globigeriniformis* showed a shallow vertical distribution with average living depths (ALD_5) of 0.5 and 0.6 cm (Fig. 5), whereas species like *Saccamminid* sp. 4 and *R. bilocularis* were found alive at the 3–5 cm sediment interval and demonstrate higher ALD_5's of 1.2 and 1.3 cm. The deepest ALD_5 within the sediment was observed for *P. ovata* with 3.5 cm (Table 3).

To investigate the occurrence of the dominant species from StaM09 at different sediment depth intervals, a correspondence analysis (CA) of assemblage composition at individual depth intervals was performed for both replicate cores. Fifty-four percent of the total variance among samples was explained by the first axis. Samples from 0 to 1 cm show lowest axis 1 scores while the two replicates of the 3–5 cm horizon display highest scores for axis 1 (Fig. 6). Replicate samples of the 0–1 and 1–2 cm depth interval were closer grouped to another than the replicates from the deeper sediments. *P. ovata* demonstrated the highest axis 1 score of all species with 3.6, while lowest axis 1 scores were observed for *T. globigeriniformis*, *Eratidus foliaceus recurvus*, and *Trochammina* cf. *inflata* (Fig. 6).

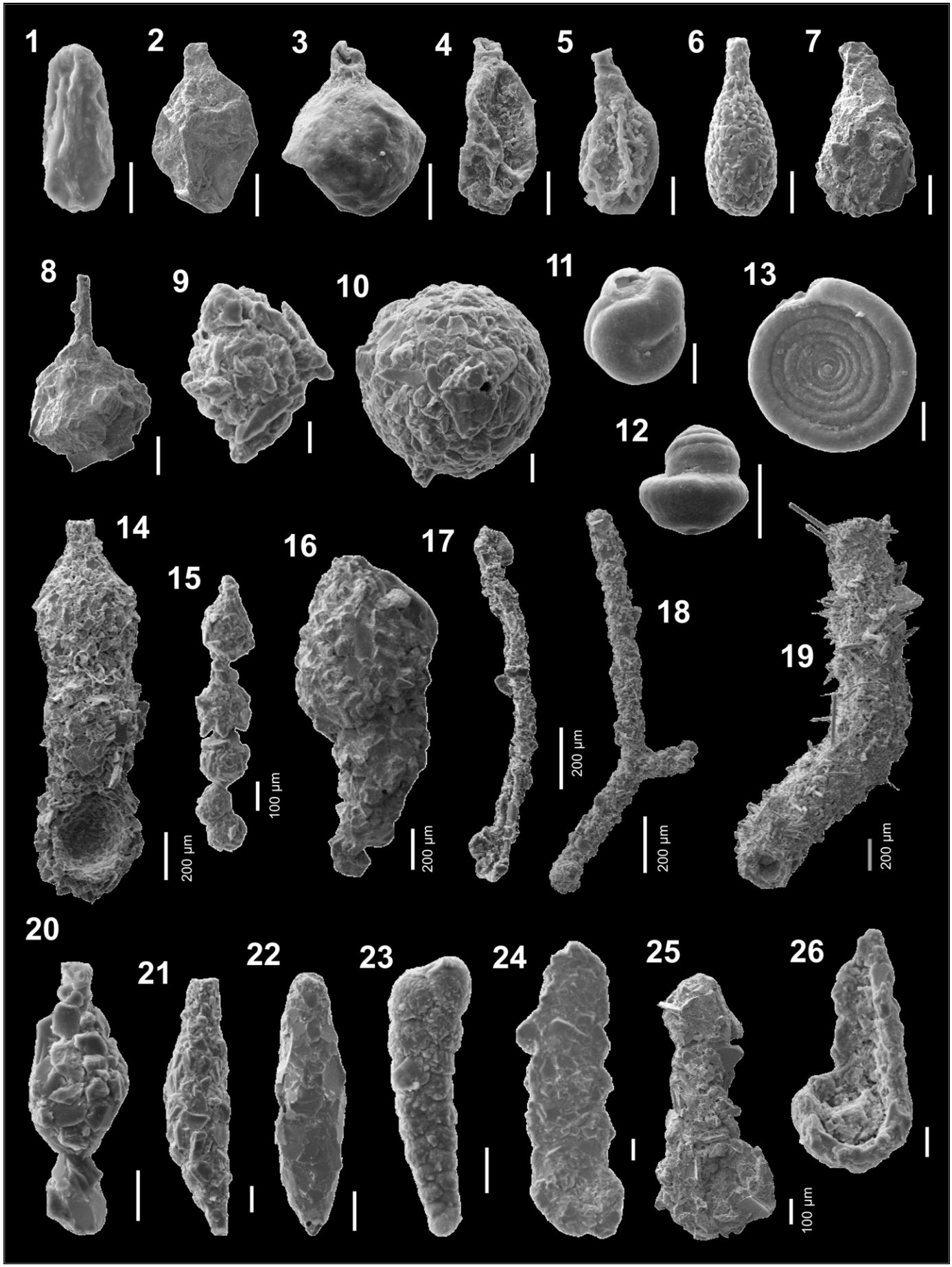
3.2. StaM07

3.2.1. Total abundances

The total number of living foraminifera in the upper 3 cm sediment differed between the four replicate cores (Table 2) and was on average 619 ± 47 ind./30 cm^3. Alive specimens were present within the entire investigated sediment section (Fig. 7), and the majority of specimens was found at 0–1 cm (45%). On average, 283 ± 78 ind./10 cm^3 were found in the uppermost centimeter (0–1 cm), 183 ± 37 ind./10 cm^3 at 1–2 cm, whereas 153 ± 37 ind./10 cm^3 were found at 2–3 cm depth. The calcareous/agglutinated assemblage at 0–3 cm depth displayed a standing stock of 268 ± 80 ind./30 cm^3. The majority (56%) of the calcareous/agglutinated assemblage was found at 0–1 cm depth, with average population density of 156 ± 60 ind./10 cm^3. With increasing sediment depth, fewer calcareous and agglutinated species were found (Fig. 7).

3.2.2. Assemblage composition

The assemblage of living foraminifera observed in September 2007 consisted of soft-walled, agglutinated and calcareous species. Soft-walled foraminifera accounted for 57% of the total specimens and 6% of all species (6 morphotypes) in the topmost 3 cm. Thirty-four percent of the observed individuals were agglutinated foraminifera, showing the highest species diversity with 72 taxa (59% of all species). Calcareous foraminifera were found to represent 10% of the total population and 35% of the species (Fig. 3). Fifty-eight percent of the total population in 0–3 cm sediment was made up by the 4 most abundant species: *Saccamminid* sp. 4 (37%), *Saccamminid* sp. 3 (13%), *A. glomeratum* (4%) and *Saccamminid* sp. 2 (4%). Species found at StaM07 and their abundances are given in Table 5.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
200 µm
100 µm
200 µm
200 µm
200 µm
200 µm
100 µm

With regard to the vertical distribution of foraminifera in the sediment, the highest number of taxa was found in the topmost cm in all four replicate cores. With increasing sediment depth, species richness decreased from an average of 73 taxa (0–1 cm) to 45 taxa (2–3 cm). All sediment depths were dominated by soft-walled foraminifera by 50% (0–1 cm) to 71% (2–3 cm).

3.2.3. Diversity

Total species richness ranged between 67 and 82 taxa at 0–3 cm sediment depth among the four replicate cores. H' values ranged between 2.2 and 3.0 and Fisher's α was found between 13.2 and 16.5 (Table 6). Dominance and evenness for entire assemblages yielded mean values of 0.2 (D) and 0.2 (E). Rarefaction curves display similar species richness between replicates (Fig. 8). The presence of the few but abundant morphotypes of soft-walled foraminifera within the assemblage increased the dominance and decreased the evenness of the assemblage, leading to lower H' and α of the total assemblage when compared with the agglutinated/calcareous taxa only (Table 6). In the uppermost sediment layer (0–1 cm), diversity of the entire foraminiferal community was found to display mean H' values of 2.9 and mean Fisher's α values of 15.4. Distribution of species within the assemblage in the top cm is characterized by mean D of 0.1, mean E of 0.3, and S was observed to range between 47 and 74 taxa (Table 5).

3.2.4. Habitat depth of species

The presence of foraminifera within the sediment column (3 cm depth) and their average living depth (ALD_3) varied between species (Table 5). Most species demonstrated an abundance maximum at the sediment surface (0–1 cm) and decreasing numbers with increasing sediment depth (e.g. Fig. 9). Other species like *Saccamminid* sp. 4, *T. globigeriniformis* and *Cribrostomoides subglobosum* were found with no distinct abundance maximum at an investigated sediment depth (Fig. 9). The shallowest ALD_3 was observed for *Quinqueloculina pygmeae* (0.7 cm) while *P. ovata*'s ALD_3 was at 2.2 cm the overall deepest.

4. Discussion

4.1. Recognition of living individuals

StaM09 samples were treated with rose Bengal (rB), the most common stain used in foraminiferal studies as proxy for living foraminifera (Bernhard, 2000). As the pink-colored chemical binds to proteins (Walton, 1952), such as those present in foraminiferal cytoplasm, the resulting pinkish coloring of the foraminiferal tests is used as indicator for living foraminifera whereas unstained tests are considered to represent dead individuals. In this study, specimens were either picked in water or wetted which increased transparency of the tests and hence the visibility of the stained cytoplasm. Nevertheless, the method holds several weaknesses (reviewed in Bernhard, 2000), such as staining necrotic tissue or cytoplasm from heat-killed foraminifera for up to weeks after the death of the individuals (Bernhard, 1988) and failing to differentiate between indigenous cytoplasm and foreign occupation of the shell (Grimm et al., 2007). Hence, the number of rB-stained individuals is likely to overestimate the number of living individuals at the time of sampling. A direct method comparison conducted by Bernhard et al. (2006) indicate that as much as half of the rB-stained number of foraminifera may have been dead at the time of collection as determined by the vital fluorogenic probe CellTracker Green. Despite these problems, rB remains a simple, easy applicable and cheap method for the recognition of living foraminifera, and its application in this study allows comparison with a range of earlier investigations. In order to minimize the effect of staining of necrotic tissue, in this study, in addition to the coloring of the cytoplasm, we also examined the distribution of the stained cytoplasm within the tests. Foraminifera were counted as living when the oldest chambers were filled with stained cytoplasm and when in total at least half of the test was filled with stained cytoplasm without any break. This methods considers the observation that when foraminifera are disturbed (e.g. by sediment movement during sampling), cytoplasm can be withdrawn deeper into the test.

The second method used in this study was based on visual inspection of the cytoplasm. Staining of the StaM07 samples at 0–3 cm depth with rB was not possible because carbon isotopic analysis was carried out on the foraminiferal cytoplasm (see Enge et al., 2011). As rB is a carbon containing molecule, its binding to the cytoplasmic proteins may cause changes in the carbon isotopes content. Hence, the non-destructive method of examination of cytoplasm color (Bernhard, 2000) was applied. Here, the presence and absence of the yellowish protoplasm was used to distinguish living from dead foraminifera whereby single specimens of the same species were compared to each other to evaluate differences in the cytoplasmatic visibility. As applied by Cornelius and Gooday (2004), the state of the test was also considered to separate living from dead foraminifera, especially for soft-walled specimens. As these do not possess thick test walls like calcareous or thick-walled agglutinated species, their fragile and often loose-agglutinated test will more easily degrade after the individuals' death. If the soft-walled test was intact and cytoplasm was visible inside, this suggested that specimens were alive at the time of sampling. The visual cytoplasm inspection method is of course to a certain degree subjective. For example, we observed that the color of the cytoplasm among the species differed, including forms with almost transparent or whitish color, making it possible that more faintly colored species like *Chilostomella oolina* were underrepresented in our inventory of living faunas. However, the results of stable isotopic analyses of specimens identified as living with this method by Enge et al. (2011) indicate that the method must have been successful for selecting living specimens, otherwise they would have not contained enough analyzable cytoplasm.

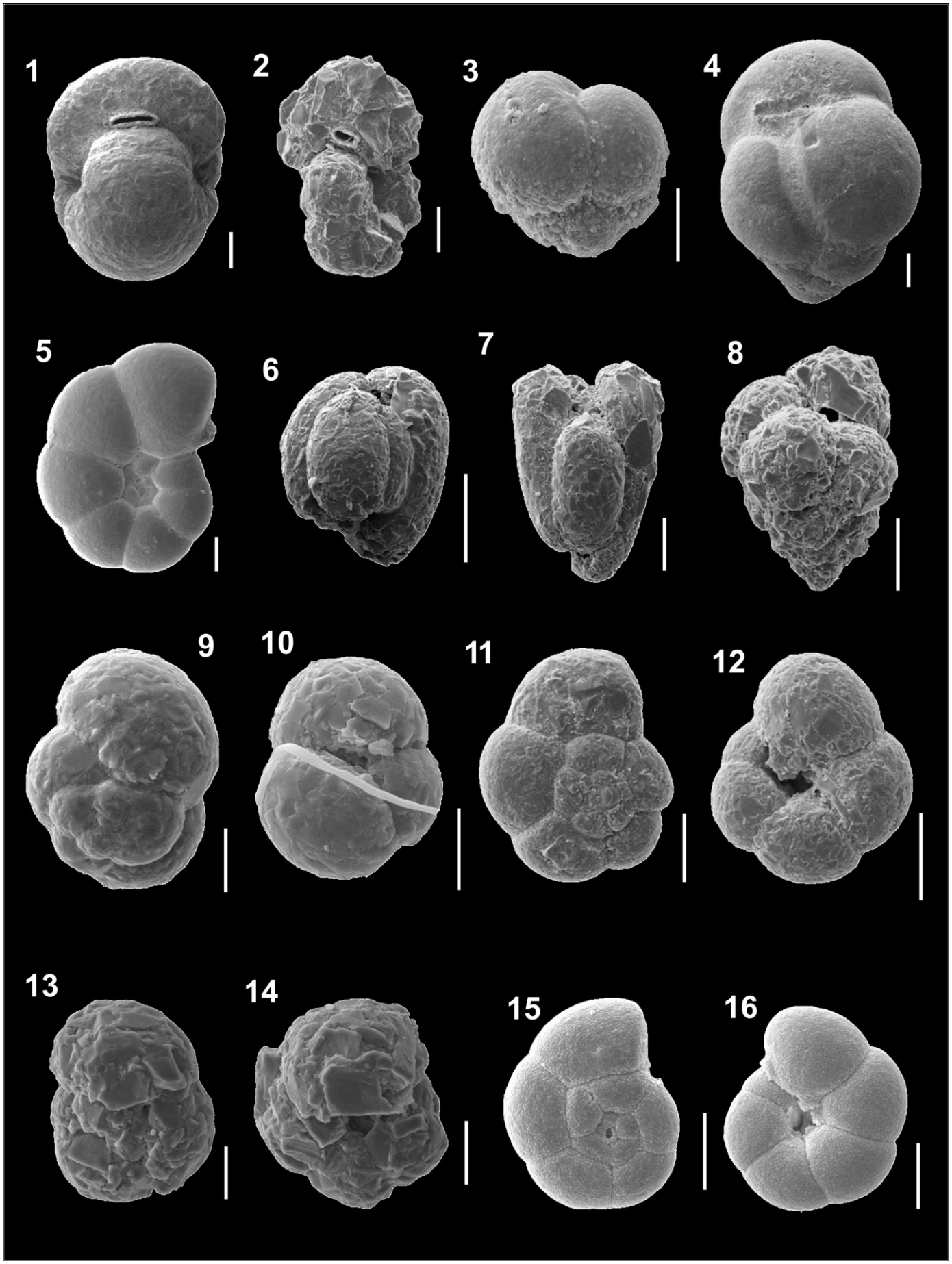
Since both methods of recognizing living individuals could have been biased in a different direction, we present the results from the two stations separately. Considering the overall similarity between the results from the two sampling events, both in terms of the population density and species composition (Table 2, Fig. 3) it seems likely that the difference due to methodology was not large, but we cannot exclude the possibility that some of the results are not fully comparable between the two sampling events.

4.2. Small-scale heterogeneity at Station M

Patchiness can make it difficult to determine whether individual samples truly represent the average regional assemblage. A heterogeneous distribution of foraminifera on a small spatial scale has been observed in the deep North Pacific by Bernstein et al. (1978), Bernstein and Meador (1979), Schroeder et al. (1988), Drazen et al. (1998), and Ohkawara et al. (2009). Being aware of these earlier observations, data presented in this study were based on replicate samples of four (StaM07) and two cores (StaM09), which had been taken within a range of about 10 m.

In our study, the overall abundances of all investigated cores were in a similar range (Figs. 2, 7), but replicate results were neither

Plate 1. Scanning electron microscope pictures of (1) *Saccamminid* "silver", (2) *Saccamminid* sp. 1, (3) *Saccamminid* sp. 2, (4) *Saccamminid* sp. 3, (5) *Saccamminid* sp. 4, (6–7) *Lagenammina difflugiformis*, (8) *Lagenammina tubulata*, (9) *Psammosphaera fusca*, (10) *Saccammina sphaerica*, (11) *Glomospira gordialis*, (12) *Glomospira charoides*, (13) *Ammodiscus anguillae*, (14) *Hormosina bacillaris*, (15) *Hormosinella guttifera*, (16) *Reophax scorpiurus*, (17) *Rhizammina* sp.1 , (18) *Rhabdammina abyssorum*, (19) *Saccorhiza ramosa*, (20) *Reophax bilocularis*, (21) *Reophax helenae*, (22) *Reophax micaceus*, (23) *Textularia porrecta*, (24) *Ammobaculites agglutinans*, (25) *Eratidus foliaceus*, (26) *Eratidus foliaceus recurvus.* Bar scale = 50 μm, unless stated otherwise.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

entirely identical for StaM07 nor for StaM09, showing that a certain amount of heterogeneity is present on the scale of meters within foraminiferal population densities at *Station M*. The variance in total abundances between the four StaM07 cores was especially pronounced in the uppermost cm (highest standard deviation of all sediment layers) where two agglutinated species of branching form (*Saccorhiza ramosa*, *R. abyssorum*) showed high numbers of fragments, especially in core D (Table 2). A different degree of fragmentation in tubular branching forms leads to difficulties in estimating abundances. We assume that next to high fragmentation potential of tubular forms which can create punctual higher counts, also small-scale variation of physical properties or biological processes and structures (e.g. burrows) within the sediment can affect the distribution of foraminifera and may have caused differences between the replicates. Drazen et al. (1998) also observed a patchy distribution of foraminifera at *Station M* but they focused on macrofauna-sized (>297 μm) foraminifera and excluded small foraminiferal species which we found to be highly abundant in our study (e.g. Saccamminidae, *A. glomeratum*, or *E. pusilla*). By considering only larger species, patchiness may appear more emphasized. Schroeder et al. (1988) found a more patchy distribution of foraminifera in the abyssal central North Pacific than in the abyssal North Atlantic which the authors explained by the exclusion of smaller species in the Pacific studies.

4.3. Foraminiferal diversity in the Northeast Pacific

Our detailed and taxonomically highly resolved dataset yielded foraminiferal diversity and abundance values broadly similar to those reported in the literature from other deep-sea settings in the Pacific Ocean. However, a direct comparison of abundance and diversity measures with previous studies is difficult as a high variation in the applied methodologies exists. For instance, the use of different size fractions can result in changes in species number and diversity measures as shown by Schönfeld (2012). To allow adequate comparison, only results from StaM09 (rB-stained) samples at 0–1 cm depth will be compared to studies which were conducted at 3000–5000 m water depth on foraminifera >63 μm.

Living (rB-stained) foraminifera at StaM09 displayed standing stocks of 309–420 ind./10 cm^3 for the total and 248–346 ind./10 cm^3 for the calcareous/agglutinated assemblages. These values are in the range of standing stock estimates for calcareous/agglutinated assemblages from other abyssal sites with 35–135 ind./10 cm^3 in the Gulf of Guinea (Timm, 1992), and 111–547 ind./10 cm^3 in the North Atlantic (Smart and Gooday, 1997). Also the numbers of foraminifera including soft-walled species are in the range of earlier observations. For example, 189–314 ind./10 cm^3 (without tubular agglutinated forms) were found in the North Atlantic (Gooday, 1996) and 113–623 ind./10 cm^2 in the Weddell Sea (Cornelius and Gooday, 2004). Regional differences are present but the results suggest that the foraminiferal population at *Station M* is comparable to other abyssal sites.

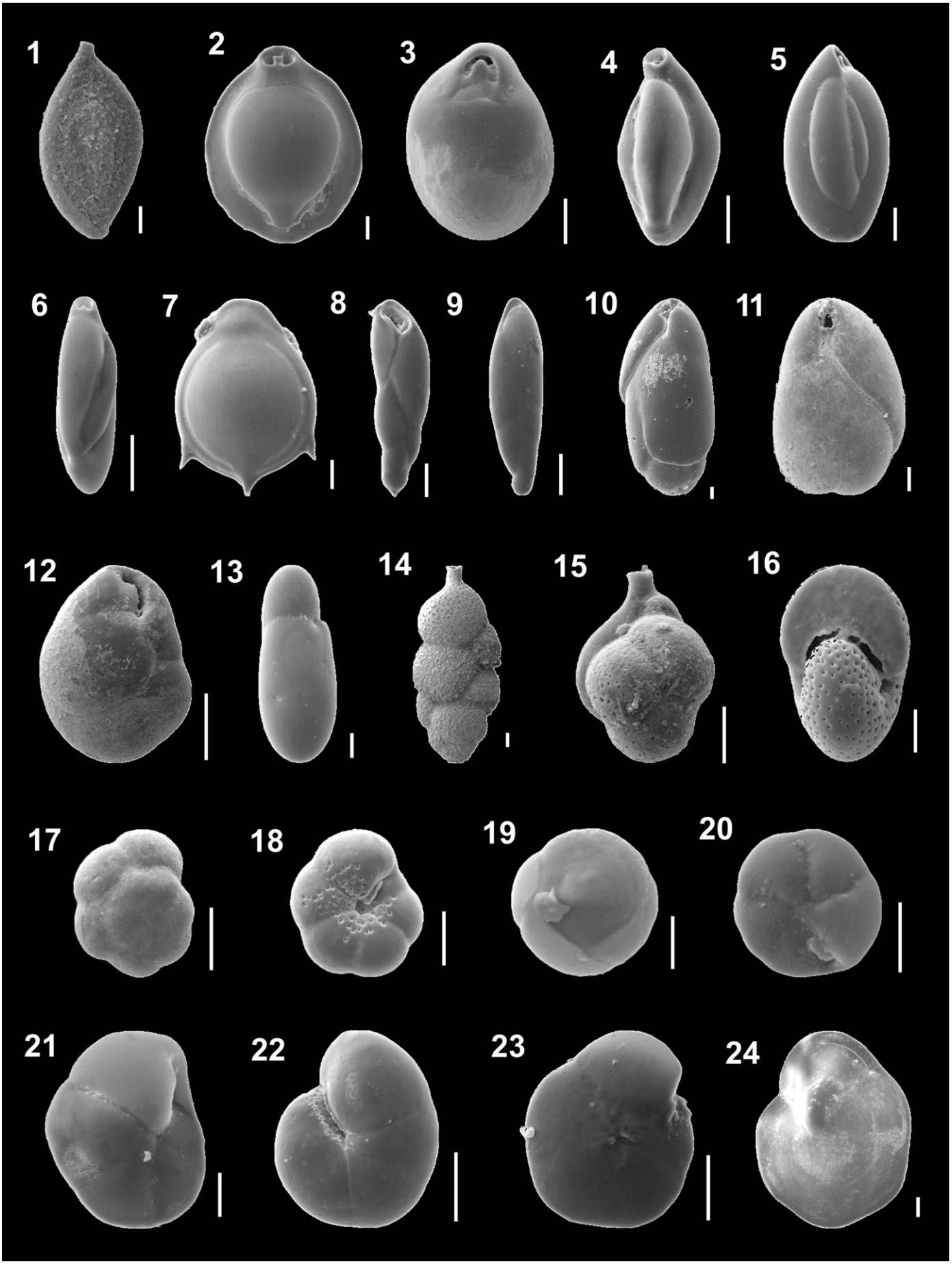
The high diversity of the total and calcareous/agglutinated assemblage is another typical attribute of deep-sea communities (Buzas and Gibson, 1969), suggested to reflect a stable deep-sea environment (Schmiedl, 1995) where co-occurrence of many species is possible and a large number of rare species is present. Average values of H' (3.6) and α (19.2) for calcareous/agglutinated StaM09 assemblages overlap with literature values for foraminiferal assemblages from the abyssal Northeast Atlantic (Smart and Gooday, 1997), the Gulf of Guinea (Timm, 1992), and Weddell Sea (Cornelius and Gooday, 2004). Considerably higher diversity ($H'_{(\log 2)}$ 6–7, α of 47–71) was calculated for assemblages in the abyssal NE Atlantic by Gooday et al. (1998). These high diversities are the result of a detailed taxonomic study by these authors of the abundant and diverse Allogromina, soft-shelled Saccamminidae, Psammosphaeridae, and Komokiacea in the assemblages. These groups have been often excluded from analyses in many other studies or were not present at such amounts in assemblages at other abyssal sites. In this study, Saccamminidae and Psammosphaeridae have been considered. Although both groups were numerically abundant, only a few taxa have been distinguished, so that the H' and α values in our fauna including those groups are lower than when excluding them.

The available amount of food and the oxygen concentration in the pore water are mainly controlling the distribution of benthic foraminifera in the deep sea (e.g. Corliss and Emerson, 1990; Bernhard, 1992). The investigated abyssal site *Station M* is located in a region with annual mean POC flux rates of 2 g $C/m^2/y$ (Smith et al., 2001) and sufficient oxygen presence in the sediment (Reimers, 1987; Smith et al., 1992). The foraminiferal assemblage at this site displayed a species richness of more than 60 taxa per sampling and values for the Shannon index and Fisher's α that are typical for deep-sea environments (Murray, 2006). In areas with an organic matter flux of 2–3 g $C/m^2/y$, species find their lower or upper nutritional thresholds for dominance in the foraminiferal community (Altenbach et al., 1999). They described these fluxes to be found for example in abyssal plains in high productivity areas which could include *Station M*, as it is located between productive waters at the coast of California (upwelling) and the more oligotroph open ocean to the west. The suggested low dominance of single species by Altenbach et al. (1999) for this transitions zone was found for *Station M* in the estimated *D* values (0.0–0.1) and *E* values (0.4–0.7). Additionally, taxa which have been related to high organic matter fluxes such as *Bolivina*, *Chilostomella*, *Uvigerina*, *Melonis*, and *Globobulimina* (e.g. Corliss, 1985; Loubere, 1996) were present, but were not clearly outnumbering other species such as suspension feeders like *S. ramosa* (Altenbach et al., 1988) and *Rhabdammina* spp. (Gooday, 1983), which are indicators for more oligotrophic conditions. But export production is not the only parameter to affect the density and composition of the foraminiferal assemblages in the studied area. As typical for a deep-sea environment of low flux of organic matter to the sea floor, the presence of oxygen deep within the sediment and in concentrations >3 ml/l (Reimers, 1987; Smith et al., 1992) allow foraminifera to populate the sediment column without restrictions by redox boundaries down to 5 cm depth and to occupy preferred microhabitats deeper in the sediment (e.g. *P. ovata*). The missing restriction to the upper sediment as in environments of high organic fluxes produces niches within the sediment for a variety of species which is also likely to have contributed to the observed high species diversity.

4.4. Soft-walled foraminifera

Soft-walled (agglutinated) saccamminids were the numerically dominant taxon at StaM07 and StaM09, present in all sediment samples and alive down to 5 cm depth. Where studied, monothalamous saccamminids have been found to be an important element of abyssal assemblages (Nozawa et al., 2006) in the deep-sea region of the Atlantic, Pacific, and Indian Ocean (Gooday et al., 2001; Sabbatini et al., 2002; Gooday et al., 2004, 2005; Radziejewska et al., 2006). However, knowledge about this group is far more limited than for agglutinated and calcareous species, and even the most detailed studies on these foraminifera leave most soft-walled (saccamminid) species in the open nomenclature (e.g. Gooday, 1996; Cornelius and Gooday, 2004; Nozawa et al., 2006). The lack of appreciation and variation in sampling methods (large size fractions) has also led to inconsistent recording of these often fragile and small foraminifera in some earlier foraminiferal

Plate 2. Scanning electron microscope pictures of (1) *Cribrostomoides subglobosum*, (2) *Evolutinella rotulata*, (3) *Karreriella bradyi*, (4) *Eggerella bradyi*, (5) *Veleronoides wiesneri*, (6–7) *Adercotryma glomeratum*, (8) Para*trochammina scotiaensis*, (9–10) *Alterammina alternans*, (11–12) *Trochammina* cf. *inflata*, (13–14) *Trochammina globigeriniformis*, (15–16) *Deuterammina grahami*. Bar scale = 50 μm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

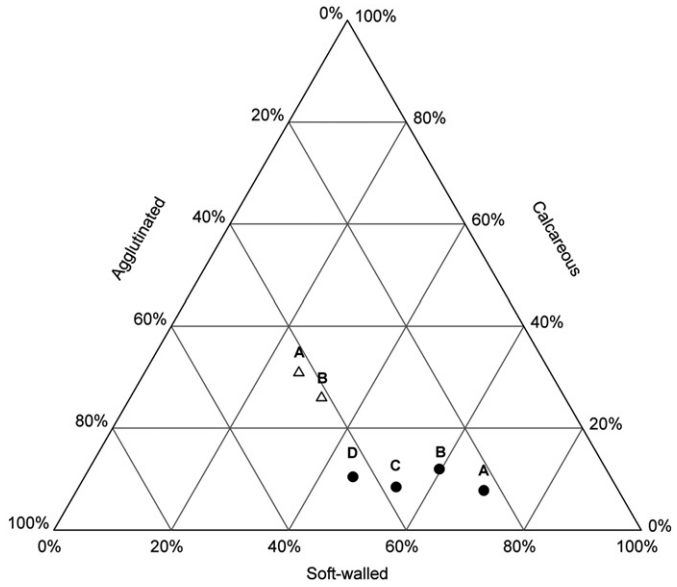


Fig. 3. Proportions of soft-walled, calcareous and agglutinated foraminifera within the total assemblage from replicate samples of StaM09 (Δ) and StaM07 (●).

investigations. As only a few studies deal with saccamminids, identification is difficult and it is likely that the diversity of this character-poor group as used in this study underestimates their true diversity (Lecroq et al., 2011). At least 15 morphotypes of monothalamous forms were described by Gooday et al. (2004) in abyssal North and Western Pacific while 23 morphotypes of saccamminids were reported from the Weddell Sea (Cornelius and Gooday, 2004). The Saccamminids sp. 1–4 found at *Station M* show high resemblance to illustrated morphospecies found in the abyssal North Pacific (Gooday et al., 2001, 2004), which were considered by the authors as cosmopolitan deep-sea species (Gooday et al., 2004).

4.5. Calcareous and agglutinated foraminifera

Both sampling events at *Station M* yielded foraminiferal assemblages of calcareous and agglutinated taxa. A number of species found at *Station M* are common in deep-sea environments: *A. glomeratum*, *C. subglobosum*, *S. ramosa*, *R. abyssorum*, *H. guttifera*, *R. bilocularis*, and calcareous species such as *Melonis barleeanum*, *Oridorsalis umbonatus*, and *Epistominella exigua* (e.g. Corliss, 1979; Burke, 1981; Schroeder et al., 1988; Timm, 1992; Gooday et al., 1996; Schmiedl et al., 1997; Kurbjeweit et al., 2000; Cornelius and Gooday, 2004; Burmistrova et al., 2007; Szarek et al., 2007). A considerable degree of similarity of abyssal foraminifera assemblages has been reported by Schroeder et al. (1988) and shown by Gooday et al. (2008).

Results of this study differ from earlier studies at *Station M* or in its near surroundings. Whereas the study by Bernhard (1992) on the deeper central California slope recorded species which were also found in our study (e.g. *M. barleeanum*, *Hoeglundina elegans*, *Pyrgo murrhina*), calcareous species represented only a small fraction of the total protozoan density (dominated by agglutinated foraminifera) in the earlier study at *Station M* by Drazen et al. (1998). On the other hand, the experimental study by Ricketts et al. (2009) reported a dominance of *Globobulimina pacifica*, *Ammodiscus latus*, *Recurvoides turbinatus*, *Uvigerina senticosa*, and *Saccammina sphaerica* in an abyssal assemblage nearby *Station M*; these species were not abundant in the assemblages reported in this study. Such differences with our species composition are probably due to the use of larger size fractions (>300, >150 μm). In these studies, smaller adult calcareous species of such as *E. pusilla* or *G. subglobosa* and the small soft-walled species that are abundant in our study, have been overlooked, resulting in lower species number and lower diversity in comparison to our results. In conclusion, we stress that when comparing assemblages, differences in sampling and sample treatment have to be considered as well as different geographical and physical properties of the studied deep-sea sites must be kept in mind. Nevertheless, it is likely that across large ecological gradients and geographical distances, the abyssal faunas of benthic foraminifera may differ. This may be due to different sediment composition and structures (e.g. manganese nodules) as well as differences in nutrient supply, water masses, oxygen concentrations, etc.

In order to visualize the similarities and differences among bathyal and abyssal North Pacific benthic foraminiferal assemblages, we compiled a matrix of species abundances for a total of 21 stations from the literature and new data presented in this study. Considering the role of methodological consistency as described above, we have only included studies which reported rB-stained foraminifera in the size fraction >63 μm and we limited our comparison to the top 1 cm of the sediment, as in some studied this was the only depth available. In addition, we have harmonized the taxonomy to the lowest common denominator (lumping to a generic level when species have not been identified) and converted all counts to percentages. Concerning the problem of tubular fragments (e.g. *Rhabdammina* sp., *Saccorhiza* sp.), which were also present in our study (see Supplementary Tables 1–3), we followed the method of Kurbjeweit et al. (2000) and therefore reclaimed our numbers in accordance with the data set of Heinz et al. (2005) (Heinz, per. communication). Other included studies did not report on tubular fragments. The resulting matrix of 22 samples and 145 species was analyzed by Nonmetrical Multidimensional Scaling with Bray–Curtis similarity (Fig. 10). The analysis shows that the assemblage at *Station M* has its nearest analogs at Suiko Seamount and Hess Rise. Studied by Ohkushi and Natori (2001), the Hess Rise is the geographically nearest oceanic abyssal site in the North Pacific. At the 3354 m station at Hess Rise, 25% of the species found were also present at *Station M* and species abundant in our study were dominating in the central North Pacific (e.g. *Lagenammina difflugiformis*, *E. exigua*, *G. subglobosa)*. However, the most abundant species *Fursenkoina cedrosensis* at the 3352 site was not present at *Station M* and it might be restricted to the Hess Rise/Suiko Seamount area (Ohkushi and Natori, 2001). Interestingly, the StaM09 fauna is clearly different from that reported by Heinz et al. (2005) from the deepest station at the Hydrate Ridge off Oregon. This station derived from 2304 m depth, but the fauna showed high affinity to the rest of the Hydrate Ridge assemblages, which in turn appear to be more similar to bathyal faunas from California margin (Mackensen and Douglas, 1989; Bernhard et al., 2001) than to *Station M*.

The results of this analysis indicate that the main trend in the faunal assemblage variation appears to be depth-related. We assume that changes in export production with water depth are mainly responsible for the observed similarity between abyssal assemblages. With increasing water depth, the flux of organic matter becomes less due to degradation processes within the water column (e.g. Suess, 1980), causing higher availability of organic matter at bathyal depths than at abyssal depths. Because species of foraminifera show different trophic requirements, the flux of organic matter controls the bathymetric distribution of species (e.g. Loubere, 1991; De Rijk et al., 2000) and different assemblage of foraminiferal species are found at bathyal depths than at abyssal depths. So were the studied sites at bathyal

Plate 3. Scanning electron microscope pictures of (1) *Spiroglutina asperula*, (2) *Pyrgo* sp. 1, (3) *Pyrgoella irregularis*, (4) *Triloculina* sp. 1, (5) *Quinqueloculina pygmaea*, (6) *Quinqueloculina bosciana*, (7) *Fissurina staphyllearia*, (8) *Fursenkoina complanata*, (9) *Fursenkoina pauciloculata*, (10) *Praeglobobulimina ovata*, (11) *Globobulimina* spp., (12) *Globocassidulina subglobosa*, (13) *Chilostomella oolina*, (14) *Uvigerina auberiana*, (15) *Uvigerina canarensis*, (16) *Melonis pompiloides*, (17–18) *Ioanella tumidula*, (19–20) *Epistominella pusilla*, (21) *Epistominella exigua*, (22) *Gyrodina soldanii*, (23) *Oridorsalis umbonatus*, (24) *Hoeglundina elegans*. Bar scale = 50 μm.

Table 3
Abundance of living (Rose Bengal-stained) foraminifera (ind./10 cm^3), diversity and average living depths (ALD, in cm; after Jorissen et al., 1995) within the upper 5 cm sediment of the two replicate cores from StaM09. Diversity measures are based on census counts and excluded taxa of lumped species such as *Reophax* spp.

StaM09	Core A (ind./10 cm^3)				Core B (ind./10 cm^3)				ALD_5 (cm)
Depth (cm)	0–1	1–2	2–3	3–5	0–1	1–2	2–3	3–5	
Saccamminid silver	3.1	–	–	–	4.2	–	–	–	0.5
Saccamminid sp. 1	–	–	2.1	–	–	–	–	–	–
Saccamminid sp. 3	8.3	5.2	–	–	6.2	5.2	2.1	–	1.0
Saccamminid sp. 4	47.1	44.7	11.4	2.1	64.4	111.2	26.0	3.1	1.3
Saccamminid spp.	2.8	–	–	–	–	–	–	–	
Bolivina sp.	–	–	2.1	–	–	–	–	–	–
Cassidulina sp.	–	–	–	–	1.0	–	–	–	–
Ceratobulimina artica	2.8	–	–	–	–	–	–	–	–
Chilostomella oolina	–	–	–	–	3.1	–	–	–	–
Cibicides spp.	2.8	2.1	–	–	6.2	–	–	–	0.7
Cibicidoides subhaidingerii	7.3	2.1	–	–	5.2	–	–	–	0.6
Epistominella exigua	–	–	4.2	1.0	8.3	–	–	–	1.8
Epistominella pusilla	30.5	3.1	2.1	–	35.3	4.2	–	–	0.6
Fissurina staphyllearia	1.4	–	–	–	–	–	–	–	–
Fursenkoina complanata	2.8	–	–	–	–	–	–	–	–
Fursenkoina pauciloculata	–	–	3.1	–	–	–	3.1	1.0	2.8
Fursenkoina sp. 1	–	–	–	–	–	–	4.2	2.1	–
Globocassidulina subglobosa	18.0	1.0	–	–	22.9	3.1	2.1	–	0.7
Gyroidina soldanii	–	–	–	–	4.2	–	–	–	–
Gyroidina sp. 1	–	–	–	–	4.2	–	–	–	–
Hoeglundina elegans	1.4	–	–	–	–	2.1	–	–	1.0
Ioanella tumidula	–	3.1	–	–	4.2	–	–	–	1.0
Lagena striata	1.4	–	–	–	–	–	–	–	–
Melonis barleeanum	6.9	–	–	–	2.1	6.2	2.1	–	1.0
Melonis pompiloides	–	2.1	–	–	6.2	–	–	–	1.0
Melonis spp.	–	–	–	–	2.1	–	–	–	–
Nodosaria spp.	0.5	–	–	–	–	–	–	–	–
Praeglobobulimina ovata	–	–	5.2	3.1	–	–	3.1	8.3	3.5
Pyrgo sp. 1	6.9	6.2	2.1	–	2.1	–	–	–	0.8
Pyrgoella irregularis	3.1	–	–	–	1.0	–	2.1	–	1.2
Quinqueloculina bosciana	8.3	–	–	–	–	–	–	–	–
Quinqueloculina pygmaea	1.4	–	–	–	2.1	–	–	–	0.5
Quinqueloculina spp.	1.4	–	–	–	–	–	–	–	–
Quinqueloculina weaveri	6.2	–	–	–	3.1	–	–	–	0.5
Robertinoides bradyi	–	–	–	–	–	2.1	–	–	–
Spiroglutina asperula	–	–	–	–	2.1	–	–	1.0	–
unidentified calcareous	1.4	–	–	–	4.2	2.1	2.1	–	0.9
Adercotryma glomeratum	6.9	–	–	–	18.7	2.1	–	–	0.6
Alterammina alternans	2.8	2.1	–	–	2.1	–	–	–	0.7
Ammobaculites sp. 2	–	–	–	–	4.2	–	–	–	–
Ammobaculitus agglutinans	2.1	–	–	–	–	–	–	–	–
Ammodiscus anguillae	1.4	4.2	1.0	–	10.4	–	3.1	1.0	1.4
Cribrostomoides sp. 1	1.4	–	–	–	–	–	–	–	–
Cyclammina cancellata	1.4	–	–	–	–	–	–	–	–
Deuterammina grahami	1.4	2.1	–	–	–	–	–	–	–
Deuterammina montagui	1.4	–	–	–	–	–	–	–	–
Eratidus foliaceus	–	–	–	–	3.1	–	–	–	–
Eratidus foliaceus recurvus	11.1	2.1	–	–	10.4	–	–	–	0.6
Evolutinella rotulata	2.8	–	–	–	6.2	–	2.1	–	0.8
Glomospira charoides	1.4	–	–	–	–	–	–	–	–
Glomospira gordialis	1.4	–	–	–	2.1	–	–	–	0.5
Haplophragmoides sp. 1	2.8	–	–	–	2.1	–	–	–	0.5
Hormosina distans	2.1	–	–	–	3.1	–	–	–	0.5
Hormosina sp. 1	–	–	2.1	–	6.2	–	–	–	1.5
Hormosinella guttifera	6.1	–	–	–	23.3	0.8	–	–	0.5
Hyperammina spp.	5.1	–	–	–	–	–	–	–	–
Lagenammina difflugiformis	4.2	2.1	2.1	–	14.5	4.2	–	–	1.0
Lagenammina tubulata	1.4	–	–	–	6.2	–	–	–	0.5
Marsipella cylindrica	0.5	–	–	–	–	–	–	–	–
Paratrochammina scotianensis	1.4	–	–	1.0	4.2	–	–	–	1.6
Reohpax subfusiformis	2.1	–	–	–	–	–	–	–	–
Reophax bilocularis	6.9	–	4.2	2.1	18.7	2.1	–	–	1.2
Reophax helenae	11.1	11.4	–	–	4.8	9.4	–	–	1.1
Reophax micaceus	–	–	–	–	–	6.2	2.1	–	–
Reophax nodulosus	–	–	–	–	0.3	–	–	–	–
Reophax scorpiurus	2.8	–	–	–	2.1	–	–	–	0.5
Reophax spp.	3.0	–	0.7	–	12.5	2.4	0.3	0.5	0.9
Rhabdammina abyssorum	12.9	4.2	2.1	–	17.7	2.1	–	–	0.8
Rhabdammina linearis	0.5	1.4	–	–	–	–	–	–	–
Rhizammina sp. 1	2.3	0.7	–	–	0.7	–	–	–	0.6
Saccammina socialis	–	–	–	–	2.1	–	–	–	–

Table 3 (*continued*)

StaM09	Core A (ind./10 cm^3)				Core B (ind./10 cm^3)				ALD_5 (cm)
Depth (cm)	0–1	1–2	2–3	3–5	0–1	1–2	2–3	3–5	
Saccammina sphaerica	–	–	–	–	2.1	–	–	–	–
Saccorhiza ramosa	0.5	–	–	–	2.1	1.0	–	–	0.7
Spiroplectammina sp. 1	4.2	–	2.1	–	3.1	–	–	–	0.8
Textularia porrecta	–	–	–	–	5.2	–	–	–	–
Thurammina albicans	–	1.0	–	–	6.2	–	–	–	1.0
Thurammina papillata	1.4	–	–	–	–	–	–	–	–
Trochammina globigeriniformis	30.5	2.1	–	–	20.8	–	–	–	0.5
Trochammina cf. *inflata*	4.2	–	–	–	10.4	–	–	–	0.5
Trochammina sp. 5	–	–	–	–	1.0	–	–	–	–
Trochammina sp. 6	–	4.2	–	–	–	–	–	–	–
Trochammina spp.	2.8	–	–	–	–	–	–	–	–
Trochammina squamata	–	2.1	–	–	–	–	–	–	–
Trochamminopsis parvus	–	–	2.1	–	–	–	–	–	–
Unidentified non–tubular aggl	–	–	–	–	–	1.0	–	–	–
Veleronoides wiesneri	6.9	–	–	–	18.7	2.1	–	–	–
Species richness *S*	53	22	16	5	53	18	12	7	–
Shannon index *H'*	3.4	2.3	2.6	1.5	3.4	1.5	1.9	1.5	–
Fisher's α	19.0	8.5	8.6	2.3	16.3	5.2	4.9	2.7	–

depths off the California margin dominated by the calcareous species *Bolivina*, *Buliminella*, *Chilostomella*, *Epistominella*, *Globobulimina*, and *Nonionella* (Mackensen and Douglas, 1989; Silva et al., 1996; Sheperd et al., 2007) which are typical forms found in organic rich sediments (e.g. Corliss, 1985; Loubere, 1996).

The analysis shows that the foraminiferal assemblage at *Station M* reflects its abyssal setting and is constituted of species adapted to reduced carbon flux to the sea floor. The very low presence of calcareous species at *Station M* with 10–30% of the total fauna and its setting at about 4000 m, suggests that the water depth of *Station M* site also plays a role. We assume that our investigated site is located close to the lysocline where the carbonate saturation of water is low and calcareous species are less successful than in shallower water depths where sufficient carbonate is present for the building of calcite tests. In the central North Pacific (~15°N, 119°W), the calcite compensation depth was suggested to be at ~4100 m due to lacking calcareous foraminifera (Nozawa et al., 2006).

4.6. Vertical habitats in the sediment

In general, benthic foraminifera at *Station M* were not homogenously distributed in the sediment column. Abundances at different sediment depths varied for single species as well as between species (Tables 3, 5). It has been established earlier that deep-sea foraminiferal species prefer specific microhabitats within the sediment column where they find their required oxygen concentration and amount of food (Corliss, 1985; Mackensen and Douglas, 1989; Corliss, 1991; Gooday, 1996; Jorissen et al., 1998). The peak abundance of foraminifera was found in the uppermost sediment layer at *Station M*, which is in agreement with observations from the deep-sea North Pacific (Snider et al., 1984; Gooday et al., 2001) and North Atlantic (Corliss and Emerson, 1990; Corliss, 1991). As predicted by the TROX model (Jorissen et al., 1995), food limitation forces foraminifera to stay closer to the sediment surface because no food is present at deeper depths. At the sediment surface, the deposited organic matter is immediately available and oxygen concentration is highest. That most species prefer these conditions is highlighted by the highest species richness in the upper sediment column (Table 3). But within this general near-surface distribution, foraminiferal species at *Station M* were found to demonstrate different depth preferences (Figs. 5, 9). That species are not distributed diffuse throughout the sediment but prefer a certain sediment depth was shown by the correspondence analysis (Fig. 6). More than half of the variance in species distribution can be explained by depth (and related changes such as in food or oxygen), being more important than spatial heterogeneity (represented by the two replicate cores). A strong linkage to the uppermost sediment layer and therefore an epifaunal or shallowest-infaunal microhabitat was observed for several species

Table 4
Diversity of living (Rose Bengal-stained) foraminifera at 0–5 cm sediment depth from four replicate sediment cores taken during sampling StaM09. The total assemblage includes soft-walled, calcareous (calc) and agglutinated (aggl) species.

StaM09	Core A		Core B		Mean	
	Total	Calc + aggl	Total	Calc + aggl	Total	Calc + aggl
Taxa *S*	63	59	58	55	61	57
Dominance *D*	0.1	0.0	0.1	0.0	0.1	0.0
Shannon index *H'*	3.4	3.7	3.1	3.6	3.3	3.6
Evenness *E*	0.5	0.7	0.4	0.7	0.4	0.7
Fisher's α	20.2	21.5	15.6	17.0	17.9	19.2

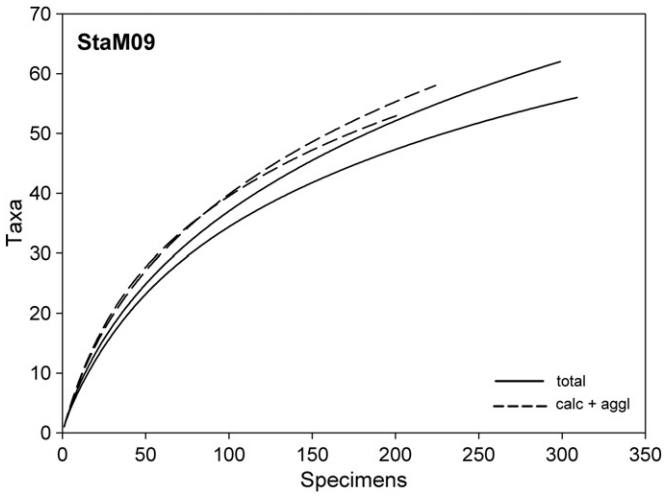


Fig. 4. Rarefaction curves, based on census counts of the living foraminifera at 0–5 cm sediment depth from two replicate cores sampled during StaM09. Total counts (solid line) include soft-walled, calcareous (calc) and agglutinated (aggl) species.

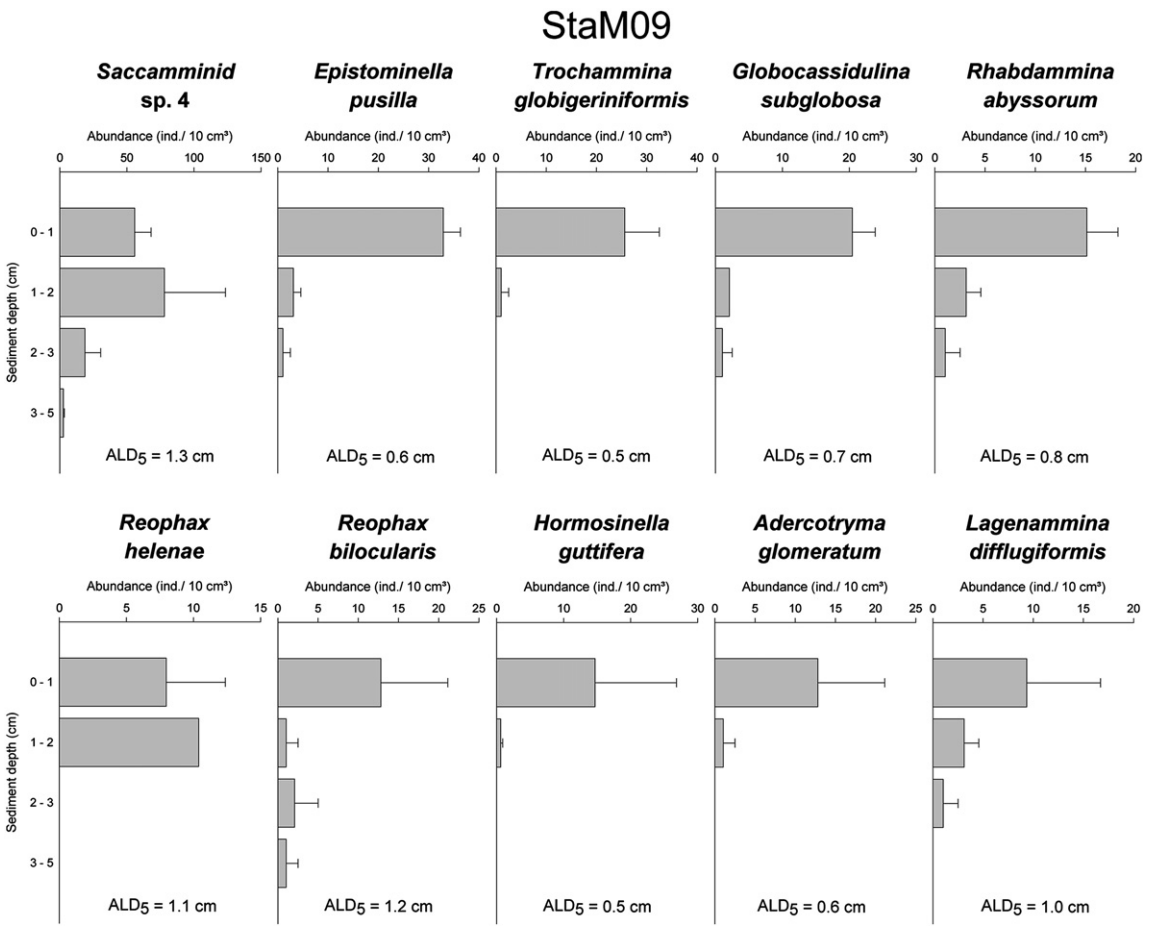


Fig. 5. Vertical distribution pattern of the dominant species from the StaM09 sampling. Total abundance (ind./10 cm^3 + SD) and the average living depth (ALD_5, after Jorissen et al., 1995) are given for the upper 5 cm sediment.

(Table 1, Fig. 6). Of these, the preferred occurrence close to the sediment surface or on the sediment has been observed before for *A. glomeratum* (e.g. Gooday, 1993; Heinz et al., 2002) and *R. abyssorum* (Jones and Charnock, 1985). Similarly, the deeper-infaunal habitat of *P. ovata* inferred in this study (Figs. 6, 9) is consistent with observations for the closely related genus *Globobulimina* (Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991; Bernhard, 1992). In general, our observations fit with previous findings and underline the existence of well-developed habitat partitioning among species in well-oxygenated abyssal sediments.

Interestingly, we observe that several species show a different ALD for StaM07 and StaM09 (see Tables 3 and 5 for comparison). As summarized in the TROX-model, it is assumed that foraminifera can find their optimal living conditions within the sediment column, and change their position due to fluctuations in external forcing. Species which prefer the deep-infaunal habitat under mesotrophic condition are found closer to the surface in an eutrophic environment as a result of shallower anoxia conditions in the sediment. Our observation of changes in the vertical distribution of species suggests that conditions on the sea floor and in the sediment at *Station M* were not identical between September 2007 and May 2009.

We realize that a direct comparison of the two sampling events is difficult because of differences in methodology (see Section 4.1.) Of the 142 species found in this study at *Station M*, 61 species (43%) were present at both samplings. The same species were dominant at StaM07 and StaM09. Sixty-one of the remaining eighty-one taxa appeared in samples from September 2007. One reason for the differences might be the higher number of replicate cores and higher numbers of specimens counted in September 2007. The rarefaction curve analysis of StaM09 (Fig. 4) indicates that the total number of species was not reached at StaM07 with the applied sampling effort (steeper slope of the rarefaction curves). Aware of these limitations, we focus the comparison between the two samplings on the abundant species. Whereas *Saccamminid* sp. 4 was dominant at both StaM07 and StaM09, other species showed different abundances between both samplings. While *Saccamminid* sp. 2, *Saccamminid* sp. 3 and *A. glomeratum* were abundant in StaM07, samples taken in May 2009 were characterized by higher abundances of *E. pusilla*, *T. globigeriniformis* and *G. subglobosa*. One possible explanation for this difference could be a difference in the availability of food. POC flux at *Station M* is typically highest in June/July and lowest in February (Smith et al., 1994). The presence of phytodetritus on the sea floor in May 2009 might have caused the more prominent appearance of the phytodetritus-associated species *E. pusilla* and *E. exigua* (e.g. Gooday, 1988, 1993; Heinz et al., 2001, 2002) and occupation of shallower microhabitats of the majority of species than at StaM07. The occurrence close to the surface facilitates faster access to freshly deposited phytodetritus for infaunal species that have been exposed to nutrient-poor conditions in the sediment reflecting low POC flux throughout the winter. In this scenario, the May 2009 samples would reflect conditions at the beginning of POC flux increase after the spring bloom, with first appearance of freshly deposited phytodetritus on the sea floor.

5. Conclusions

This study presents the results of an analysis of the total living community of benthic foraminifera at *Station M* in the abyssal

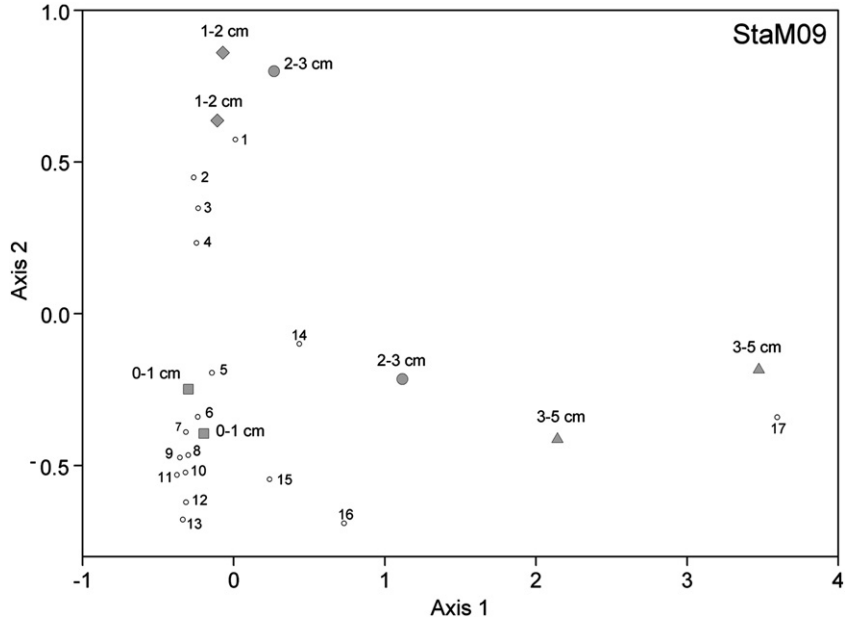


Fig. 6. Correspondence analysis of the census counts of the dominant living foraminifera ($n=17$) at different sediment depths from replicate cores ($n=2$) from sampling StaM09. 1) *Saccamminid* sp. 4, 2) *Reophax helenae*, 3) *Melonis barleeanum*, 4) *Saccamminid* sp. 3, 5) *Lagenammina difflugiformis*, 6) *Rhabdammina abyssorum*, 7) *Globocassidulina subglobosa*, 8) *Epistominella pusilla*, 9) *Eratidus foliaceus recurvus*, 10) *Adercotryma glomeratum*, 11) *Trochammina globigeriniformis*, 12) *Hormosinella guttifera*, 13) *Trochammina* cf. *inflata*, 14) *Ammodiscus anguillae*, 15) *Reophax bilocularis*, 16) *Epistominella exigua*, and 17) *Praeglobobulimina ovata*.

Northeast Pacific. Combining two different methodological treatments of multiple replicates with a detailed taxonomic study at >63 μm including soft-walled taxa, we discuss both the affinities and ecological significance of the fauna as well as the ecological requirements of single species within the sediment. We found a high resemblance of the standing stocks, species composition and microhabitat preferences with studies at other abyssal sites, with the highest assemblage affinity to data from Hess Rise. Specifically, the results allow us to conclude the following:

- Although two different methods were applied for the identification of living and dead specimens, the results revealed similar patterns of foraminiferal abundance. All assemblages were dominated by soft-walled and agglutinated foraminifera and the diversity pattern at both samplings was characterized by the occurrence of few abundant and many rare species.
- The diverse foraminiferal assemblage reflects the well-oxygenated and food limited conditions in the abyssal North Pacific and includes many species which are common in other abyssal deep-sea areas. The higher resemblance of the *Station M* fauna to open ocean regimes in the central abyssal North Pacific compared to bathyal assemblages in the proximity to *Station M* shows that the species are adapted to low fluxes of organic carbon and that the assemblage composition is related to the export production as a function of depth.
- Despite a strong affinity of most of the fauna for the very top of the sediment, a clear vertical habitat partitioning within the sediment was observed. Epifaunal species with their abundance maximum at the surface sediment (e.g. *A. glomeratum*) were present as well as infaunal species such as *P. ovata*.
- Differences of living assemblage at *Station M* between the two samplings might be related to temporal variability, although different sample treatment could explain part of the differences. Variability in POC flux to the sea floor is known for this abyssal site and indication for phytodetritus presence is suggested for the May sampling due to higher abundance of *E. exigua* and *E. pusilla*.

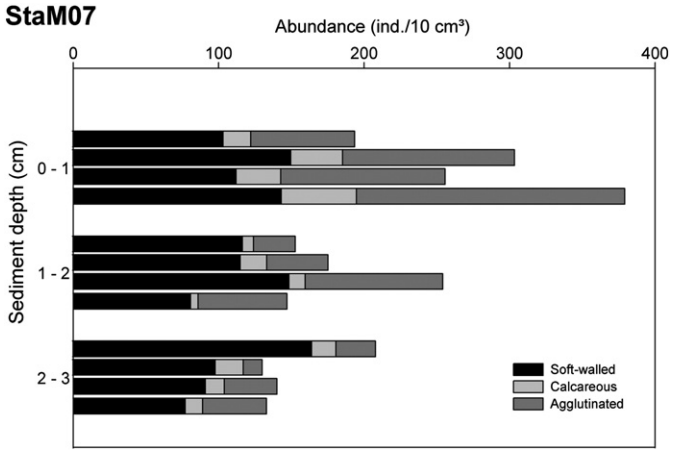


Fig. 7. Absolute abundances of living foraminifera (soft-walled, calcareous, agglutinated) in the upper 3 cm sediment (StaM07 sampling, 4 cores).

Acknowledgments

The authors would like to thank K.L. Smith Jr., the captain and the crew of the research vessel Western Flyer for their work and ship time. We are also thankful to M.M. Moeseneder and U. Witte for sampling and processing the sediment cores. Many thanks go to H. Schulz and P. Fittkau for their competent help with the SEM. We appreciate the comments by W. Joyce on the article and we also highly acknowledge the work of the three anonymous reviewers and the editor Frans Jorissen to improve this article. This research was supported by the Deutsche Forschungsgemeinschaft (grant HE-2460/5-1 for A. Enge).

Appendix A. Faunal reference list

The reference list includes all species and taxa of living foraminifera found at *Station M*. For the named species, a reference is given for the identification source and (for the dominant species) an illustration

Table 5
Abundance of living foraminifera (ind./10 cm^3), diversity and average living depths (ALD, in cm; after Jorissen et al., 1995) within the upper 3 cm sediment of the four replicate cores from StaM07. Diversity measures are based on census counts and excluded taxa of lumped species such as *Reophax* spp.

StaM07	Core A (ind./10 cm^3)			Core B (ind./10 cm^3)			Core C (ind./10 cm^3)			Core D (ind./10 cm^3)			ALD_3 (cm)
Depth (cm)	0–1	1–2	2–3	0–1	1–2	2–3	0–1	1–2	2–3	0–1	1–2	2–3	
Saccamminid silver	–	–	–	–	–	–	–	–	–	1.6	0.5	–	–
Saccamminid sp. 1	0.5	1.0	1.0	0.8	–	16.4	0.3	6.8	0.8	9.6	4.4	7.3	1.8
Saccamminid sp. 2	12.2	5.7	6.2	13.0	7.0	4.7	7.8	9.4	6.8	8.8	7.5	8.6	1.3
Saccamminid sp. 3	48.9	17.4	4.4	46.5	44.4	12.0	33.5	18.4	36.6	17.7	34.6	9.6	1.2
Saccamminid sp. 4	41.3	92.2	153.0	89.9	63.7	65.5	68.6	113.8	46.8	104.5	34.0	52.0	1.5
Saccamminid sp. 5	–	0.3	–	0.3	–	–	1.8	–	–	1.3	–	–	0.8
Saccamminid spp.	1.0	0.5	–	–	0.5	–	–	–	–	–	–	–	–
Anomalidnoides sp. 1	–	–	–	–	–	–	–	–	–	0.5	–	–	–
Astrononion spp.	–	–	–	–	–	0.3	0.3	–	–	–	–	–	–
Bolivina pacifica	–	–	–	–	–	–	0.3	–	–	–	–	–	–
Bolivina pseudopunctata	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Brizalina catanensis	–	0.3	–	0.3	–	0.3	–	–	–	–	–	–	–
Bulimina spp.	–	–	–	1.0	–	–	0.3	–	–	–	–	–	–
Cibicides spp.	–	–	0.8	–	–	–	–	0.3	–	–	–	–	–
Cibicidoides subhaidingerii	0.5	0.3	0.8	0.5	0.3	0.3	0.8	0.5	–	1.8	–	–	1.1
Cibicidoides wuellerstorfi	0.3	–	–	–	–	–	0.3	–	–	–	–	–	–
Epistominella pusilla	2.6	2.1	3.4	9.4	2.3	4.2	5.7	3.1	2.1	16.9	0.5	3.6	1.2
Fissurina sp. 1	–	–	–	0.3	–	0.3	–	–	–	0.3	–	–	–
Fissurina staphyllearia	–	–	–	–	–	–	0.3	–	–	0.5	–	–	–
Globocassidulina subglobosa	7.3	1.0	0.5	2.9	2.3	3.4	2.9	2.9	0.3	14.0	2.1	1.8	1.0
Gyroidina soldanii		–	0.8	0.5	–	–	1.0	0.5	–	0.8	–	0.8	1.3
Gyroidina sp. 1		–	–	0.5	–	–	–	–	–	0.3	–	–	–
Hoeglundina elegans		–	–	0.3	0.5	–	0.8	–	–	1.6	–	–	–
Ioanella tumidula	3.1	0.5	1.3	4.2	–	0.8	3.9	0.3	0.3	4.4	–	–	0.8
Lagena lateralis	–	–	–	–	–	–	–	0.3	–	0.8	–	–	–
Lagena sp.	–	0.3	–	–	–	–	–	–	–	–	–	–	–
Lenticulina sp. 1	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Melonis barleeanum	0.8	–	0.3	2.9	3.1	0.3	1.0	1.8	2.3	2.3	1.8	0.3	1.2
Miliolid spp.	–	–	–	0.8	–	–	0.8	0.3	0.5	0.5	0.5	–	–
Nonion pacificum	–	–	–	1.0	–	–	–	–	–	–	–	–	–
Nonion sp.	–	0.3	–	–	–	–	–	–	–	–	–	–	–
Oridorsalis umbonatus	–	–	–		–	–	–	–	–	0.5	–	–	–
Osangulariella umbonifera	–	0.3	–		–	0.3	0.3	–	–	–	–	–	–
Praeglobobulimina ovata	–	0.5	2.9	0.8	2.9	3.6	–	–	2.3	0.8	–	2.1	2.2
Procerolagena gracillima	–	–	–	0.3	–	–	–	–	–		–	–	–
Pyrgo sp. 1	0.5	–	0.3	1.3	–	0.3	2.1	–	–	0.3	–	–	0.8
Pyrgo sp. 2	–	–	–		–	–	0.5	–	–	0.5	–	–	–
Pyrgo sp. 3	0.5	–	–	0.5	–	–	–	–	–	–	–	–	–
Pyrgo spp.	0.3	–	–		–	–	0.3	–	0.3	0.8	–	–	–
Pyrgoella irregularis	–	–	–	–	–	–	0.3	–	–	–	–	0.3	–
Quinqueloculina pygmaea	0.8	–	–	0.3	0.5	–	1.3	–	–	0.5	–	–	0.7
Quinqueloculina seminulum	0.3	–	–	–	–	–	0.5	–	0.3	–	–	–	–
Quinqueloculina spp.	0.3	–	–	0.3	–	–	–		–	0.5	–	0.3	–
Robertina subcylindrica	–	–	–	0.3			0.5				–	–	–
Spiroglutina asperula	–	1.3	1.8	3.1	1.8	2.1	2.3	0.5	1.0	1.8	–	–	1.3
Triloculina sp. 2	0.5	0.3	–	2.3	0.3	0.3	1.0	–	0.3	0.3		–	0.8
Unidentified calcareous	–	–	–	–	0.5	–	1.6	–	1.3	–	0.3	–	–
Uvigerina canariensis	1.3	0.5	3.9	1.3	3.1	3.1	1.8	0.5	1.8	0.8	–	2.6	1.8
Uvigerina sp.	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Uvigerina sp. 1	–	–	–	–	0.5	–	–	0.3	0.3	0.3	–	0.3	–
Adercotryma glomeratum	10.9	5.5	6.8	13.5	6.5	4.2	11.2	9.1	6.0	13.5	7.5	3.1	1.2
Alterammina alternans	4.9	0.3	1.6	3.9	0.5	0.5	3.1	7.0	1.6	10.1	1.8	3.4	1.1
Ammobaculites spp.	0.5	–	–	–	–	–	–	–	0.3	–	–	–	–
Ammobaculitus agglutinans	–	–	–	0.3	–	–	0.3	0.3	–	0.3	–	–	–
Ammobaculitus americanus	–	–	0.5	0.3	0.3	–	0.3	–	–	–	–	–	–
Ammodiscus anguillae	3.1	–	0.5	1.8	0.3	0.5	0.5	0.8	0.3	1.8	–	0.5	1.0
Ammolagena clavata	0.8	–	–	–	–	–	–	–	–	–	–	–	–
Aschemonella sp. 1	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Bathysiphon filiformis	–	0.2	–	–	0.8	0.2	0.2	0.3	–	–	–	–	–
Bathysiphon sp. 2	–	–	–	0.1	–	–	0.5	0.4	–	0.5	–	–	–
Cribrostomoides subglobosum	4.4	2.1	0.3	8.1	7.3	–	4.2	10.4	2.1	8.6	6.0	3.1	1.1
Cyclammina cancellata	–	–	–	–	–	–	–	–	–	0.3	–	–	–
Deuterammina grahami	–	–	–	–	–	–	–	–	–	0.8	–	–	–
Deuterammina montagui	–	0.3	0.5	0.3	–	–	0.5	–	0.5	0.5	–	1.3	1.5
Egerella bradyi	–	–	0.3	–	–	–	0.8	–	–	–	–	0.3	–
Eggerelloides scaber	1.0	–	–	–	–	–	–	–	–	–	–	–	–

Table 5 (*continued*)

StaM07	Core A (ind./10 cm^3)			Core B (ind./10 cm^3)			Core C (ind./10 cm^3)			Core D (ind./10 cm^3)			ALD_3 (cm)
Depth (cm)	0–1	1–2	2–3	0–1	1–2	2–3	0–1	1–2	2–3	0–1	1–2	2–3	
Eratidus foliaceus	–	–	–	0.5	1.0	0.3	1.3	0.5	1.3	1.8	–	0.8	–
Eratidus foliaceus recurvus	1.6	1.6	1.3	2.1	2.1	1.0	4.4	2.6	1.3	4.4	1.6	1.8	1.3
Evolutinella rotulata	0.3	–	–	3.1	–	–	3.1	0.5	1.6	–	–	–	–
Glomospira charoides	2.1	–	0.3	0.8	0.5	–	1.6	0.3	–	0.5	0.3	–	0.8
Glomospira gordialis	1.0	0.3	0.8	0.5	–	0.3	–	0.3	–	1.0	1.6	0.3	1.8
Haplophragmium sp. 1	–	–	–	–	–	–	–	0.3	–	–	–	–	–
Haplophragmium sp. 2	–	–	–	–	–	–	–	–	–	2.1	–	–	–
Haplophragmoides sp. 2	4.2	–	–	–	–	–	–	–	–	–	–	–	–
Haplophragmoides spp.	0.3	–	–	0.3	–	–	–	–	–	–	–	–	–
Hormosina bacillaris	–	–	–	–	–	–	0.7	–	–	3.6	0.8	0.3	–
Hormosina distans	–	0.3	–	–	–	–	0.3	–	–	0.5	–	–	–
Hormosina globulifera	0.3	1.0	1.6	1.0	0.3	0.3	0.5	1.3	1.0	0.5	0.8	–	1.4
Hormosinella guttifer	5.9	2.7	1.4	8.8	2.4	1.3	9.4	4.3	2.9	11.0	0.9	2.8	1.0
Hormosinella ovicula	0.1	–	–	0.1	–	–	–	0.1	–	0.1	–	0.3	1.1
Hyperammina fragilis	1.2	0.3	0.2	0.7	0.2	0.1	1.0	0.9	0.1	1.6	0.4	0.1	0.9
Hyperammina friabilis	0.1	0.1	0.2	0.8	0.1	–	0.3	–	0.3	0.1	0.5	0.1	1.3
Karreriella bradyi	–	–	–	–	0.3	–	1.0	0.3	–	0.3	–	0.5	–
Karrerulina conversa	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Lagenammina diffugiformis	1.6	2.3	0.8	4.9	2.1	1.0	2.6	5.2	1.8	3.1	5.2	0.8	1.3
Lagenammina tubulata	1.0	0.3	–	1.6	–	–	2.1	0.8	0.3		0.8		1.1
Paratrochammina scotianensis	2.1	–	0.8	1.6	0.3	0.5	1.8	1.6	0.8	3.6	1.8	0.5	1.1
Psammmosphaera sp.	–	0.3	–	–	–	–	–	–	–	–	0.5	–	–
Psammosphaera fusca	0.3	0.3	0.8	1.3	0.5	0.3	3.4	1.3	0.3	4.2	0.8	1.8	1.2
Recurvoides sp.	–	–	0.3	–	–	–	–	–	–	–	–	–	–
Reophax bilocularis	–	0.5	0.3	–	0.8	–	0.5	1.0	0.5	0.3	1.3	1.8	1.7
Reophax helenae	0.3	–	–	1.0	2.9	0.3	3.1	0.8	0.5	–	0.5	3.4	1.3
Reophax mortensis	1.6	0.3	0.3	1.3	–	–	1.2	0.9	0.7	1.8	1.4	1.5	1.1
Reophax nodulosus	–	–	0.5	0.1	0.2	–	–	0.8	–	–	–	–	–
Reophax scorpiurus	–	–	–	–	–	–	–	0.8	–	3.4	0.5	0.3	–
Reophax spp.	1.8	–	1.0	0.4	1.3	–	8.1	0.3	0.8	0.5	–	–	0.9
Rhabdammina abyssorum	5.6	1.8	0.4	21.7	3.7	0.1	–	16.3	0.3	32.8	3.0	–	0.9
Rhabdammina sp. 1	–	–	0.2	–	–	–	1.0	0.9	0.3	2.6	0.8	0.7	–
Rhizammina sp.	–	–	–	–	–	–	0.3	–	–	0.7	–	0.5	–
Rhizammina sp. 1	–	–	–	–	0.3	–	0.9	0.1	–	1.6	–	–	–
Saccammina spp.	–	–	–	0.3	–	–	1.3	–	–	–	–	0.8	–
Saccorhiza ramosa	2.8	2.1	0.4	5.5	3.3	0.3	2.7	3.1	1.6	17.5	2.5	0.6	1.0
Spiroplectammina biformis	–	–	–	–	–	–	0.5	–	–	0.5	0.3	–	–
Subreophax aduncus	–	–	–	1.0	–	–	0.5	0.3	–	–	0.3	–	–
Textularia porrecta	0.5	–	–	–	0.3	–	0.5	1.0	–	0.8	–	0.5	1.1
Textularia sp. 1	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Thurammina albicans	–	–	–	0.3	0.3	–	0.3	–	–	1.0	–	–	–
Thurammina papillata	–	–	–	–	–	–	0.3	–	–	–	–	–	–
Trochammina globigeriniformis	1.8	3.1	0.8	1.6	1.6	0.8	3.1	4.4	0.8	12.5	10.7	8.6	1.3
Trochammina cf. *inflata*	3.4	1.6	1.0	3.4	0.3	–	3.6	4.2	0.3	16.9	4.9	0.3	0.9
Trochammina sp. 1	–	–	–	0.5	–	–	1.8	–	–	–	–	–	–
Trochammina sp. 2	–	–	–	–	–	–	–	–	–	0.8	–	–	–
Trochammina sp. 3	0.5	–	–	0.5	–	–	1.6	–	–	–	–	–	–
Trochammina sp. 4	–	–	–	1.6	–	–	0.3	–	–	–	–	–	–
Trochammina spp.	0.5	0.5	1.3	16.1	–	0.5	18.4	4.7	4.2	7.3	1.3	–	1.0
Trochammina squamata	1.0	0.5	1.6	0.3	0.3	–	0.8	0.5	–	2.1	1.6	0.5	1.2
Unidentified non–tubular aggl	–	0.3	0.3	4.7	–	–	2.6	3.9	1.6	3.9	–	0.8	1.12
Unidentified tubular aggl	0.5	0.1	0.2	0.3	–	–	0.3	0.7	–	0.3	–	1.7	1.3
Veleroninoides jeffreysii	0.5	–	0.3	–	–	0.5	0.5	–	–	1.0	0.8	–	1.3
Veleroninoides sp. 1	2.6	–	0.3	0.3	1.8	0.3	3.1	1.0	1.8	–	–	–	–
Veleronoides wiesneri	0.3	0.3	–	0.3	–	–	0.8	0.5	0.5	1.6	–	0.3	0.9
Verneuilinulla propinqua	–	–	–	0.3	–	–	–	–	–	–	–	–	–
Species richness *S*	47	41	45	68	43	34	74	52	41	69	38	42	
Shannon index *H'*	2.7	1.8	1.4	2.3	2.0	3.0	3.0	2.4	2.3	3.1	2.7	2.6	
Fisher's α	11.2	10.1	10.3	16.0	10.3	8.3	19.3	11.8	10.5	15.2	9.2	10.9	

reference which is representative for the species. The following literature for identification was used: (a) Cushman (1913), (b) Phleger et al. (1953), (c) Brönnimann and Whittaker (1988), (d) Nienstedt and Arnold (1988), (e) Timm (1992), (f) Sgarrella and Moncharmont Zei (1993), (g) Jones (1994), (h) Schmiedl (1995), (i) Kuhnt et al. (2000), and (j) Majewski et al. (2005).

Astrorhizida

Aschemonella sp. 1. Similar to *Aschemonella scabra* in Jones (1994, Pl. 27, Fig. 1) but body more is slender and appendages are more defined from the body.

Bathysiphon filiformis M. Sars, 1872[g].

Bathysiphon sp. 2. Fragile, thin-walled test with definite constrictions.

Hyperammina fragilis Höglund, 1947[j].

Hyperammina friabilis Brady, 1884[g].

Table 6
Diversity of living foraminifera at 0–3 cm sediment depth from four replicate sediment cores taken during sampling StaM07. The total assemblage includes soft-walled, calcareous (calc) and agglutinated (aggl) species. Paired *t*-tests were performed between total and the calcareous/agglutinated assemblage. Differences of significance ($p \geq 0.05$) are indicated with *.

StaM07	Core A		Core B		Core C		Core D		Mean		*t*-Test	
	Total	Calc + aggl	Total	Calc + aggl	Total	Calc + aggl	Total	Calc + aggl	Total	Calc + aggl	*t*	*p*
Species richness *S*	67	62	78	73	82	77	78	72	76	71	21	>0.01*
Dominance *D*	0.3	0.1	0.2	0.1	0.2	0.0	0.1	0.1	0.2	0.1	4.89	0.02*
Shannon index *H'*	2.2	3.5	2.6	3.5	2.8	3.7	3.0	3.4	2.6	3.5	−4.75	0.02*
Evenness *E*	0.1	0.5	0.2	0.4	0.2	0.5	0.3	0.4	0.2	0.5	−3.87	0.03*
Fisher's α	13.2	17.1	15.7	19.0	16.5	19.5	15.3	16.3	15.2	18.0	−4.46	0.02*

Lagenammina difflugiformis (Brady, 1879)[g]. We found two morphotypes of this species, a yellowish, more finely agglutinated type (as illustrated in Jones, 1991, Pl. 30, Fig. 1–3) as well as a more coarsely agglutinated type of more whitish test material (resemblance to Timm, 1992, Pl. 1, Fig. 13a, b). Both types are illustrated in Pl. 1, Figs. 6–7.

Lagenammina tubulata Rhumbler, 1931[i]. Illustrated in Pl. 1, Fig. 8.

Marsipella cylindrica Brady, 1882[g].

Psammosphaera fusca Schulze, 1875[g]. Illustrated in Pl. 1, Fig. 9.

Psammosphaera sp.

Rhabdammina abyssorum M. Sars, 1869[g]. Illustrated in Pl. 1, Fig. 18.

Rhabdammina linearis Brady, 1879[g].

Rhabdammina sp. 1

Rhizammina sp. 1. Very thin in diameter, appears very fragile. Illustrated in Pl. 1, Fig. 17.

Saccammina socialis Brady, 1884[g].

Saccammina sphaerica Brady, 1871[g]. Illustrated in Pl. 1, Fig. 10.

Saccamminid "silver." Small soft-walled species with one aperture and silvery glance on the test surface. It likely corresponds to "Silver Saccamminid" described by Gooday et al. (1996) from Antarctic sediments in shallow depths. Illustrated in Pl. 1, Fig. 1

Saccamminid sp. 1. Soft-walled species, flask-shaped with one aperture and a short neck. Surface appears roughened, not smooth. Illustrated in Pl. 1, Fig. 2.

Saccamminid sp. 2. Soft-walled monothalamous species whose test appears more spherical, very smooth and shiny. Long neck. Illustrated in Pl. 1, Fig. 3.

Saccamminid sp. 3. Soft-walled, monothalamous species in shape more elongated, and with sediment particles attached to the surface. Illustrated in Pl. 1, Fig. 4.

Saccamminid sp. 4. Soft-walled and flask-shaped species with one aperture, a longer neck. Sediment particles can be attached to surface. Illustrated in Pl. 1, Fig. 5.

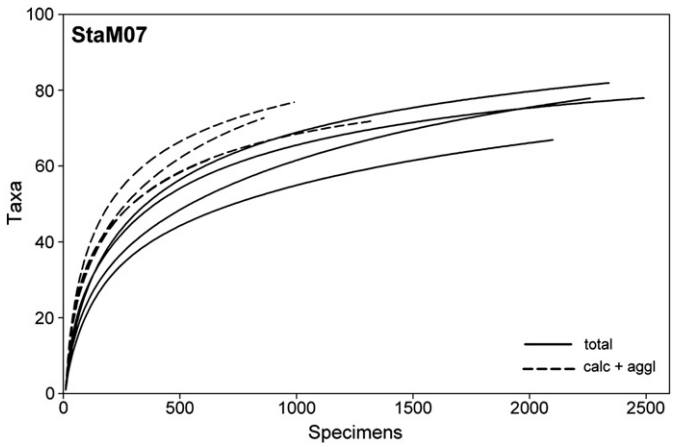


Fig. 8. Rarefaction curves, based on census counts of the living foraminifera at 0–3 cm sediment depth from four replicate cores sampled during StaM07. Total counts (solid line) include soft-walled, calcareous (calc) and agglutinated (aggl) species.

Saccamminid sp. 5. Soft-walled, flask-shaped species with one aperture and a white test color.

Saccorhiza ramosa (Brady, 1879)[g]. Illustrated in Pl. 1, Fig. 19.

Thurammina albicans Brady, 1879[g].

Thurammina papillata Brady, 1879[g].

Lituolida

Adercotryma glomeratum (Brady, 1878)[g]. Dimorphism of test observed, similar to Kuhnt et al. (2000). Both types illustrated in Pl. 2, Fig. 6–7.

Ammobaculites agglutinans (d'Orbigny, 1846)[g]. Illustrated in Pl. 2, Fig. 24.

Ammobaculites americanus d'Orbigny, 1826[d].

Ammobaculites sp. 2

Ammodiscus anguillae Høglund, 1947[g]. Illustrated in Pl. 1, Fig. 13.

Ammolagena clavata (Jones & Parker, 1860)[g].

Cribrostomoides subglobosum Cushman, 1910[g]. Illustrated in Pl. 2, Fig. 1.

Cribrostomoides sp. 1. Similar to *C. subglobosum* but thinner in shape and last whorl with aperture slightly distorted.

Cyclammina cancellata Brady, 1879[g].

Eratidus foliaceus (Brady, 1881)[g]. Illustrated in Pl. 1, Fig. 25.

Eratidus foliaceus recurvus (Earland, 1934)[i]. Illustrated in Pl. 1, Fig. 26.

Evolutinella rotulata (Brady, 1881)[g]. Illustrated in Pl. 2, Fig. 2.

Glomospira charoides (Jones & Parker, 1860)[g]. Illustrated in Pl. 1, Fig. 12.

Glomospira gordialis (Jones & Parker, 1860)[g]. Illustrated in Pl. 1, Fig. 11

Haplophragmium sp. 1

Haplophragmium sp. 2

Haplophragmoides sp. 1

Haplophragmoides sp. 2

Hormosina bacillaris (Brady, 1881)[g]. Illustrated in Pl. 1, Fig. 14.

Hormosina globulifera Brady, 1879[g].

Hormosina sp. 1

Hormosinella distans (Brady 1881)[g].

Hormosinella guttifera (Brady, 1881)[g]. Illustrated in Pl. 1, Fig. 15.

Hormosinella ovicula (Brady, 1879)[g].

Karrerulina conversa (Grzybowski, 1901)[g].

Recurvoides sp.

Reophax bilocularis Flint, 1899[e]. Illustrated in Pl 1, Fig. 20.

Reophax helenae Rhumbler, 1931[i]. Illustrated in Pl. 1, Fig. 21.

Reophax micaceus Earland, 1934[e]. Illustrated in Pl. 1, Fig. 22.

Reophax mortenseni Hofker, 1972[g].

Reophax nodulosus Brady, 1879[g].

Reophax scorpiurus Montfort, 1808[e]. Illustrated in Pl. 1, Fig. 16.

Reophax subfusiformis Earland, 1933[e].

Spiroplectammina biformis (Parker & Jones, 1865)[g]. Illustrated in Pl. 2, Fig. 14.

Spiroplectammina sp. 1. Very tiny and flat species, coarsely agglutinated.

Subreophax aduncus (Brady, 1882)[g].

Veleroninoides jeffreysii Williamson, 1856[g].

Veleroninoides wiesneri (Parr, 1950)[g]. Illustrated in Pl. 2, Fig. 5.

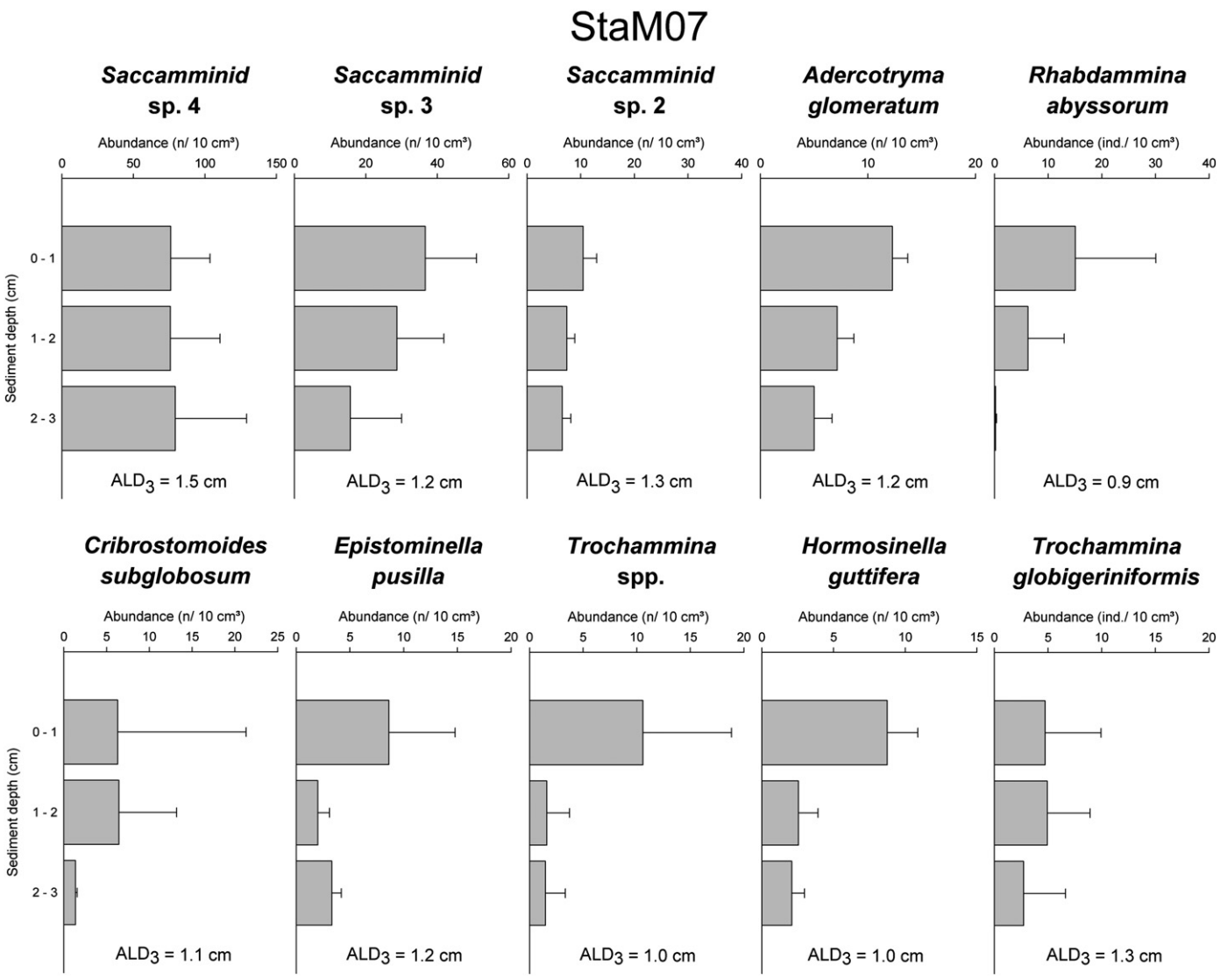


Fig. 9. Vertical distribution pattern of the dominant species from the StaM07 sampling. Total abundance (ind./10 cm^3 + SD) and the average living depth (ALD_3, after Jorissen et al., 1995) are given for the upper 3 cm sediment.

Veleroninoides sp. 1. Species with 5 chambers in the final whorl, a slightly inflated final chamber and a distinct, interio-areal located aperture.

Verneuilinulla propinqua (Brady, 1884)[g].

Textularida

Eggerella bradyi (Cushman, 1911)[g]. Illustrated in Pl. 1, Fig. 4.

Eggerelloides scaber (Williamson, 1858)[g].

Karreriella bradyi (Cushman, 1911)[g]. Illustrated in Pl. 2, Fig. 3.

Textularia porrecta (Brady, 1884)[g]. Illustrated in Pl. 1, Fig. 23.

Textularia sp. 1. Very tiny species.

Trochamminida

Alterammina alternans (Earland, 1934)[c]. Illustrated in Pl. 2, Figs. 9–10.

Deuterammina grahami Brönniman & Whittaker, 1988[c]. Test built of homogenously agglutinated baryte bodies as shown in Brönniman & Whittaker (1988). Illustrated in Pl. 2, Figs. 15–16.

Deuterammina montagui Brönnimann and Whittaker, 1988[c].

Paratrochammina scotiaensis Brönnimann and Whittaker, 1988[i]. Illustrated in Pl. 2, Fig. 8.

Trochammina globigeriniformis Parker & Jones, 1865[g]. Illustrated in Pl. 2, Figs. 13–14.

Trochammina cf. *inflata* (Montagu, 1808)[g]. Illustrated in Pl. 2, Figs. 11–12.

Trochammina squamata (Jones & Parker, 1860)[i].

Trochammina sp. 1

Trochammina sp. 2

Trochammina sp. 3

Trochammina sp. 4

Trochammina sp. 5

Trochammina sp. 6

Trochamminopsis parvus Brönnimann and Whittaker, 1988[c].

Miliolida

Pyrgo murrhina (Schwager, 1866)[a].

Pyrgo sp. 1. Similar to *Pyrgo murrhina* but showing no identation of the keel of the last chamber. Illustrated in Pl. 3, Fig. 2.

Pyrgo sp. 2. Also similar to *P. murrhina* but instead of the keel identation of the last chamber, a shaft from both chambers downwards is present.

Pyrgo sp. 3

Pyrgoella irregularis (d'Orbigny, 1839)[g]. Illustrated in Pl. 3, Fig. 3.

Quinqueloculina bosciana (d'Orbigny, 1839)[f]. Illustrated in P. 3, Fig. 6.

Quinqueloculina pygmaea Reuss, 1850[f]. Illustrated in Pl 3, Fig. 5.

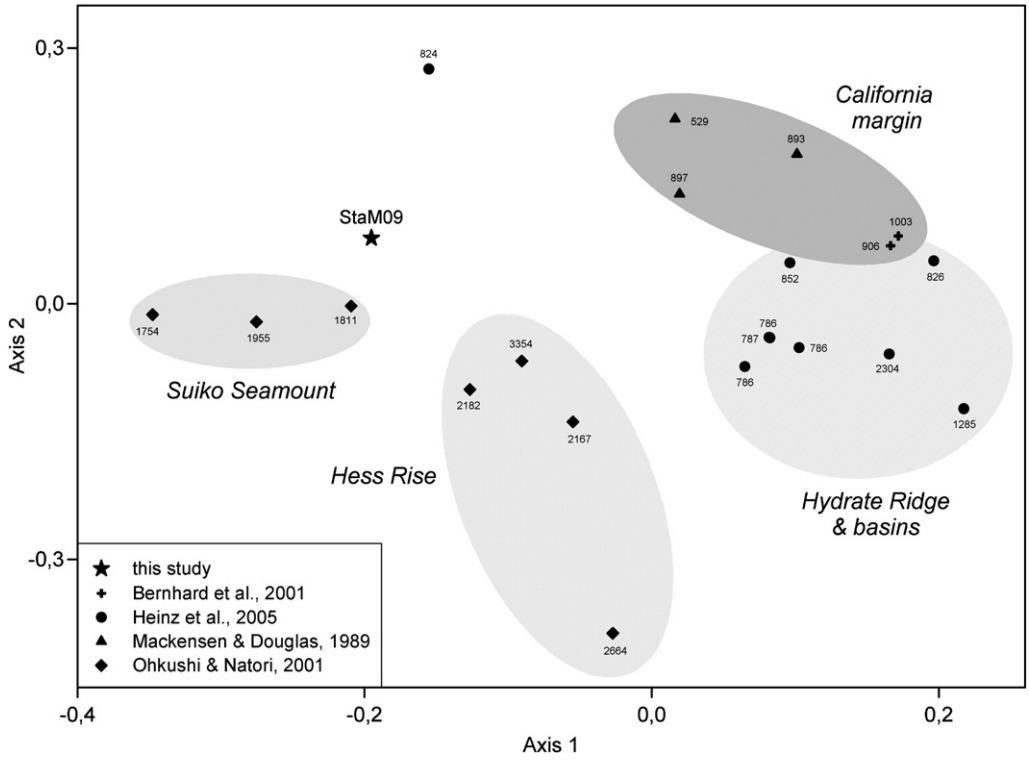


Fig. 10. Nonmetric Multidimensional Scaling (NMDS) plot based on Bray–Curtis similarity of 22 assemblages of living foraminifera in the North Pacific. The water depth (m) is given for each sampling. Under the assumption of counts of rose Bengal-stained individuals >63 μm from the 0–1 cm sediment layer, species abundances of StaM09 (3853 m depth) were compared to literature data from Mackensen and Douglas (1989), Bernhard et al. (2001), Ohkushi and Natori (2001) and Heinz et al. (2005). The matrix of relative abundances for analysis did not included Saccamminidae and Allogromina. Taxa were lumped on generic level where species have not been identified.

Quinqueloculina seminulum (Linné, 1758)[g].
Quinqueloculina weaveri Rau, 1948[g].
Spiroglutina asperula (Kerrer, 1868)[g]. Illustrated in Pl. 3, Fig. 1.
Triloculina sp. 1. Illustrated in Pl. 3, Fig. 4.
Triloculina sp. 2
Lagenida
Fissurina incomposita (Patterson & Pettis, 1986)[g].
Fissurina staphyllearia Schwager, 1866[g]. Illustrated in Pl. 3, Fig. 7.
Fissurina sp. 1
Lagena lateralis (Cushman, 1913)[a].
Lagena striata (d'Orbigny, 1839)[g].
Lagena sp.
Lenticulina sp. 1
Procerolagena gracillima (Seguenza, 1862)[g].
Buliminida
Bolivina pacifica Cushman & McCulloch, 1942[e].
Bolivina pseudopunctata Höglund, 1947[b].
Bolivina sp.
Brizalina catanensis (Seguenza, 1862)[f].
Fursenkoina complanata (Egger, 1893)[g]. Illustrated in Pl. 3, Fig. 8.
Fursenkoina pauciloculata (Brady, 1884)[g]. Illustrated in Pl. 3, Fig. 9.
Fursenkoina sp. 1.
Globobulimina spp. Illustrated in Pl. 3, Fig. 11.
Praeglobobulimina ovata (d'Orbigny, 1846)[g]. Illustrated in Pl. 3, Fig. 10.
Uvigerina auberiana (d'Orbigny, 1839)[g]. Illustrated in Pl. 3, Fig. 14.
Uvigerina canariensis (d'Orbigny, 1839)[g]. Illustrated in Pl. 3, Fig. 15.
Uvigerina sp. 1
Uvigerina sp.
Rotaliida
Anomalinoides sp. 1
Cassidulina sp.
Ceratobulimina arctica Green, 1959[f].
Chilostomella oolina Schwager, 1878[g]. Illustrated in Pl. 3, Fig. 13.
Cibicidoides subhaidingerii (Parr, 1950)[g].
Cibicidoides wuellerstorfii (Schwager, 1866)[g].
Epistominella exigua (Brady, 1884)[b]. Illustrated in Pl. 3, Fig. 21.
Epistominella pusilla (Parr, 1950)[e]. Illustrated in Pl. 3, Figs. 19–20.
Globocassidulina subglobosa (Brady, 1881)[g]. Illustrated in Pl. 3 Fig. 12.
Gyroidina soldanii (d'Orbigny, 1826)[g]. Illustrated in Pl. 3, Fig. 22.
Gyroidina sp. 1.
Ioanella tumidula (Brady, 1884)[g]. Illustrated in Pl. 3, Figs. 17–18.
Melonis barleeanum (Williamson, 1858)[h].
Melonis pompilioides (Fichtel & Moll, 1798)[g]. Illustrated in Pl. 3, Fig. 16.
Nonion pacificum (Cushman, 1924)[e].
Nonion sp.
Oridorsalis umbonatus Reuss, 1851[g]. Illustrated in Pl. 3, Fig. 23.
Osangulariella umbonifera (Cushman, 1933)[g].
Robertinida
Hoeglundina elegans (d'Orbigny, 1826)[g]. Illustrated in Pl. 3, Fig. 24.
Robertina subcylindrica (Brady, 1881)[g].
Robertinoides bradyi (Cushman and Parker, 1936)[g].

Appendix B. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marmicro.2012.08.004.

References

Altenbach, A.V., Unsoeld, G., Walger, E., 1988. The hydrodynamic environment of *Saccorhiza ramosa* (Brady). Meyniana 40, 119–132.
Altenbach, A.V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S., Trauth, M., 1999. Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon. Journal of Foramineferal Research 29 (3), 173–185.

Beaulieu, S., 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep-Sea Research I 48 (4), 1121–1137.
Beaulieu, S., Baldwin, R., 1998. Temporal variability in currents and the benthic boundary layer at an abyssal station off central California. Deep-Sea Research II 45 (4–5), 587–615.
Bernhard, J.M., 1988. Postmortem vital staining in benthic foraminifera: duration and importance in population and distributional studies. Journal of Foraminiferal Research 18 (2), 143–146.
Bernhard, J.M., 1992. Benthic foraminiferal distribution and biomass related to pore water oxygen content—central California continental slope and rise. Deep-Sea Research A 39 (3–4), 585–605.
Bernhard, J.M., 2000. Distinguishing live from dead foraminifera: methods review and proper applications. Micropaleontology 46 (supplement no. 1), 38–46.
Bernhard, J.M., Buck, K.R., Barry, J.P., 2001. Monterey Bay cold-seep biota: assemblages, abundance, and ultrastructure of living foraminifera. Deep-Sea Research I 48 (10), 2233–2249.
Bernhard, J.M., Ostermann, D.R., Williams, D.S., Blanks, J.K., 2006. Comparison of two methods to identify live benthic foraminifera: a test between Rose Bengal and CellTracker Green with implications for stable isotope paleoreconstructions. Paleoceanography 21 (PA4210), 1–8.
Bernstein, B., Meador, J., 1979. Temporal persistence of biological patch structure in an abyssal benthic community. Marine Biology 51, 179–183.
Bernstein, B., Hessler, R., Smith, R., Jumars, P., 1978. Spatial dispersion of benthic foraminifera in the abyssal central north Pacific. Limnology and Oceanography 23 (3), 401–416.
Brady, H.B., 1884. Report on the Foraminifera dredged by H. M. S. Challenger during the years 1873–1876. Report of the scientific results of the voyage of H.M.S. Challenger, 1873–1876. Zoology 1–814 part 22.
Brönnimann, P., Whittaker, J.E., 1988. The Trochamminacea of the Discovery Reports. A review of the Trochamminacea (Protozoa: Foraminiferida) described from south Atlantic and Antarctic waters by Heron-Allen & Earland (1932) and Earland (1933; 1934; 1936). British Museum (Natural History), London 1–152.
Burke, S., 1981. Recent benthic foraminifera of the Ontong Java Plateau. Journal of Foraminiferal Research 11 (1), 1–19.
Burmistrova, I.I., Khusid, T.A., Belyaeva, N.V., Chekhovskaya, M.P., 2007. Agglutinated abyssal foraminifers of the equatorial pacific. Oceanology 47 (6), 824–832.
Buzas, M.A., Gibson, T.G., 1969. Species diversity: benthonic foraminifera in western north Atlantic. Science 163 (3862), 72–75.
Corliss, B.H., 1979. Taxonomy of recent deep sea benthonic foraminifera from the southeast Indian Ocean. Micropaleontology 25 (1), 1–19.
Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. Nature 314 (6010), 435–438.
Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. Marine Micropaleontology 17 (3–4), 195–236.
Corliss, B.H., Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep-Sea Research A 37 (3), 381–400.
Cornelius, N., Gooday, A.J., 2004. 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. Deep-Sea Research II 51 (14–16), 1571–1602.
Cushman, A.J., 1913. A monograph of the foraminifera of the North Pacific Ocean. Part 3, Lagenidae. Bulletin of the United States National Museum 71 (3), 1–125.
Cushman, J.A., 1927. Recent foraminifera from off the west coast of America. Bulletin of the Scripps Institution of Oceanography of the University of California, Technical Series 1 (10), 119–188.
De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. Marine Micropaleontology 40 (3), 151–166.
Drazen, J.C., Baldwin, R.J., Smith, K.L., 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II 45 (4–5), 893–913.
Enge, A.J., Nomaki, H., Ogawa, N., Witte, U., Moeseneder, M., Lavik, G., Ohkouchi, N., Kitazato, H., Kucera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Marine Ecology Progress Series 438, 129–142.
Fisher, R.A., Steven Corbert, A., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12 (1), 42–58.
Gooday, A.J., 1983. Primitive Foraminifera and Xenophyophorea in IOS epibenthic sledge samples from the northeast Atlantic. Institute of Oceanographic Sciences 33.
Gooday, A.J., 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep-sea. Nature 332 (6159), 70–73.
Gooday, A.J., 1993. Deep-sea benthic foraminiferal species which exploit phytodetritus: characteristic features and controls on distribution. Marine Micropaleontology 22 (3), 187–205.
Gooday, A.J., 1996. Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes. Deep-Sea Research I 43 (9), 1395–1421.
Gooday, A.J., Bowser, S.S., Bernhard, J.M., 1996. Benthic foraminiferal assemblages in Explorers Cove, Antarctica: a shallow-water site with deep-sea characteristics. Progress in Oceanography 37 (2), 117–166.
Gooday, A.J., Bett, B.J., Shires, R., Lambshead, P.J.D., 1998. Deep-sea benthic foraminiferal species diversity in the NE Atlantic and NW Arabian Sea: a synthesis. Deep-Sea Research II 45 (1–3), 165–201.
Gooday, A.J., Kitazato, H., Hori, S., Toyofuku, T., 2001. Monothalamous soft-shelled foraminifera at an abyssal site in the north Pacific: a preliminary report. Journal of Oceanography 57, 377–384.
Gooday, A.J., Hori, S., Todo, Y., Okamoto, T., Kitazato, H., Sabbatini, A., 2004. Soft-walled, monothalamous benthic foraininiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. Deep-Sea Research I 51 (1), 33–53.
Gooday, A.J., Bowser, S., Cedhagen, T., Cornelius, N., Hald, M., Korsun, S., Pawlowski, J., 2005. Monothalamous foraminiferans and gromiids (Protista) from western Svalbard: a preliminary survey. Marine Biology Research 1 (4), 290–312.
Gooday, A.J., Nomaki, H., Kitazato, H., 2008. Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity. Biogeochemical Controls on Paleoceanographic Environmental Proxies: In: Austin, W.E.N., James, R.H. (Eds.), Geological Society, London, Special Publications, London, pp. 97–119.
Grimm, G.W., Stogerer, K., Ertan, K.T., Kitazato, H., Kucera, M., Hemleben, V., Hemleben, C., 2007. Diversity of rDNA in *Chilostomella*: molecular differentiation patterns and putative hermit types. Marine Micropaleontology 62 (2), 75–90.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 4 (1) 9 pp.
Heinz, P., Kitazato, H., Schmiedl, G., Hemleben, C., 2001. Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions. Journal of Foraminiferal Research 31 (3), 210–227.
Heinz, P., Hemleben, C., Kitazato, H., 2002. Time-response of cultured deep-sea benthic foraminifera to different algal diets. Deep-Sea Research I 49 (3), 517–537.
Heinz, P., Sommer, S., Pfannkuche, O., Hemleben, C., 2005. Living benthic foraminifera in sediments influenced by gas hydrates at the Cascadia convergent margin, NE Pacific. Marine Ecology Progress Series 304, 77–89.
Hessler, R.R., Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Research 21 (3), 185–209.
Hurlbert, S., 1971. The nonconcept of species diversity: a critique and alternative paramters. Ecology 52 (4), 577–586.
Jones, R., 1994. The Challenger Foraminifera. Oxford University Press, Oxford . 149 pp.
Jones, R., Charnock, M., 1985. "Morphogroups" of agglutinating foraminifera. Their life positions and feeding habits and potential applicability in (paleo)ecological studies. Revue de Paléobiologie 4 (2), 311–320.
Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Marine Micropaleontology 26 (1–4), 3–15.
Jorissen, F.J., Wittling, I., Peypouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cape Blanc, NW-Africa: community structure and microhabitats. Deep-Sea Research I 45 (12), 2157–2188.
Kuhnt, W., Collins, E., Scott, D., 2000. Deep water agglutinated foraminiferal assemblages across the Gulf Stream: distribution patterns and taphonomy. Proceedings of the Fifth International Workshop on Agglutinated Foraminifera: In: Hart, M., Kaminski, M., Smart, C. (Eds.), Grzybowski Foundation Special Publication, 7, pp. 261–298.
Kurbjeweit, F., Schmiedl, G., Schiebel, R., Hemleben, C., Pfannkuche, O., Wallmann, K., Schafer, P., 2000. Distribution, biomass and diversity of benthic foraminifera in relation to sediment geochemistry in the Arabian Sea. Deep-Sea Research II 47 (14), 2913–2955.
Lecroq, B., Lejzerowicz, F., Bachar, D., Christen, R., Esling, P., Baerlocher, L., Osteras, M., Farinelli, L., Pawlowski, J., 2011. Ultra-deep sequencing of foraminiferal microbarcodes unveils hidden richness of early monothalamous lineages in deep-sea sediments. Proceedings of the National academy of Sciences of the United States of America 108 (32), 13177–13182.
Loubere, P., 1991. Deep-sea benthic foraminiferal assemblage response to a surface ocean productivity gradient: a test. Paleoceanography 6 (2), 193–204.
Loubere, P., 1996. The surface ocean productivity and bottom water oxygen signals in deep water benthic foraminiferal assemblages. Marine Micropaleontology 28 (3–4), 247–261.
Mackensen, A., Douglas, R., 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland. Deep-Sea Research A 36 (6), 879–900.
Majewski, W., Pawlowski, J., Zajaczkowski, M., 2005. Monothalamous foraminifera from West Spitsbergen fjords, Svalbard: a brief overview. Polish Polar Research 26, 269–285.
Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M.J., Heip, C.H.R., 2002. Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Marine Ecology Progress Series 236, 23–29.
Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge . 426 pp.
Nienstedt, J., Arnold, A., 1988. The distribution of benthic foraminifera on seamounts near the East Pacific Rise. Journal of Foraminiferal Research 18 (3), 237–249.
Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: *in situ* tracer experiments. Limnology and Oceanography 50 (1), 134–146.
Nozawa, F., Kitazato, H., Tsuchiya, M., Gooday, A.J., 2006. 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. Deep-Sea Research I 53 (8), 146–1422.
Ohkawara, N., Kitazato, H., Uematsu, K., Gooday, A.J., 2009. A minute new species of Saccammina (monothalamous Foraminifera; Protista) from the abyssal Pacific. Journal of Micropalaeontology 28, 143–151.
Ohkushi, K., Natori, H., 2001. Living benthic foraminifera of the Hess Rise and Suiko Seamount, central north Pacific. Deep-Sea Research I 48 (5), 1309–1324.
Phleger, F.B., Parker, F.L., Peirson, J.F., 1953. North Atlantic Foraminifera. In: Pettersson, H. (Ed.), Reports of the Swedish deep-sea expedition 1947-1948. Elanders Boktryckeri Aktiebolag, Göteborg. 122 pp.
Radziejewska, T., Gooday, A.J., Koltan, M., Szyrwiel, E., 2006. Deep-sea non-calcareous foraminifera: some examples from the Pacific's abyssal nodule field. Meiofauna Marina 15, 3–10.

Reimers, C.E., 1987. An *in situ* microprofiling instrument for measuring interfacial pore water gradients: methods and oxygen profiles from the north Pacific Ocean. Deep-Sea Research II 334 (12), 2019–2035.
Ricketts, E.R., Kennett, J.P., Hill, T.M., Barry, J.P., 2009. Effects of carbon dioxide sequestration on California margin deep-sea foraminiferal assemblages. Marine Micropaleontology 72 (3–4), 165–175.
Sabbatini, A., Morigi, C., Negri, A., Gooday, A., 2002. Soft-shelled benthic foraminifera from a hadal site (7800 m water depth) in the Atacama Trench (SE Pacific): preliminary observations. Journal of Micropalaeontology 21, 131–135.
Schmiedl, G., 1995. Rekonstruktion der spätquartären Tiefenwasserzirkulation und Produktivität im östlichen Südatlantik anhand von benthischen Foraminiferenvergesellschaftungen = Late Quaternary benthic foraminiferal assemblages from the eastern South Atlantic Ocean: reconstruction of deep water circulation and productivity changes. Berichte zur Polarforschung (Reports on Polar Research), Bremerhaven, Alfred Wegener Institute for Polar and Marine Research 160, 207.
Schmiedl, G., Mackensen, A., Muller, P.J., 1997. Recent benthic foraminifera from the eastern South Atlantic Ocean: dependence on food supply and water masses. Marine Micropaleontology 32 (3–4), 249–287.
Schönfeld, J., 2012. History and development of methods in recent benthic foraminiferal studies. Journal of Micropalaeontology 31, 53–72.
Schroeder, C., Scott, D., Medioli, F., Bernstein, B., Hessler, R., 1988. Larger agglutinated foraminifera—comparison of assemblages from central North Pacific and western North-Atlantic (Nares Abyssal-Plain). Journal of Foraminiferal Research 18 (1), 25–41.
Sgarrella, F., Moncharmont Zei, M., 1993. Benthic foraminifera of the Gulf of Naples (Italy): systematics and autoecology. Bollettino della Società Paleontologica Italiana 32 (2), 145–264.
Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL . 144 pp.
Sheperd, A., Rathburn, A., Pérez, M., 2007. Living foraminiferal assemblages from the Southern California margin: a comparison of the >150, 63–150, and >63 μm fractions. Marine Micropaleontology 65, 54–77.
Silva, K.A., Corliss, B.H., Rathburn, A.E., Thunell, R.C., 1996. Seasonality of living benthic foraminifera from the San Pedro Basin, California borderland. Journal of Foraminiferal Research 26 (1), 71–93.
Simpson, E., 1949. Measurement of diversity. Nature 163, 688.
Smart, C.W., Gooday, A.J., 1997. Recent benthic foraminifera in the abyssal northeast Atlantic ocean: relation to phytodetrital inputs. Journal of Foraminiferal Research 27 (2), 85–92.
Smith, P.B., 1973. Foraminifera of the North Pacific Ocean. Geological Survey Professional Paper 766. United States Government Printing Office, Washington . 37 pp.
Smith, K.L., Druffel, E.R.M., 1998. Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. Deep-Sea Research II 45 (4–5), 573–586.
Smith, K.L., Baldwin, R.J., Williams, P.M., 1992. Reconciling particulate organic carbon flux and sediment community oxygen consumption in the deep North Pacific. Nature 359 (6393), 313–316.
Smith, K.L., Kaufmann, R.S., Baldwin, R.J., 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern north Pacific Ocean. Limnology and Oceanography 39 (5), 1101–1118.
Smith, K.L., Kaufmann, R.S., Baldwin, R.J., Carlucci, A.F., 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. Limnology and Oceanography 46 (3), 543–556.
Smith, K.L., Baldwin, R., Karl, D., Boetius, A., 2002. Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre. Deep-Sea Research I 49 (6), 971–990.
Smith, K.L., Ruhl, H., Kaufmann, R., Kahru, M., 2008. Tracing abyssal food supply back to upper-ocean processes over a 17-year time series in the northeast Pacific. Limnology and Oceanography 53 (6), 2655–2667.
Snider, L.J., Burnett, B.R., Hessler, R.R., 1984. The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep-Sea Research A 31 (10), 1225–1249.
Suess, E., 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. Nature 288, 260–263.
Szarek, R., Nomaki, H., Kitazato, H., 2007. Living deep-sea benthic foraminifera from the warm and oxygen-depleted environment of the Sulu Sea. Deep-Sea Research II 54 (1–2), 145–176.
Tendal, O.S., Hessler, R.R., 1977. An introduction to the biology and systematics of Komokiacea (Textulariina, Foraminiferida). Galathea Report, pp. 165–194.
Timm, S., 1992. Rezente Tiefsee-Benthosforaminiferen aus Oberflächensedimenten des Golfes von Guinea (Westafrika): taxonomie, Verbreitung, Ökologie und Korngrößenfraktionen = Recent deep-sea benthic foraminifera from surface sediments of the Gulf of Guinea (West Africa): taxonomy, distribution, ecology, and grain size fractions. Berichte (Universität Kiel, Geologisch-Paläontologisches Institut und Museum) 59, 192.
Walton, W.R., 1952. Techniques for recognition of living foraminifera. Contributions from the Cushman Foundation 3 (2), 56–60.
Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.R., Jorgensen, B.B., Pfannkuche, O., 2003. *In situ* experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424 (6950), 763–766.

Publication 3

Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin

Response to a simulated phytodetritus pulse by benthic foraminifera in oxygen minimum zone sediments of the Indian Margin

Annekatrin J. Enge [1,*], Ursula Witte [2], Michal Kucera [3], Petra Heinz [1]

[1] Department for Geosciences, University of Tübingen, Hölderlinstrasse 12, 72074 Tübingen, Germany
[2] Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, United Kingdom
[3] MARUM – Center for Marine Environmental Sciences, Leobener Strasse, 28359 Bremen, Germany
* *corresponding author*: annekatrin.enge@uni-tuebingen.de (A.Enge)

Abstract

Benthic foraminifera in sediments of the Indian Margin of the Arabian Sea where the oxygen minimum zone (OMZ) impinges on the continental slope are exposed to particularly severe levels of oxygen depletion. Food supply for the benthic community is high but delivered in distinct pulses during upwelling and water mixing events associated with summer and winter monsoon periods. In order to investigate how benthic foraminifera respond to such pulsed food delivery under oxygen concentrations of <0.1 ml/l (OMZ core), an *in-situ* isotope labeling experiment (^{13}C, ^{15}N) was performed at the Western continental slope of India at 540 m water depth. The assemblage of living foraminifera (>125 µm) at 0-1 cm in the core region of the OMZ is characterized by an unexpectedly high population density of 3982 ind./10 cm² and a strong dominance by a few calcareous species. The presence of labeled ^{13}C and ^{15}N in their cytoplasm indicates that all nine investigated species which constitute 93% of total foraminiferal population, have taken up the labeled phytodetritus during the 4-day experimental phase. In total, these nine species had assimilated 101 mg C/m² (15.5% of the total added carbon). The uptake of nitrogen was investigated on the three most abundant species (*Bolivina* aff. *B. dilatata*, *Cassidulina* sp., *Bulimina gibba*) and resulted in 2.7 mg N/m² (2% of the total added nitrogen). The short-term response to the offered phytodetritus varied largely among foraminiferal species with *Uvigerina schwageri* being by far the most important species in short-term processing whereas the most abundant species *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. showed comparably low uptake of the offered food. We suggest that the observed species-specific differences are related to individual biomass of species and to specific feeding preferences. The high numbers of living foraminifera and their rapid response to deposited fresh phytodetritus demonstrate the importance of foraminifera in the short-term carbon cycling under oxygen-depleted conditions. We propose that foraminifera at the studied site benefit from unique adaptations in their metabolisms to nearly anoxic conditions as well as from the exclusion of macrofauna and the resulting relaxed food competition, and predation pressure.

Key words

Foraminifera; isotope labeling experiment; $\delta^{13}C$; $\delta^{15}N$; oxygen depletion; Arabian Sea; phytodetritus; deep-sea carbon cycling

1 Introduction

Most benthic deep-sea organisms depend on organic matter that settles onto the sea floor as their food source. The sinking organic matter derives from phytoplankton in surface water. Following primary productivity peaks in surface waters, phytoplankton detritus (phytodetritus) sinks periodically through the water column to the sea floor (Haake et al., 1993) where it forms the main food source for benthic foraminifera (Lambshead and Gooday, 1990; Gooday and Hughes, 2002). Such pulsed delivery of phytodetritus generally occurs in areas of highly seasonal surface productivity (Gooday and Turley, 1990; Gage and Tyler, 1991; Beaulieu and Smith, 1998; Gooday, 2002). Once it settles on the sea floor, benthic foraminifera are one of the major groups involved in processing the fresh, labile organic matter. Where the deposition of phytodetritus is seasonal or occurs in pulsed events, its availability on the sediment surface is short-lived. Because benthic foraminifera can respond very quickly to the pulses of phytodetritus to the sediment surface (Graf, 1989; Gooday and Turley, 1990; Altenbach, 1992; Linke et al., 1995; Drazen et al., 1998; Enge et al., 2011) and they are common inhabitants of marine sediments, they play a quantitatively important role in short-term processing of phytodetritus on the sea floor of the world oceans (Moodley et al., 2002).

In general, sediments rich of organic matter are found predominantly on continental margins (e.g. Demaison and Moore, 1980). High surface production and limited water replenishment (Kamykowski and Zentara, 1990) results in low-oxygen midwater bodies (oxygen minimum zones, OMZs). These natural hydrographic features with dissolved oxygen concentrations of <0.5 ml/l are especially well-developed at intermediate water depths in the North Pacific, the Arabian Sea, and the Bay of Bengal (Wyrtki, 1971; Helly and Levin, 2004). Where these low-oxygen water masses impinge on the continental margins at shelf to upper bathyal depths, sediments with dysoxic to anoxic conditions are found. Benthic organisms found within OMZ sediments may appear to be blessed with abundance of organic matter but they must be able to tolerate the very low oxygen concentrations that are permanently present in the core region of OMZs.

An unusually high tolerance to hypoxia among eukaryotic benthos has been observed for benthic foraminifera in veracious oxygen-depleted areas such as the Southern California borderland, Scandinavian fjords, and OMZ sediments (Bernhard and Sen Gupta, 1999). Being able to perform respiration by denitrification in the absence of oxygen was first observed for

two benthic species by (2006). This unusually ability to accumulate nitrate and its respiration to dinitrogen gas was later confirmed in benthic foraminifera in OMZ sediments at the Chilean coast (Hogslund et al., 2008) and later demonstrated in laboratory experiments (Pina-Ochoa et al., 2010). Since most other eukaryotic organisms, especially macrofauna, are not as tolerant to hypoxia as foraminifera (Josefson and Widbom, 1988), they often are absent from sediments at the core of the OMZ (Gooday et al., 2009). Due to their unique metabolism, combined with the absence of macrofaunal competition, foraminifera are thus able to proliferate under extreme low-oxygen conditions. In the OMZ sediments in the Arabian Sea, recent foraminifera are abundant components of the benthic community as observed by studies performed at the Pakistan margin (Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007; Gooday et al., 2009) and Oman margin (Hermelin and Shimmield, 1990; Gooday et al., 2000).

Their abundant occurrence in OMZ sediments, combined with the ability to utilize fresh labile organic matter and tolerate low oxygen concentrations suggest that benthic foraminifera might play an important role in carbon cycling in OMZ sediments in the Arabian Sea. *In-situ* feeding experiments using ^{13}C-labeled food have been shown to be an effective approach to study the metabolic response of foraminifera to phytodetritus deposition under natural conditions. Previous *in-situ* feeding experiments on foraminifera (Moodley et al., 2002; Kitazato et al., 2003; Witte et al., 2003; Nomaki et al., 2005; Nomaki et al., 2006; Enge et al., 2011; Nomaki et al., 2011) show that the response to phytodetritus by foraminifera can occur within hours, but can strongly vary between habitats and species. In OMZ sediments at the Pakistan Margin, Woulds et al. (2007) and Andersson et al. (2008) performed 16 feeding experiments along a depth transect (140-1850 m) with 2 and 5 days incubation. Both studies showed variation in the response of the foraminiferal community to phytodetritus between the different water depths. Analysis on species level was not focus of these studies except *Uvigerina* ex. gr. *U. semiornata* who was the dominant foraminifera at 140 and 300 m depth within the OMZ.

All of the existing *in-situ* feeding experiments on foraminifera, including those in the OMZ influenced sediments of Pakistan were carried out under conditions with oxygen concentrations higher than 0.17 ml/l. Under these conditions, the advantages of nitrate metabolism in foraminifera and the exclusion of competition by macrofauna are not yet obvious. Therefore, the aim of our study was to investigate benthic foraminifera and their response to phytodetritus at almost anoxic conditions of <0.1 ml/l by performing an *in-situ* feeding experiment in an OMZ core region. Using an isotope labeling experiment set up at the Indian Margin, we followed the fate of the organic matter in form of the labeled diatom *T. weissflogii* in single species of foraminifera. In addition to ^{13}C as tracer material, we simultaneously tracked ^{15}N. Such dual experiments are very limited in number and have been so far carried out in the intertidal of the North Sea (Rossi, 2007; Evrard et al., 2010) and at OMZ sediments of the Indian Margin (Hunter et al., 2012). Unfortunately, foraminifera have not

been investigated towards their ^{15}N uptake during these approaches. This is the first approach to test another tracer on foraminifera than the commonly used ^{13}C isotope. Because carbon and nitrogen are essential for biomass buildup, we assume that foraminifera will show uptake of both during the experiment.

2 Material and Methods

2.1 Study area

The experimental study was carried out in October 2008 during the post-monsoon period in the Eastern Arabian Sea at 16° 58' N, 71° 55' E (Fig. 1). The open-water OMZ of the Arabian Sea expands for 285000 km³ and impinges on the continental margin of India at water depths of about 120-1100m (Helly and Levin, 2004). The formation and sustainment of the OMZ results from a combination of several factors such as the high primary production, strong stratification of the upper 200m water column and low water mixing rates (Slater and Kroopnick, 1984). The intense productivity in the Arabian Sea is driven by monsoon-induced upwelling in summer (SW monsoon, June-September) and deep mixing of water masses in winter (NE monsoon, December-April), resulting in a distinct seasonality of sea surface conditions and organic matter flux. Where the OMZ waters impinge on the continental margin, the benthic community is thus exposed to the combination of low-oxygen concentrations and pulsed input of organic matter to the sea floor.

The investigated depth of 540m is located in the core region of the OMZ at the Indian Margin (Hunter et al., 2011). Environmental data at this site are available from recordings during the dives by the submersible *Shinkai* 6500 (JAMSTEC, 2007) and derive from CTD recordings and measurements with an optical oxygen sensor (Hunter et al., 2011). The site of sampling exhibited *in-situ* oxygen concentrations during the two sampling dives of 0.02 - 0.05 ml/l, an average temperature of 12°C (Tab. 1), and is located in an area of moderate to high average yearly productivity of >0.5 - 0.75 g C/m²/d (Babu et al., 1999).

2.2 Preparation of ^{13}C and ^{15}N-labeled algae

Before the cruise, an axenic clone of the diatom *Thalassiosira weissflogii* (CCMP, Bigelow Laboratories for Ocean Science, U.S.A.) was cultured in artificial seawater and *L*1 culture medium, enriched with 99%-^{13}C-bicarbonate ($NaH^{13}CO_3$, Cambridge Isotope Laboratories, Inc., U.S.A.) and 50%-^{15}N-sodium nitrate ($Na^{15}NO_3$, Cambridge Isotope Laboratories, Inc.). Algae were cultured at 16°C for 28 d (light: dark = 16:8; 35 PSU), harvested by centrifugation (500 G; 30 min), sonicated (2000 Hz; 5 min) and rinsed three times in ultrapure water to remove inorganic salts and dissolved organic carbon. Harvested algae were lyophilised (-60°C; -0.0001 mbar; 24 h) to produce phytodetritus containing 27.75 atom%^{13}C and 33.70 atom %^{15}N (Hunter et al., 2012).

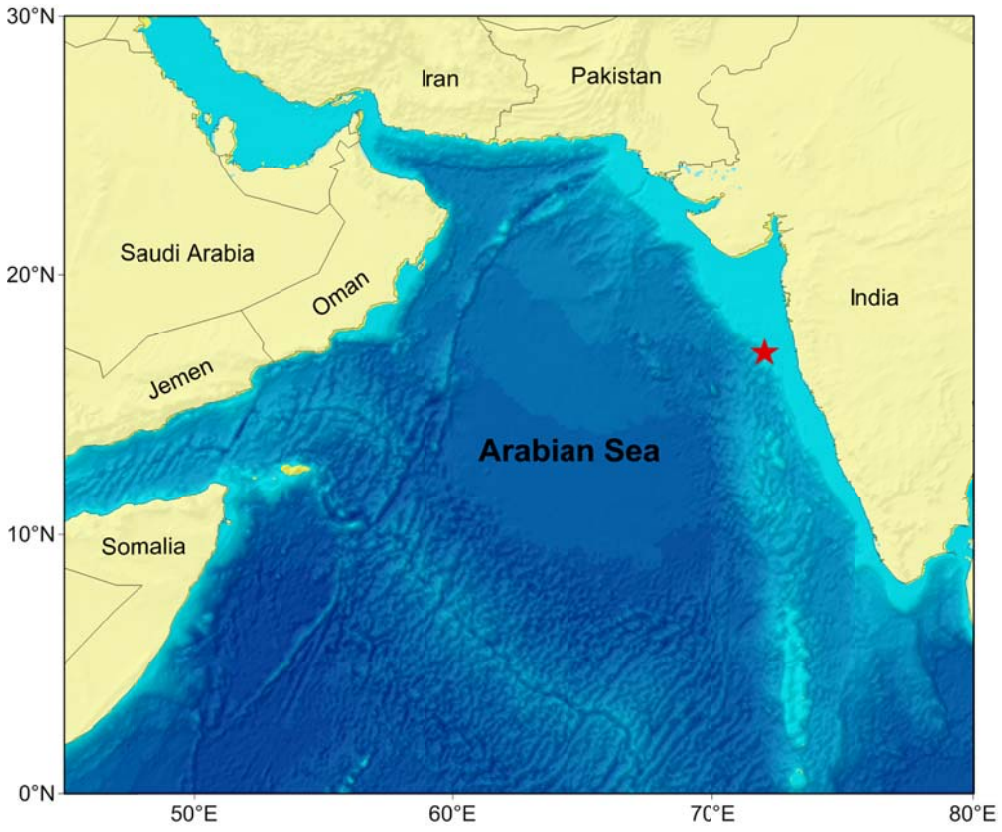


Figure 1 Topographic map of the Arabian Sea and location of the study area at the Western continental margin of India.

2.3 Experimental setup

This experiment was carried out as a part of an international study on benthic ecology, geochemistry and biogeochemical processes across the oxygen minimum zone at the Indian margin of the Arabian Sea. The collaborative research cruise “YK08-11” aboard the R/V *Yokosuka* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) took place between September and November 2008.

The feeding experiment was carried out from 9 through 13 October 2008 using an Oceanlab spreader system. This *in-situ* mesocosm consists of a transparent polycarbonate tube (25 cm inner diameter, 30 cm length) and a lid. More detailed information about the construction can be found in Hunter et al. (2012). On 9 October 2008, the tube was pushed straight into the undisturbed sea floor by the manipulator arm of the manned submersible *Shinkai* 6500, until standing firmly upright. The spreader lid held a container with the suspension of *T. weissflogii* (650 mg C/m², 160 mg N/m²) which was applied to the enclosed sediment surface by pushing a plunger that subsequently released the algae. The spreader lid was removed several hours after the deployment of the spreader to ensure that the algae slurry had completely deposited onto the sediment surface. Incubation of the enclosed sediment surface with the labeled diatoms lasted four days. The applied amount of food and the open system with continuous water exchange guaranteed a set up optimally emulating natural conditions. After four days, push cores (plastic tubes, 70 mm inner diameter) from the inside of the spreader were recovered by the submersible and the Oceanlab spreader system was removed. On board of the research vessel, the sediment cores were immediately horizontally sliced in 1 cm intervals down to 3 cm depth and frozen at -80°C. The sediment samples were then kept frozen at -25°C until analysis. For our study, the assemblage and the isotope composition of foraminifera from one push core was investigated. Over 15000 individuals per sediment sample (1 cm thickness) and the need for up to 1500 individuals for a single measurement were limiting replication due to time and manpower restrictions. Profiting of these high numbers, we were able to produce duplicates of measurements for carbon for four species. From the sediment cores, we concentrated on the upper 1 cm of the sediment, as the living foraminifera assemblage in OMZ sediments of the Arabian Sea is largely restricted to the uppermost sediment layer (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009).

2.4 Sample preparation

In the laboratory at the University of Tübingen, the 0-1 cm sediment sample was thawed and washed over a mesh (125 µm) with artificial seawater of 34-35 PSU (23.4 g NaCl, 4.0 g $MgSO_4 \times 7\ H_2O$, 0.8 g KCl, 0.26 g $CaCl_2$ and distilled water up to 1 l final volume). After sieving, the residue was frozen at -25°C until further processing. Separation of living and dead specimens was based on visual assessment of cytoplasm presence and the degree to which it filled the

test (Moodley et al., 2002; Nomaki et al., 2005; Nomaki et al., 2006; Sweetman et al., 2009). Foraminifera were wet-picked under cooled conditions and identified to species level as far as possible. The entire sample of 0-1 cm depth was investigated for the faunal composition of living foraminifera. The taxonomy followed Jones (1994) and Schumacher et al. (2007). For organic matter uptake analyses, the 9 most abundant foraminiferal species were analyzed, as only these were present in sufficient number and biomass to allow an isotopic analysis: *Bolivina* aff. *B. dilatata, Bulimina gibba, Cassidulina* sp., *Ehrenbergina pacifica*, *Epistominella rugosa*, *Hoeglundina elegans*, *Lenticulina* sp., *Uvigerina peregrina*, and *Uvigerina schwageri*. Because isotope measurements require a certain value of foraminiferal biomass, analyzes could not be performed on single specimens. Hence to obtain measurements with sufficient organic material present, individuals of one species were pooled. The required number of individuals varied among species due to different size and biomass and accounted for up to 1500 individuals per silver cup (see Tab. 2).

Before processing, material for isotopic analysis, glassware and silver cups were combusted (450°C, 5 h) and picking tools were cleaned with a mixture of Dichloromethane and Methane (1:1, v:v) to be free of organic contaminants. All foraminifera were carefully brushed to remove organic matter adhering on the outside of the test and washed twice in filtered artificial seawater. After filling silver cups with 10 µL of filtered seawater, foraminifera were transferred into these cups with a brush. Subsequently, the filled cups were dried at 50°C for several hours before adding Hydrochloric acid (6.25%) to ensure complete dissolution of carbonate. Because the decalcification process involves CO_2 production and can cause overflow of organic matter out of the silver cup, the transfer of foraminifera into cups had to be performed stepwise and not at once. Thus, transferring specimens to silver cups, heating and adding Hydrochloric acid had to be repeated until all calcareous parts of the foraminifera were dissolved. Finally, samples were kept at 50°C for three days to allow complete drying. Measurements of the carbon and nitrogen concentrations and isotopic ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of the foraminiferal cytoplasm were carried out using an elemental analyzer/isotope-ratio mass spectrometer (EA/IRMS) at SI Science Co., Ltd. (Japan).

2.5 Calculation of phytodetritus uptake

The total C and N content of foraminiferal cytoplasm as well as $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were measured using an EA/IRMS. The ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$ will be expressed as atom%^{13}C and atom%^{15}N further on in the text. Formulas given in this chapter apply to the calculation of carbon uptake. The assimilation of nitrogen was calculated the same way with differing standards and natural background values from carbon calculations.

Carbon isotope composition was measured against the international Vienna Pee Dee Belemnite standard (VPDB, atom%^{13}C = 0.0112372) and the nitrogen isotope composition

relative to the atmospheric nitrogen (air, atom%^{15}N = 0.003676). Differences between sample and standard are expressed in the δ-notation:

$$\delta^{13}C\ [‰] = \frac{\text{atom\%}^{13}C_{sample}}{\text{atom\%}^{13}C_{VPDB}} - 1) \times 1000.$$

Incorporation of ^{13}C and ^{15}N by foraminifera was defined as excess above background (natural signatures of δ^{13}C and δ^{15}N). Natural isotope (background) signatures for carbon and nitrogen of foraminiferal cytoplasm and algae were taken from literature. Living foraminifera display background values of δ^{13}C = -20.3 and δ^{15}N = 8.0 (for both see Tab. 2), while the diatom *Thalassiosira weissflogii* shows natural signatures of δ^{13}C = -21.2 and δ^{15}N = 4.9 (Aberle and Malzahn, 2007). Uptake (mg C) was calculated as the product of the excess in the sample and the total carbon/nitrogen content in the sample, divided by the excess of the labeled alga.

$$\text{Excess}_{sample} = \frac{\text{atom\%}^{13}C_{sample} - \text{atom\%}^{13}C_{background\ foram}}{100}$$

$$\text{Excess}_{alga} = \frac{\text{atom\%}^{13}C_{alga} - \text{atom\%}^{13}C_{background\ alga}}{100}$$

$$\text{C uptake [mg C]} = \frac{\text{excess}_{sample}}{\text{excess}_{alga}} \times \text{TOC}_{sample}$$

Calculation for species uptake per sea-floor area (mg C/m²) was obtained by dividing the uptake per sample (mg C) by the number of analyzed specimens (see Tab. 3) and then multiplying the individual uptake (mg C/ind.) with abundance (ind./m²) found in the uppermost centimeter. The fraction (*f*) of carbon and nitrogen originating from added alga material in the TOC/TON of the analyzed foraminifera was calculated after Nomaki et al. (2006) as following:

$$f_C = \frac{\text{atom\%}^{13}C_{sample} - \text{atom\%}^{13}C_{background\ foram}}{\text{atom\%}^{13}C_{alga} - \text{atom\%}^{13}C_{background\ alga}}$$

The calculated *f* also represents the biomass-normalized uptake of species which is the same as the total C uptake per sample (mg C) divided by the TOC content of the sample (mg C). Because *f* values were very small, we used *f* × 100 (%).

Table 1 Environmental parameters at the sampling site, obtained during deployment and recovery of spreaders and push cores. Surface sediment characteristics (% TOC, % TN, porosity) are given in Hunter et al. (2011). Data presented show means for the 540 m depth because recordings were continuous during dives.

Date	Water depth (m)	Longitude	Latitude	O_2 (µmol/l)	O_2 (ml/l)	Temp. (°C)	Salinity (PSU)
2011/10/09	540	16° 58.8' N	71° 55.3' E	0.9	0.02	11.7	35.2
2011/10/13	540	16° 58.8' N	71° 55.3' E	2.4	0.05	12.1	35.2

Table 2 Sample list of measured benthic foraminifera at 0-1 cm sediment depth at 540 m water depth which had been incubated with ^{13}C and ^{15}N-labeled organic matter.

Species	Measured individuals	C content (µg/ind.)	N content (µg/ind.)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bolivina aff. *B. dilatata*	400	0.124	-	700.4	-
	400	0.128	-	723.4	-
	1500	-	0.010	-	5258.3
Bulimina gibba	250	0.312	-	2630.3	-
	600	-	0.023	-	14924.7
Cassidulina sp.	300	0.108	-	505.0	-
	300	0.103	-	374.7	-
	1500	-	0.010	-	7191.0
Ehrenbergina pacifica	350	0.251	-	174.6	-
	300	0.226	-	115.5	-
Epistominella rugosa	400	0.140	-	674.6	-
Hoeglundina elegans	200	0.235	-	6182.6	-
Lenticulina sp.	200	0.565	-	230.9	-
Uvigerina schwageri	200	1.363	-	9516.3	-
Uvigerina peregrina	350	0.265	-	4903.4	-
	300	0.232	-	5000.7	-

3 Results

3.1 Foraminiferal assemblage at 0-1 cm

The analyzed sediment corresponding to 38.5 cm³ contained 15322 living foraminifera. This amounts to a population density of 3982 ind./10 cm³ in the uppermost cm at 540 m water depth. Abundances of species ranged between 0.3 and 1081 ind./10 cm^3. The assemblage was constituted almost entirely of calcareous species (99.5%). Agglutinated foraminifera made up the rest of the assemblage (0.5%) and Miliolids, Allogromids, Xenophyophores and soft-walled (agglutinated) foraminifera were not present at this water depth in the >125 µm fraction. The community of living foraminifera in the analyzed size class was dominated by a small number of species (Fig. 2). *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. were the numerically most important species with densities of 1015 and 1081 ind./10 cm³ (Tab. 4). Those two species alone accounted for over half (53%) of the entire foraminiferal abundances. Furthermore, *Bulimina gibba* (10%), *Ehrenbergina pacifica* (9%), *Uvigerina peregrina* (8%), *Epistominella rugosa* (5%), *Hoeglundina elegans* (4%), *Uvigerina schwageri* (4%), and *Lenticulina* sp. (2%) were also abundant (Fig. 3).

The TOC content of species (calculated from the total TOC in the sample and the analyzed number of individuals) varied largely among species, ranging from 0.1 to 1.3 µg TOC per individual on average. (Tab. 2). Lowest cytoplasmatic TOC content was found in *Cassidulina* sp. and *Bolivina* aff. *B. dilatata* whereas *Uvigerina schwageri* demonstrated the overall highest TOC content of all investigated species and was also largest in size. Based on the calculated individual TOC content and the total abundances of specimens in the uppermost cm, we estimated the mean individual TOC content of each species in relation to the area of sediment (which will be referred to as species biomass from now on in the text). The total biomass also varied largely between investigated species (Fig. 3), and *Uvigerina schwageri* demonstrated the highest biomass at the investigated site with 160 mg TOC/m². Lowest contribution to the foraminiferal biomass was found for *Epistominella rugosa* and *Hoeglundina elegans*.

3.2 Response to added carbon

Because of the high dominance of a few species at the studied site within the OMZ sediments, only the response of the most abundant species to the labeled algal material has been studied. In total, the cytoplasm of 7550 living individuals (Tab. 2) was analyzed for the $^{13}C/^{12}C$ (9 species) and $^{15}N/^{14}N$ ratio (3 species). Measured $\delta^{13}C$ values of 375‰ to 9304‰ were exceeding natural isotopic values (-20‰), and indicate uptake of labeled phytodetritus during the experimental phase by all species analyzed. The total uptake (as product of individual uptake and abundance) after four days of incubation for all species is shown in Fig. 4 and varied largely among the analyzed species.

Table 3 Values for natural $\delta^{13}C$ and $\delta^{15}N$ of sedimentary organic matter and benthic foraminiferal cytoplasm from relevant studies performing isotopic tracer experiments. When $\delta^{13}C$ for foraminiferal cytoplasm was available for different sediment depths and foraminiferal species, only calcareous species at 0-1 cm sediment depth were included.

Study area	**Water depth** (m)	$\delta^{13}C_{foram}$ (‰)	$\delta^{15}N_{foram}$ (‰)	**Reference**
Sagami Bay	1445	-18.0 ± 3.2	-	Nomaki et al. (2005)
	1445	-23.5 ± 2.6	-	Nomaki et al. (2006)
	1430	-19.3 ± 0.4	8.7 ± 1.4	Nomaki et al. (2008)
	750	-19.1 ± 1.2	7.2 ± 1.6	Nomaki et al. (2008)
Northeast Pacific	3953	-18.7 ± 3.2	-	Enge et al. (2011)
Norwegian fjord	685	-24.7 ± 0.6	-	Sweetman et al. (2009)

Table 4 Abundances (ind./10 cm³), carbon and nitrogen uptake N uptake and the fractions of carbon (f_C) and nitrogen (f_N) originating from added algal material in foraminiferal cytoplasm.

Species	**Abundance** (ind./10 cm³)	**C uptake** (ng C/ind.)	**Total C uptake** (mg C/m²)	f_C **× 100** (%)	**N uptake** (ng N/ind.)	**Total N uptake** (mg N/m²)	f_N **× 100** (%)
Bolivina aff. *B. dilatata*	1081	3.8 ± 0.2	4.1 ± 0.2	3.0	0.6	0.6	5.6
Bulimina gibba	391	33.2	13.0	10.6	3.6	1.4	15.5
Cassidulina sp.	1015	2.0 ± 0.5	2.0 ± 0.5	1.9	0.7	0.7	7.7
Ehrenbergina pacifica	356	1.6 ± 0.5	0.6 ± 0.2	0.7	-	-	-
Epistominella rugosa	188	4.0	0.7	2.8	-	-	-
Hoeglundina elegans	154	56.2	8.7	23.9	-	-	-
Lenticulina sp.	102	5.8	0.6	1.0	-	-	-
Uvigerina schwageri	117	484.4	56.7	35.6	-	-	-
Uvigerina peregrina	302	48.2 ± 3.9	14.6 ± 1.1	19.4	-	-	-

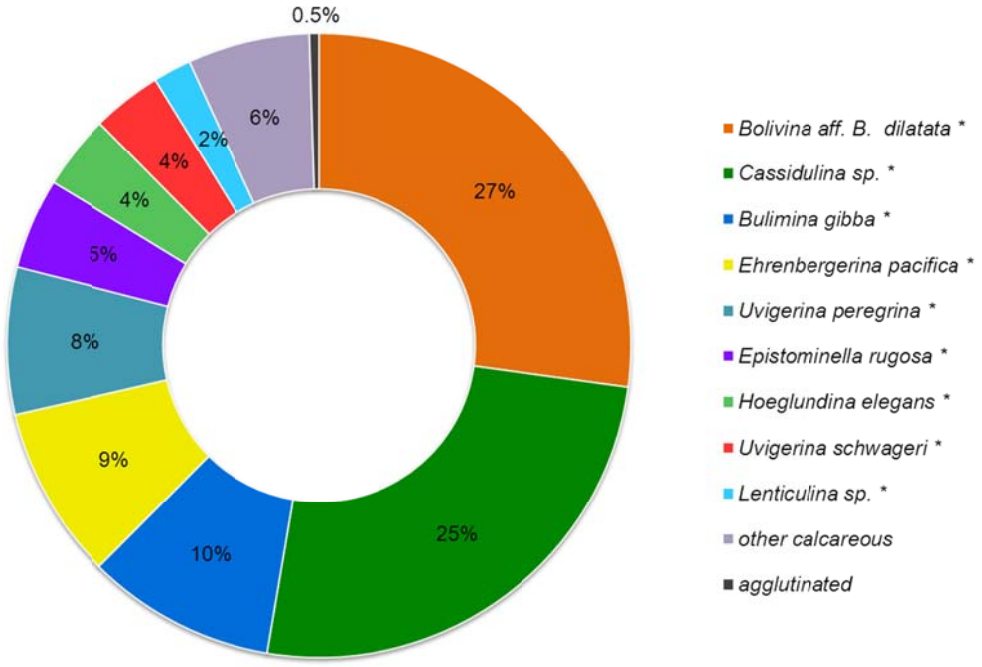


Figure 2 Relative abundances of the dominant species of living foraminifera (>125 µm) at 0-1 cm sediment depth. Uptake of phytodetritus was measured for marked species (*).

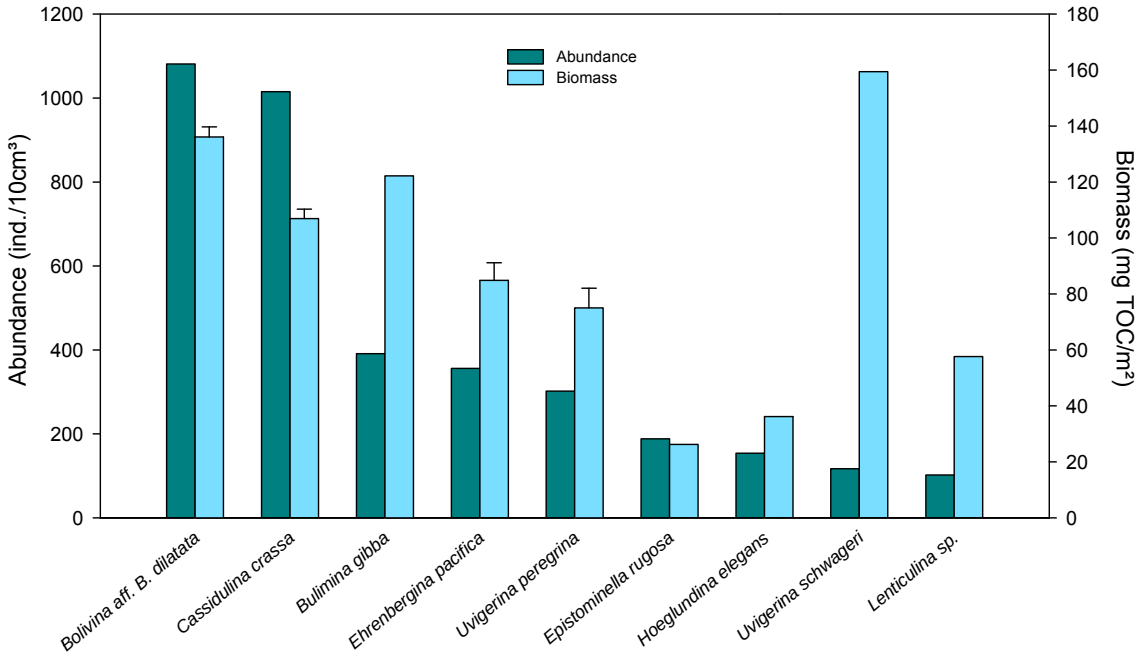


Figure 3 Abundances of living foraminifera (>125 µm) in the uppermost cm of the sediment and the total TOC content of species per area.

Total C uptake was highest for *Uvigerina schwageri* with 56.7 mg C/m² (Tab. 4). *Bulimina gibba*, *Hoeglundina elegans* and *Uvigerina peregrina* were similar high in their uptake ranging between 8-15 mg C/m^2. Lowest uptake of <1 mg C/m^2 was observed for the two species *Ehrenbergina pacifica* and *Epistominella rugosa*. After four days, the nine dominating species had taken up 101 mg C/m^2 which accounts for 15.5% of the total added labeled carbon at the beginning of the experiment.

The uptake of labeled carbon per individual (representing an average value for all individuals of the species) varied largely between the investigated species. On average, one foraminifer ingested 71 ng C within the four days of incubation with a high range between species. Lowest individual uptake was demonstrated by *Ehrenbergina pacifica* with 1.6 ng C, while the C uptake by *Uvigerina schwageri* yielded in 484 ng C per individual (Tab. 4). In order to test whether food uptake is a function of biomass of the foraminiferal species, we calculated the biomass-normalized uptake which accounts for the fraction (*f*) of the carbon originating from the labeled food in the cytoplasm of the analyzed foraminifera. *Uvigerina schwageri* was the species with the highest labeled carbon content (f × 1000) with 36%, followed by *Hoeglundina elegans* (24%), and *Uvigerina peregrina* (19%). Lowest added carbon signal was calculated for *Ehrenbergina elegans* with 0.7% (Fig. 3). A significant correlation was found between individual TOC content and biomass-normalized uptake if *Uvigerina schwageri* was included into the analysis (linear regression analysis, p = 0.04) (Fig. 5). A linear regression analysis without *U. schwageri* found no correlation between individual biomass and uptake independent of species biomass (p = 0.97).

3.3 Response to added nitrogen

Nitrogen isotope measurements were carried out successful for all of the three analyzed species (*Bolivina* aff. *B. dilatata*, *Cassidulina* sp., *Bulimina gibba*) which represent the most abundant species found in the study. Uptake of labeled nitrogen was twice as high for *Bulimina gibba* (1.4 mg N/m^2) as for *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. (Fig. 6). The uptake of nitrogen by the three species of 2.7 mg N/m^2 represents 1.7% of the applied 160 mg N/m² at the start of the experiment. In comparison to the carbon uptake, the three species (*Bolivina* aff. *B. dilatata*, *Cassidulina* sp., *B. gibba*) had taken up 19.1 mg C/m² which accounts for 2.9% of the 650 mg C/m².

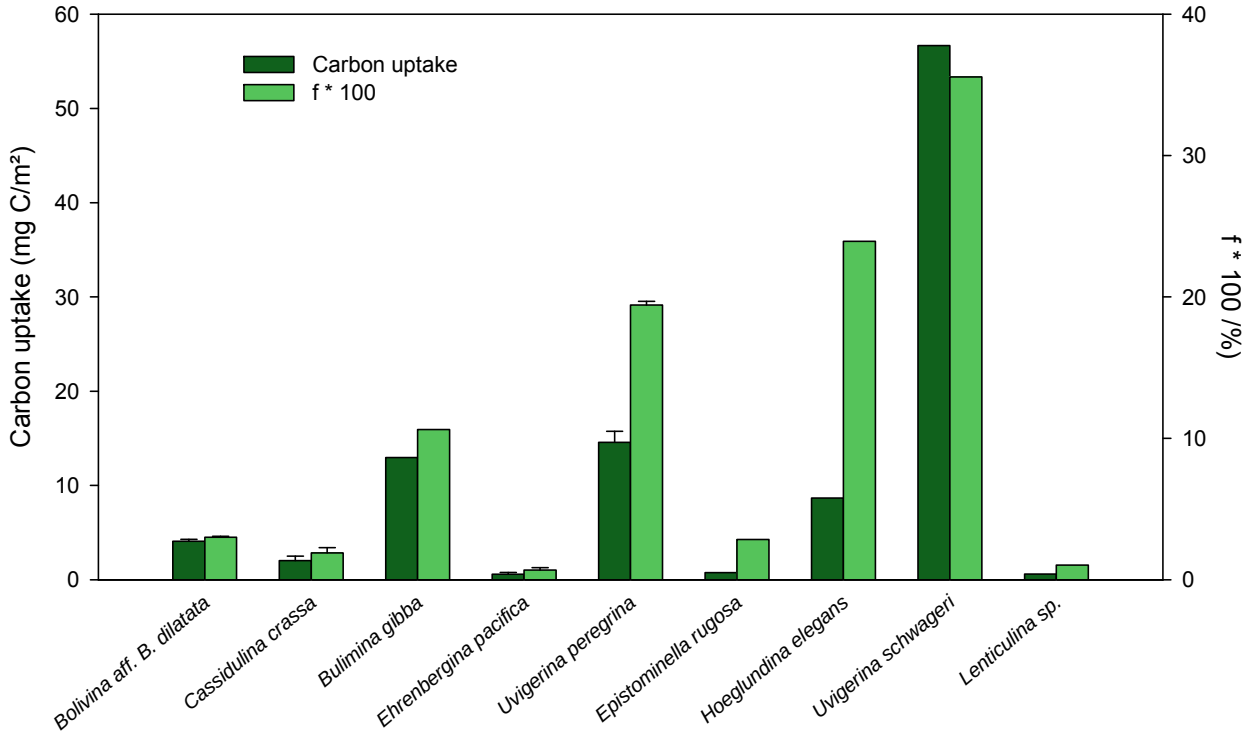


Figure 4 Total carbon uptake of species and the percentage fraction of carbon originating from labeled algae in the analyzed TOC of the foraminiferal cytoplasm.

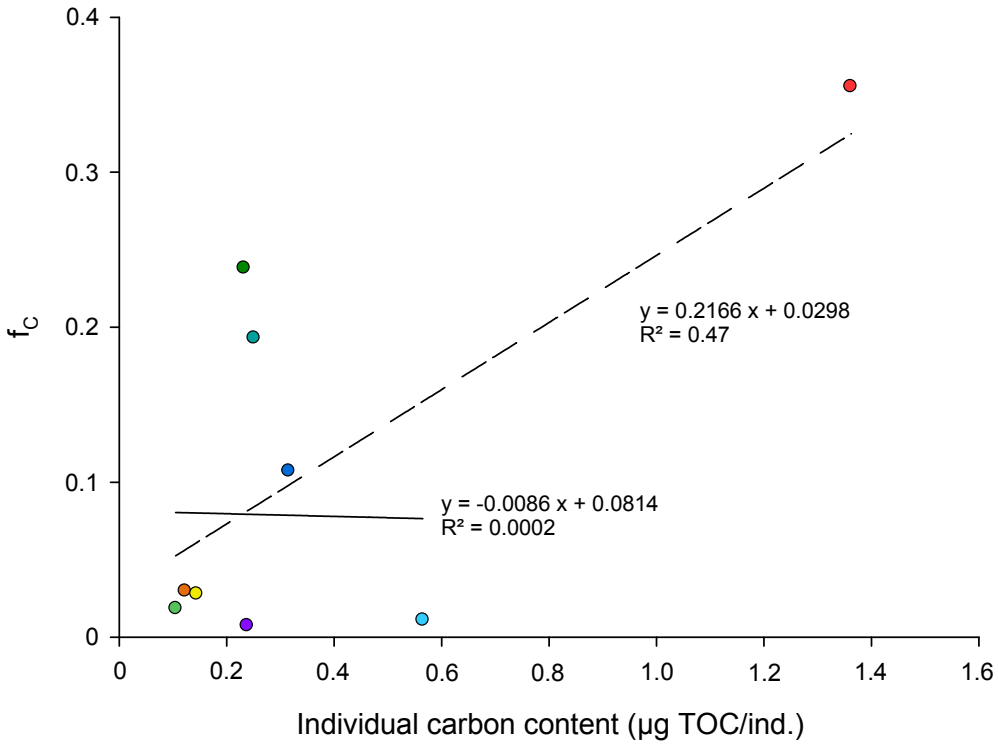


Figure 5 Estimated individual TOC content of the investigated nine species in relation to the biomass-normalized carbon uptake of species (f_C). A linear regression analysis was performed with all species (dashed line) and with 8 species excluding *Uvigerina schwageri* (red circle).

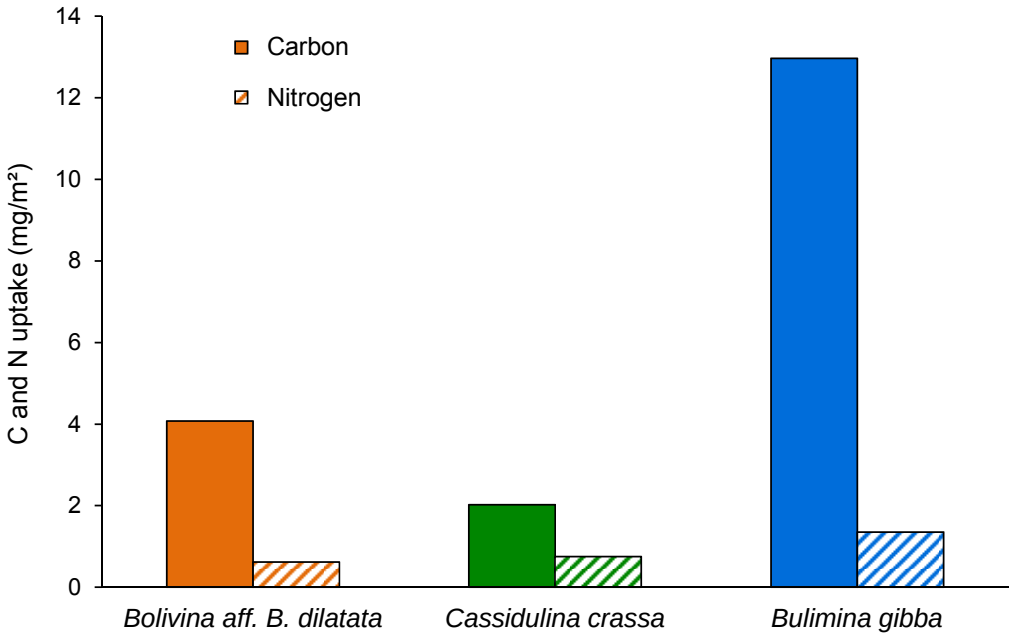


Figure 6 Uptake of carbon (solid) and nitrogen (striped) of the three most abundant species in the uppermost cm at 540 m depth.

4 Discussion

4.1 Species-specific response to phytodetritus

The individual response to the added phytodetritus displayed high variation among the investigated nine species. These differences combined with the differing total abundances of species yielded in a total per-species uptake varying considerably between species (Tab. 4), from 0.6 mg C/m² for *Ehrenbergina pacifica* to 56.7 mg C/m² for *Uvigerina schwageri*. Similar pronounced differences in short-term processing of phytodetritus between foraminiferal species under *in-situ* experimental conditions have been also observed in the bathyal Sagami Bay (Kitazato et al., 2003; Nomaki et al., 2005), the abyssal North Pacific (Enge et al., 2011) as well as at the Carolina margin (Levin et al., 1999). We suspect that several factors contribute to the occurrence of species-specific uptake of fresh phytodetritus in an environment of sufficient food supply.

As the calculation of total per-species uptake (per area) in our study was based on individual abundances, we expected that the numerically dominating species *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. would have shown highest uptake of all species. But both species demonstrated uptake lower than the average value, being less important to short-term carbon cycling than species which contribute far less to foraminiferal numbers at this site. This observation shows that the number of individuals is not controlling the success of a species in phytodetritus uptake and that other parameter are responsible for species-specific differences towards the utilization of fresh phytodetritus.

The rate of uptake of a species might be to some extent related to the specific biomass of foraminifera. In our study, *Uvigerina schwageri* demonstrated the highest uptake of all species (Fig. 4) and also the largest biomass (TOC content) per individual. Species with the lowest individual biomass (*Cassidulina* sp., *B*. aff. *B*. *dilatata*, *E. rugosa*) were the species with the lowest carbon uptake. But for the species (*B*. *gibba*, *U*. *peregrina*, *H*. *elegans*) who were feeding well besides *U. schwageri* no correlation was found between individual biomass and uptake. Possibly, once a certain threshold value in individual biomass is crossed, a direct correlation between biomass and uptake is given. But below the threshold value, biomass would not be the dominating influence on food ingestion, and uptake also relies on further parameters. Whereupon we would exclude body size because test thickness is very different and larger specimens can contain less biomass than smaller species due to thicker tests (e.g. *Uvigerina schwageri*, *Lenticulina* sp.)

As suggested by Nomaki et al. (2005) for foraminiferal populations from Sagami Bay, feeding preferences might play a very important role. The phytoplankton community found in the Eastern Arabian Sea consists of about 30 eukaryotic taxa with a variable distribution throughout the year even though diatoms are the dominating element throughout the year (Sawant and Madhupratap, 1996). Hence, phytodetritus deposits on the sea floor after

productivity maxima in summer and winter contain several phytoplankton groups. In our experiment we used the diatom species *Thalassiosira weissflogii* as food source, fitting in the spectrum of possible food for this location. Very high uptake by *Uvigerina schwageri* suggests a preference for these diatoms whereas *T*. *weissflogii* might not be the favorite food source for the species that demonstrated lowest uptake in our experiment such as *Ehrenbergina pacifica* or *Lenticulina* sp. Heinz et al. (2002) found higher numbers of individuals of foraminifera species after feeding on *Amphiprora* sp. (diatom) and *Pyramimonas* sp. (green alga) than after feeding on *Dunaliella tertiolecta* (green alga), all three being common algae species. In their *in-situ* experiment, Nomaki et al. (2006) were able to identify selective feeders and random feeders of phytodetritus and sedimentary organic matter. Thus *Uvigerina akitaensis* was one of the phytophageous species that ingested phytodetritus selectively. Differential feeding preferences among species could be of advantage in an environment where competition for space and food must be very high among foraminiferal individuals, considering the standing stock of about 4000 individuals per 10 cm^3.

In our study, *U*. *schwageri* showed highest uptake of all species by far and one third of this species' carbon content originated from labeled food. This is evidence that this species shows phytophageous feeding in OMZ sediment at the Indian Margin. The association of the genera *Uvigerina* and *Bulimina* to high productivity was suggested by Loubere and Fariduddin (1999) and an *in-situ* feeding experiment performed in the eutrophic Sagami Bay found *Uvigerina akitaensis* and *Bulimina aculeata* to dominate the foraminiferal response to phytodetritus (Nomaki et al., 2005). The highest uptake of all species by *Uvigerina* ex gr. *U. semiornata*, *Uvigerina peregrina*, and *Bulimina gibba* in our experiment is in agreement with these earlier observations. *Uvigerina* species with outstanding impact on short-term phytodetritus processing was observed by Woulds et al. (2007) in the core region of OMZ sediments at the Pakistan Margin. These taxa seem to be highly adapted to high food concentration and be able to react and ingest large amounts of organic material very fast.

The species *Bolivina* aff. *B. dilatata, Cassidulina* sp., *Ehrenbergina pacifica*, *Epistominella rugosa,* and *Lenticulina* sp. showed lowest uptake during the experiment. They might demonstrate slower metabolism or feeding behavior and reaction would be higher after a longer incubation time. Such time-delayed responses have been observed before. On the other hand these species might not be able to digest fresh diatoms or recognize them as a potential food source. Differential feeding preferences among species could be of advantage in an environment where competition for space and food must be very high among foraminiferal individuals.

4.2 Impact of foraminifera on carbon cycling in OMZ sediments

Although the amount of phytodetritus ingested during the experiment differed among species, the experiment revealed that all species investigated from the upper sediment cm reacted

quickly and strong to the phytodetritus presence. Within four days, nine foraminiferal species had taken up 101 mg C/m² with *Uvigerina schwageri* as the most important contributor. The here presented uptake represents the assimilation of labeled phytodetritus by the nine most abundant species in the size fraction >125 µm. As we do not know the uptake of the remaining species present at this sediment depth and excluded the size fraction <125 µm, our results are minimum values of carbon assimilation. Uptake by the entire foraminiferal community might be even higher and the impact on the benthic community utilization of fresh organic matter greater.

The observed response to fresh phytodetritus during the experiment at the Indian Margin shows that even under dysoxic conditions foraminifera are able to utilize food rapidly. In particular, *Uvigerina schwageri* ingested high amounts of labeled material and might be best adapted to the environmental conditions simulated by the experiment: the presence of fresh phytodetritus arriving in a pulsed event. That deep-sea foraminifera are able to react very quickly to offered organic matter was observed during *in-situ* feeding experiments by Kitazato et al. (2003), Nomaki et al. (2005), Enge et al. (2011), and Nomaki et al. (2011). Foraminifera at 2170 m depth in the North Pacific had ingested ~2 mg C/m² within 35 hours (Moodley et al., 2002). In Sagami Bay, *Uvigerina akitaensis* and *Bulimina aculeata* were the most important rapidly responding species, responsible for utilizing 31 mg C/m² within 11 days (Nomaki et al., 2005). Comparison of uptake between foraminifera at our investigated site and these mentioned habitats is difficult because of strong differences between site, regarding oxygen concentration, food supply, or foraminiferal assemblage composition and abundances).

The only comparable approach to investigate the response of foraminifera to phytodetritus deposition in OMZ sediments was realized northerly of our study site at the Pakistan Margin by Woulds et al. (2007) and Andersson et al. (2008). During a jointed cruise, ^{13}C-labeled phytodetritus was offered *in-situ* and *ex-situ* to the benthic community (e.g. foraminifera) along a depth transect including OMZ influenced sediments (140-1850 m). At 300 m depth where the core region of the Pakistan OMZ is found, the uptake of the entire foraminiferal community after 5 days of incubation ranged between 6 and 20 mg C/m². These values are at least five times lower than observed in our experiment at the Indian Margin at 540 m. And while *Uvigerina schwageri* was the most important species in our experiment, it was *Uvigerina* ex gr. *U. semiornata* who demonstrated remarkable uptake during the Pakistan Margin experiment. Considering that both experiments were carried out both at a similar habitat (OMZ sediments) and both in the Arabian Sea, we expected uptake of foraminifera to show resemblance to one another. The observed variation in the response of the benthic foraminifera under oxygen-depleted conditions to freshly deposited phytodetritus may result from differences in foraminiferal numbers, and water depth. First, the calculation of carbon uptake per area is based on the number of living foraminifera found at the study site. The higher abundances of 3982 ind./10 cm³ at the Indian Margin at 540 m depth in comparison to 200-336 ind./10 cm³ at

the Pakistan Margin (300 m) may be responsible for the calculated uptake. Assuming that at the Indian Margin only 336 specimens per 10 cm³ were present, the estimated uptake of about 9 mg C/m² would be very similar to the measured uptake at the Pakistan Margin with 6-20 mg C/m². The observed high uptake at the Indian Margin is hence a product of the large population densities by living foraminifera at this site. On the other hand, our study site at 540 m depth is located in the center of the OMZ (Hunter et al., 2011) with oxygen concentrations of less than 0.1 ml/l and missing macrofauna (Hunter et al., 2012), whereas the site at 300 m investigated by Woulds et al. (2007) and Andersson et al. (2008) is at the upper edge of the core region where oxygen conditions are not as stable and adaptation of foraminifera to environmental conditions might not be as strong as for foraminifera under constant suboxic conditions (such as at 540 m at the Indian Margin).

As shown above, benthic foraminifera in sediments with oxygen concentrations of <0.1 lm/l are able to utilize organic matter as fast as foraminifera from non oxygen-depleted environments. This suggests that foraminifera in the core region of OMZ sediments at the Indian Margin must be highly adapted to low oxygen in order to be able to ingest large amounts of food. In eutrophic environments, foraminifera are adjusted to the presence of organic matter and do not need time-consuming activation of metabolism due to starvation as it has been suggested for deep-sea foraminifera by Nomaki et al. (2005), to explain their delayed response to phytodetritus pulse. The higher uptake by foraminifera at our site in comparison to the Pakistan margin assemblage could also result from the absence of the macrofauna at the investigated water depth in our study (Hunter et al., 2012). Where present at continental margins, macrofaunal organisms are important consumers of phytodetritus reacting very quickly to its deposition (Blair et al., 1996; Levin et al., 1999; Woulds et al., 2007; Andersson et al., 2008; Hunter et al., 2012). Due to the macrofaunal absence, foraminifera at 540 m at the Indian margin are less exposed to competitors for food and space. Knowledge about the presence and population size of meiofaunal organism at this depth is not given so far, hence competition through the meiofauna might be present. Macrofauna assemblages at the Indian margin from 800 and 1100 m depth include polychaetes, nematodes, crustaceans, molluscs (Hunter et al., 2012) of which some representatives in other marine sites have been found to selectively feed on foraminifera (Lipps, 1983; Nomaki et al., 2008). To this day, nothing is known about selective feeding on foraminifera in this area of the Arabian Sea by other benthic organisms, but also detritiviore predation has been noted to regulate foraminiferal densities (Lipps, 1983; Gooday, 1986). Reduced predation pressure on foraminifera by the missing macrofauna at 540 m depth cannot be excluded and might have also contributed to the successful reaction of foraminifera to phytodetritus und their abundant presence.

Their high abundances and ability to rapidly ingest large amounts of organic material suggests that benthic foraminifera must play a very important role in the early decomposition of sinking organic carbon in the core region of OMZ sediments. Other possible consumers of

phytodetritus at this site would be bacteria which we assume to be higher than the uptake by foraminifera. In oxygen-depleted environments where high amounts of organic matter are present, bacteria are also very likely to occur in high numbers. At the OMZ sediments at the Pakistan margin at 300m depth, no uptake was found for the macrofauna which was represented by less than 0.5 g wet weight/m² (Woulds et al., 2007). The largest pool of labeled carbon was respired (41 mg C/m²) and uptake by bacteria was higher than by foraminifera (Andersson et al., 2008). While Moodley et al. (2002) found bacteria and foraminifera to account for 50% of short-term response to phytodetritus in the North Atlantic, Witte et al. (2003) observed low impact of foraminifera in the abyssal North Atlantic on the total faunal uptake during the first week, but highest uptake of carbon by foraminifera of all investigated benthic groups after 3 weeks. Apparently, the role of foraminifera in cycling of organic matter on the sea floor can show much variation between different environments where the foraminifera are exposed to differing physico-chemical conditions (e.g. oxygen content, nutrient supply, water depth) and biological interactions (competition, predation) which have an influence on phytodetritus assimilation by benthic foraminifera.

4.3 Uptake of nitrogen by foraminifera

All three foraminiferal species presented high labeling with ^{15}N after the experiment which shows that all tested species had ingested nitrogen during the experimental phase and that ^{15}N can be used as a suitable marker in feeding experiments to track the food to the consumer. However, the sensitivity of the analyzing devices today is lower to nitrogen than to carbon why more foraminiferal biomass is required for the analysis of the nitrogen isotopic composition. Hence, analysis of nitrogen uptake on species level requires high abundances of species or high individual biomass. For example, in our experiment we pooled 1500 living individuals of *Cassidulina* sp. for one measurement. This limits the use of ^{15}N as marker, and its application on foraminiferal assemblages at abyssal or hadal depths could be hampered by the generally lower number of living foraminifera at these depths (e.g. Gooday, 1996; Ohkushi and Natori, 2001) in comparison to assemblages at the continental margin.

The nitrogen uptake by *Bolivina* aff. *B. dilatata*, *Cassidulina* sp., and *Bulimina gibba* in the uppermost cm at 540 m is characterized by similar responses and by lower interspecific differences than observed for the carbon uptake. And all three species demonstrated lower absolute nitrogen (2.7 mg N/m²) than carbon uptake (19.1 mg C/m²) after four days (Fig. 6). This might be due the applied dose of both components at the beginning of the experiment. The phytodetritus (*T. weissflogii*) deployed at the sea floor contained 650 mg C/m² and 160 mg N/m², and nitrogen and carbon uptake by the three foraminifera hence responds to 1.7% and 2.9% of the phytodetrital dose mass. And although the difference in the relative uptake of carbon and nitrogen is less than the absolute uptake, foraminifera still ingested almost twice the amount of carbon than nitrogen. Because no dual labeling experiment has been

successfully performed with foraminifera so far, comparison is made to other benthic faunal groups. The observed higher uptake of carbon by foraminifera in comparison to nitrogen is in contrast with observations made for the meio- and macrofauna of the intertidal in the North Sea (Rossi 2007, Evrard et al. 2010). While Rossi (1007) found nitrogen to be faster ingested and to greater extent than carbon by the investigated macrofauna, the study by Evrard et al. (2010) revealed a preferred ingestion of nitrogen by the meiofauna, while macrofauna-sized organisms rather assimilated carbon or ingested material with higher carbon content, respectively. The only other study using ^{13}C and ^{15}N in deep-sea experiments was performed by Hunter et al. (2012) on the macrofauna during the same cruise in the Indian Margin where our experiment was performed. At 800 and 1100 m depth (no macrofauna present at 540 m), macrofauna had also ingested more carbon than nitrogen. Their carbon assimilation accounted for ~1% of the phytodetritus dose, while only ~0.4% of the offered nitrogen were ingested. The results of these studies show strong discrepancies in the relationship between carbon and nitrogen assimilation of nitrogen between faunal groups and sites.

Organic carbon and nitrogen are important components of all organic compounds such as proteins, nucleic acid, lipids, but carbon is present at much larger amounts and is also the one of the main elements of polysaccharides which are catabolized by foraminifera for energy production. Nitrogen is particularly needed during growth and reproductive processes. The larger requirements of organic carbon might hence explain the higher uptake of carbon during the experiment. But it also needs to keep in mind that foraminifera not only ingest organic material to meet their nutritional demands, they also remove particles or compounds from their body. Foraminifera are small eukaryotic organisms that do not possess a stomach to store food for a long time. Hence we cannot be certain that all food ingested during the experiment was also present within the cytoplasm analyzed for isotopic composition. The applied method does not discriminate between ingested carbon/nitrogen atoms and atoms assimilated into the foraminiferal biomass. Excretion of nitrogenous waste products could have also occurred during the experimental period and the measured nitrogen amounts present in the foraminiferal cytoplasm would not reflect the total amount ingested during the entire time.

5 Acknowledgements

We are grateful to Hiroshi Kitazato for the possibility to participate in the research cruise “YK08-11”. Many thanks go to the captain and crew of the R/V Yokohama as well as to the pilots of the submersible Shinkai 6500 for the skillful operations. We also highly appreciate the help of Hidetaka Nomaki in organizing and helping in the isotopic measurements. This research was supported by the Deutsche Forschungsgemeinschaft (grant HE-2460/5-1 for A. Enge) and the Carnegie Trust (grant no. 008427 to U. Witte).

6 References

Aberle, N., Malzahn, A.M., 2007. Interspecific and nutrient-dependent variations in stable isotope fractionation: experimental studies simulating pelagic multitrophic systems. Oecologia 154 (2), 291-303.

Altenbach, A.V., 1992. Short-term processes and patterns in the foraminiferal response to organic flux rates. Marine Micropaleontology 19 (1-2), 119-129.

Andersson, J.H., Woulds, C., Schwartz, M., Cowie, G.L., Levin, L.A., Soetaert, K., Middelburg, J.J., 2008. Short-term fate of phytodetritus in sediments across the Arabian Sea Oxygen Minimum Zone. Biogeosciences 5, 43-53.

Babu, C.P., Burmsack, H.-J., Schnetger, B., 1999. Distribution of organic carbon in surface sediments along the eastern Arabian Sea: a revisit. Marine Geology 162, 91-103.

Beaulieu, S.E., Smith, K.L. Jr, 1998. Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition. Deep-Sea Research II 45 (4-5), 781-815.

Bernhard, J.M., Sen Gupta, B.K., 1999. Foraminifera of oxygen-depleted environments, in: Sen Gupta, B.K. (Ed.), Modern Foraminifera, Kluwer Publishers, Great Britain, pp. 201-216.

Blair, N.E., Levin, L.A., DeMaster, D.J., Plaia, G., 1996. The short-term fate of fresh algal carbon in continental slope sediments. Limnology and Oceanography 41 (6), 1208-1219.

Demaison, G.J., Moore, G.T., 1980. Anoxic environments and oil source bed genesis. Organic Geochemistry 2 (1), 9-31.

Drazen, J.C., Baldwin, R.J., Smith, K.L. Jr, 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II 45 (4-5), 893-913.

Enge, A.J., Nomaki, H., Ogawa, N.O., Witte, U., Moeseneder, M.M., Lavik, G., Ohkouchi, N., Kitazato, H., Kucera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Marine Ecology-Progress Series 438, 129-142.

Evrard, V., Soetaert, K., Heip, C.H.R., Huettel, M., Xenopoulos, M.A., Middelburg, J.J., 2010. Carbon and nitrogen flows through the benthic food web of a photic subtidal sandy sediment. Marine Ecology-Progress Series 416, 1-16.

Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: A natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, 504 pp.

Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (north-east Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. Deep-Sea Research I 33 (10), 1345-1375.

Gooday, A.J., 1996. Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes. Deep-Sea Research I 43 (9), 1395-1421.

Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: A review. Journal of Oceanography 58 (2), 305-332.

Gooday, A.J., Bernhard, J.M., Levin, L.A., Suhr, S.B., 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. Deep-Sea Research II 47 (1-2), 25-54.

Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. Marine Micropaleontology 46 (1-2), 83-110.

Gooday, A.J., Levin, L.A., da Silva, A.A., Bett, B.J., Cowie, G.L., Dissard, D., Gage, J.D., Hughes, D.J., Jeffreys, R., Lamont, P.A., Larkin, K.E., Murty, S.J., Schumacher, S., Whitcraft, C., Woulds, C., 2009. Faunal responses to oxygen gradients on the Pakistan margin: A comparison of foraminiferans, macrofauna and megafauna. Deep-Sea Research II 56 (6-7), 488-502.

Gooday, A.J., Turley, C.M., 1990. Response by benthic organisms to inputs of organic material to the ocean-floor - A review. Philosphical Transactions of the Royal Society of London Series 331 (1616), 119-138.

Graf, G., 1989. Benthic pelagic coupling in a deep-sea community. Nature 341 (6241), 437-439.

Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R.R., Curry, W.B., 1993. Seasonality and interannual variability of particulate fluxes to the deep Arabian Sea. Deep-Sea Research I 40 (7), 1323-1344.

Heinz, P., Hemleben, C., Kitazato, H., 2002. Time-response of cultured deep-sea benthic foraminifera to different algal diets. Deep-Sea Research I 49 (3), 517-537.

Helly, J.J., Levin, L.A., 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Research I 51 (9), 1159-1168.

Hermelin, J.O.R., Shimmield, G.B., 1990. The importance of the oxygen minimum zone and sediment geochemistry in the distribution of recent benthic foraminifera in the northwest Indian Ocean. Marine Geology 91 (1-2), 1-29.

Hogslund, S., Revsbech, N.P., Cedhagen, T., Nielsen, L.P., Gallardo, V.A., 2008. Denitrification, nitrate turnover, and aerobic respiration by benthic foraminiferans in the oxygen minimum zone off Chile. Journal of Experimental Marine Biology and Ecology 359 (2), 85-91.

Hunter, W.R., Levin, L.A., Kitazato, H., Witte, U., 2012. Macrobenthic assemblage structure and organismal stoichiometry control faunal processing of particulate organic carbon and nitrogen in oxygen minimum zone sediments. Biogeosciences 9 (3), 993-1006.

Hunter, W.R., Oguri, K., Kitazato, H., Ansari, Z.A., Witte, U., 2011. Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin. Deep-Sea Research I 58 (6), 699-710.

Jannink, N.T., Zachariasse, W.J., Van der Zwaan, G.J., 1998. Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea). Deep-Sea Research I 45 (9), 1483-1513.

Jones, R.W., 1994. The Challenger Foraminifera. Oxford University Press, Oxford, 149 pp.

Josefson, A.B., Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. Marine Biology 100, 31-40.

Kamykowski, D., Zentara, S.J., 1990. Hypoxia in the world ocean as recorded in the historical data set. Deep-Sea Research A 37 (12), 1861-1874.

Kitazato, H., Nomaki, H., Heinz, P., Nakatsuka, T., 2003. The role of benthic foraminifera in deep-sea food webs at the sediment-water interface: Results from *in situ* feeding experiments in Sagami Bay. Frontier Research on Earth Evolution 1, 227-232.

Lambshead, P.J.D., Gooday, A.J., 1990. The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic - the assemblage response. Deep-Sea Research A 37 (8), 1263-1283.

Larkin, K.E., Gooday, A.J., 2009. Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300 m water depth in the NE Arabian Sea. Deep-Sea Research II 56 (6-7), 403-421.

Levin, L.A., Blair, N.E., Martin, C.M., DeMaster, D.J., Plaia, G., Thomas, C.J., 1999. Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *in situ* experiments using ^{13}C-labeled diatoms. Marine Ecology-Progress Series 182, 37-54.

Linke, P., Altenbach, A.V., Graf, G., Heeger, T., 1995. Response of deep-sea benthic foraminifera to a simulated sedimentation event. Journal of Foraminiferal Research 25 (1), 75-82.

Lipps, J.H., 1983. Biotic interactions in benthic foraminifera, in: Tevesz, M., McCall, P. (Eds.), Biotic interactions in recent and fossil benthic communities, Plenum Publishing Corporation, pp. 331-376.

Loubere, P., Fariduddin, M., 1999. Benthic foraminifera and the flux of organic carbon to the seabed, in: Sen Gupta, B. (Ed.), Modern foraminifera, Kluwer Academic Publishers, Great Britain, pp. 181-199.

Maas, M., 2000. Verteilung lebendgefärbter benthischer Foraminiferen in einer intensivierten Sauerstoffminimumzone, Indo-Pakistanischer Kontinentalrand, nördliches Arabisches Meer. Meyniana 52, 101-129.

Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M.J., Heip, C.H.R., 2002. Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Marine Ecology-Progress Series 236, 23-29.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: *In situ* tracer experiments. Limnology and Oceanography 50 (1), 134-146.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N.O., Kogure, K., Ikemoto, E., Kitazato, H., 2006. Different ingestion patterns of ^{13}C-labeled bacteria and algae by deep-sea benthic foraminifera. Marine Ecology-Progress Series 310, 95-108.

Nomaki, H., Ogawa, N.O., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., Kitazato, H., 2008. Benthic foraminifera as trophic links between phytodetritus and

benthic metazoans: carbon and nitrogen isotopic evidence. Marine Ecology-Progress Series 357, 153-164.

Nomaki, H., Ogawa, N.O., Takano, Y., Suga, H., Ohkouchi, N., Kitazato, H., 2011. Differing utilization of glucose and algal particulate organic matter by deep-sea benthic organisms of Sagami Bay, Japan. Marine Ecology-Progress Series 431, 11-24.

Ohkushi, K., Natori, H., 2001. Living benthic foraminifera of the Hess Rise and Suiko Seamount, central north Pacific. Deep-Sea Research I 48 (5), 1309-1324.

Pina-Ochoa, E., Koho, K.A., Geslin, E., Risgaard-Petersen, N., 2010. Survival and life strategy of the foraminiferan *Globobulimina turgida* through nitrate storage and denitrification. Marine Ecology-Progress Series 417, 39-49.

Risgaard-Petersen, N., Langezaal, A.M., Ingvardsen, S., Schmid, M.C., Jetten, M.S.M., Op den Camp, H.J.M., Derksen, J.W.M., Pina-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., van der Zwaan, G.J., 2006. Evidence for complete denitrification in a benthic foraminifer. Nature 443 (7107), 93-96.

Rossi, F., 2007. Recycle of buried macroalgal detritus in sediments: use of dual-labelling experiments in the field. Marine Biology 150, 1073-1081.

Sawant, S., Madhupratap, M., 1996. Seasonality and composition of phytoplankton in the Arabian Sea. Current Science 71 (11), 869-873.

Schumacher, S., Jorissen, F.J., Dissard, D., Larkin, K.E., Gooday, A.J., 2007. Live (Rose Bengal stained) and dead benthic foraminifera from the oxygen minimum zone of the Pakistan continental margin (Arabian Sea). Marine Micropaleontology 62 (1), 45-73.

Slater, R.D., Kroopnick, P., 1984. Controls on dissolved oxygen distribution and organic carbon deposition in the Arabian Sea, in: Haq, B., Milliman, J. (Eds.), Marine Geology and Oceanography of Arabian Sea and coastal Pakistan, Van Nostrand Reinhold Co., New York, pp. 305-313.

Sweetman, A.K., Sommer, S., Pfannkuche, O., Witte, U., 2009. Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord. Journal of Foraminiferal Research 39 (1), 15-22.

Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.R., Jorgensen, B.B., Pfannkuche, O., 2003. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424 (6950), 763-766.

Woulds, C., Cowie, G.L., Levin, L.A., Andersson, J.H., Middelburg, J.J., Vandewiele, S., Lamont, P.A., Larkin, K.E., Gooday, A.J., Schumacher, S., Whitcraft, C., Jeffreys, R.M., Schwartz, M., 2007. Oxygen as a control on seafloor biological communities and their roles in sedimentary carbon cycling. Limnology and Oceanography 52 (4), 1698-1709.

Wyrtki, K., 1971. Oceanographic atlas of the International Indian Ocean Expedition, National Science Foundation, Washington, DC, 542 pp.