UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

National Oceanography Centre
School of Ocean and Earth Science

Community and trophic responses of benthic Foraminifera to oxygen gradients and organic enrichment

by

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'As objects of beauty they (Foraminifera) arrest the attention of even the casual observer by the delicacy of their structure as well as the symmetry and variety of their forms' (JM Flint 1899).

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ABSTRACT

FACULTY OF ENGINEERING, SCIENCE & MATHEMATICS
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Doctor of Philosophy

COMMUNITY AND TROPHIC RESPONSES OF BENTHIC FORAMINIFERA TO OXYGEN CONCENTRATION AND ORGANIC ENRICHMENT

by Kate E. Larkin

Global warming and eutrophication are driving an expansion of hypoxia in the World Ocean. This will favour organisms, such as Foraminifera (testate protists), that tolerate low-oxygen conditions and may lead to an overall decline in marine biodiversity. With this in mind, community and trophic responses of benthic Foraminifera were investigated at two contrasting sites in the upper boundary (140 m water depth; bottom-water oxygen concentrations = 2.05 ml^{-1} during the spring intermonsoon and 0.11 ml^{-1} during the SW monsoon) and the core (300 m water depth; bottom-water oxygen concentration consistently ~ 0.11 ml^{-1}) of an intense, natural, mid-water oxygen minimum zone (OMZ) on the Pakistan Margin, NE Arabian Sea. Live macrofaunal (>300 µm fraction) Foraminifera (including soft-walled species) and metazoans were examined at each site during the 2003 spring intermonsoon (April) and SW monsoon (October) seasons (4 replicate multicores/site/season, 25.5cm^2 surface area, 0-5 cm depth). Wet-sorting revealed a low diversity assemblage dominated (> 60 %) by calcareous Foraminifera at both sites. A total of 36 species was recognised and diversity was not greatly affected by water depth or season. At both sites, >86 % of Foraminifera were restricted to the upper 0-1 cm layer of sediment and the Average Living Depth (ALD) decreased from the spring intermonsoon to the SW monsoon (140 m, ALD_5 = 0.41 to 0.33; 300 m, ALD_5 = 0.65 to 0.44). Foraminifera increased in mean abundance from 124 to 153 individuals per 10 cm^2 from the spring intermonsoon to the SW monsoon at 140 m and from 86 to 122 individuals per 10 cm^2 at 300 m. The calcareous species *Uvigerina* ex. gr. *semiornata* dominated communities and increased in mean abundance from 54 to 118 individuals (140 m) and from 41 to 69 individuals (300 m) per 10 cm^2 following the SW monsoon. At 140 m, Foraminifera were 3.6 times more abundant than metazoans during the spring intermonsoon, rising to 13.9 times during the SW monsoon. The corresponding proportions at 300 m, where metazoans were rare, were 12.4 and 14.5. Fatty acid biomarkers suggest that foraminiferal diets vary between species. The calcareous species *U.* ex. gr. *semiornata*, *Bolivina* aff. *dilatata* and *Globobulimina* cf. *G. pyrula* selectively ingested phytodetrital material, whereas the agglutinated species, *Ammodiscus* aff. *cretaceus*, *Bathysiphon* sp. nov. 1, and *Reophax dentaliniformis* favoured bacteria. Moreover, *U.* ex. gr. *semiornata*, rapidly ingested (within two days) ^{13}C-labelled diatoms in shipboard laboratory and *in situ* pulse-chase experiments at the 140-m site following the SW monsoon. This enabled the uptake and processing of organic matter (OM) to be tracked in the foraminiferal cell into individual fatty acids, using Gas Chromatography - Mass Spectrometry (selective ion scan). These results suggest that calcareous Foraminifera, in particular *U.* ex. gr. *semiornata*, play a central role in OM cycling on the sea-floor in the upper part of the Pakistan margin OMZ.

Declaration of Authorship

I, **Kate Elisabeth Larkin**, declare that the thesis entitled **Community and trophic responses of benthic Foraminifera to oxygen gradients and organic enrichment** and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University;
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- Where I have consulted the published work of others, this is always clearly attributed;
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- None of this work has been published before submission.

Signed: Kate E Larkin

Date: 30/7/2006

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1 Introduction

1.1 Global oceanic regime shifts: a cause for concern

The current acceleration in the production and release of carbon dioxide (CO_2) into the atmosphere is largely a direct result of the burning of fossil fuels, which is currently increasing concentrations in the atmosphere by c.1.5ppm yr^{-1} (Herzog et al. 2000). The global ocean has an unrivalled capacity to act as a natural reservoir for atmospheric carbon dioxide (CO_2). However, the uptake of this greenhouse gas is changing the physical and chemical characteristics of global water masses. Individual studies and long-term time series observatories are capturing temperature and salinity anomalies in water masses (e.g. Bryden et al. 2005). The oceans are becoming increasingly acidic through increased air-sea flux exchanges of CO_2, lowering the pH of water masses. High CO_2 concentrations and increased levels of organic pollution in the coastal and intermediate waters are stimulating primary productivity, and thus increasing the biological oxygen demand, depleting the oceans in oxygen and promoting the spread of hypoxia in the pelagic and benthic environment.

The global ocean is a complex natural system, displaying some degree of internal variability and positive feedback but with delicate balances and exchanges. However, there is evidence that increasing levels of CO_2 in the oceans, coupled with global warming in the atmosphere, are profoundly influencing the global oceanic nutrient inventories and may create adverse effects on oceanic ecosystems and global circulation patterns (Marsh et al. 2005; McDonagh et al. 2005). What will be the consequences of these regime changes? Oceanic sediments are of central importance in answering this question. These are the world's largest sinks for organic carbon. The natural sequestering of carbon in sediments by organic matter burial leads to its exclusion from the atmosphere and the carbon cycle over time scales of 100,000

years. There have been few comprehensive studies of the relationships between the benthos, sediment geochemistry and the accumulation, cycling and burial of organic matter cycling on the seafloor. Still less is known regarding the influence of physical and chemical gradients, e.g. of temperature, oxygen concentration, pH and organic enrichment, on benthic ecosystems, or how changes in these gradients will influence the biodiversity of ecosystems and the efficiency with which they are able to process organic carbon.

1.2 Marine benthic hypoxia: a growing phenomenon

Hypoxia is a growing problem in the world's oceans. The main contributing factor appears to be an increase in anthropogenic organic pollution in many coastal waters (Turner and Rabalais 1994). Although hypoxic and anoxic basins are well known features of the world's oceans (Kamykowski and Zentara 1990; Helly and Levin 2004), the expansion of hypoxic and anoxic conditions is a cause for concern. Oxygen deficiency causes the mass mortality of many functionally important species. On a large-scale, this may lead to an overall decline in global marine biodiversity and an increase in the abundance of opportunistic organisms, such as bacteria and protists, that tolerate low-oxygen conditions. This is likely to significantly affect the structure and function of benthic communities, the biogeochemistry of benthic environments and benthic-pelagic coupling. Surprisingly little is known about the consequences of disrupting the structure and composition of ecosystems on organic matter cycling, despite the potentially disastrous ecological and economic implications of such changes for productivity and fish stocks. Without the large-scale reduction of anthropogenic nutrient input to the sea, hypoxia will continue to spread. It is therefore vital that a greater understanding is reached of biological and biogeochemical processes within oxygen-deficient environments, both natural and anthopogenically induced, so that predictions about the impact of hypoxia on the global ocean and climate can be better constrained and policy makers can be better informed.

1.3 Benthic Foraminifera

Benthic Foraminifera are the focus of this study. Foraminifera are a highly successful and diverse group of amoeboid protists which belong within the newly-established supergroup Rhizaria (Nikolaev et al. 2004). The fundamental characteristic of the Foraminifera are granuloreticulose pseudopodia that form a mobile network used in feeding, locomotion and other life processes (Travis and Bowser 1991; Bernhard and Bowser 1992; Bowser et al. 1992; Bowser and Travis 2002). Foraminifera can be divided into morphological groups depending on their test type; 'naked' (lacking a test), unilocular thecate (organic), unilocular agglutinated, multilocular agglutinated and multilocular calcareous (Hansen 1979; Loeblich and Tappan 1987). However, only the hard-shelled, readily fossilized calcareous and agglutinated taxa are extensively studied as a result of their importance in palaeontological studies (Murray 1991b; Van der Zwaan et al. 1999). Foraminifera are ubiquitous in marine environments from estuaries and lagoons (Murray 1968) to the deepest ocean trench (Todo et al. 2005), but also occur in fresh water (Holzmann et al. 2002) and even damp terrestrial conditions (Meisterfeld et al. 2001).

Foraminifera are typically smaller and more short-lived than many metazoan taxa (Pearson and Rosenberg 1978). Some species possess a tolerance to hypoxia and display opportunistic life histories, developing high population densities in some low oxygen environments, particularly in areas associated with high organic enrichment (Phleger and Soutar 1973; Bernhard 1986). In low-oxygen environments, many metazoan groups are eliminated and Foraminifera may be of ecological significance as they dominate the eukaryotic biomass in the benthic ecosystem (Moodley et al. 1997; Gooday et al. 2000a). Therefore, as areas of hypoxia continue to expand in the world's oceans, Foraminifera may become key players in benthic OM cycling across increasing areas of the sea floor, with consequences for the cycling and burial of organic matter and the carbon budget of the ocean system. However, little is known about the response of Foraminifera to levels of organic enrichment and oxygen. Still

less is known about the feeding ecology and trophic responses of this important taxonomic group, or the role of these protists in the utilisation of organic matter on the seafloor.

1.4 Aims and hypotheses of this Study

This present study was undertaken within the wider context of a NERC-funded interdisciplinary project '*Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling.*' The project as a whole aimed to provide a comprehensive overview of organic matter cycling and benthic biology within low oxygen environments, specifically the Pakistan Margin Oxygen Minimum Zone (OMZ), in order to increase understanding of benthic processes within low oxygen environments and the contribution of these areas to the global nutrient inventories and cycles. The overarching aim of this study was to investigate the impact of environmental variables and ecological factors, particularly bottom-water oxygen concentration and organic matter availability, on the abundance, diversity and taxonomic composition of the benthic foraminiferal community and the ecological and trophic responses of individual species to these factors. The following hypotheses are addressed:

1) Bottom-water oxygen concentrations influence benthic foraminiferal abundances, species diversity and dominance.
2) Bottom-water oxygen concentrations influence the microhabitat (vertical distribution) of the benthic foraminiferal assemblage.
3) Food availability is an important factor controlling the abundance of benthic Foraminifera.
4) Benthic Foraminifera and Metazoa exhibit contrasting responses to environmental gradients in oxygen concentration and organic enrichment.
5) Benthic Foraminifera are unselective deposit feeders and there are no trophic differences between individual species.
6) Benthic Foraminifera respond rapidly to labile organic matter.

2 Environmental influences on deep-sea Foraminifera

2.1 Deep-sea organisms and environmental gradients

Whilst shallow-water benthic organisms are subjected to considerable variation in environmental parameters such as temperature and salinity change, the deep-sea environment is considerably more stable. Benthic organisms living in the deep sea are therefore likely to have less tolerance to change than those living in shallow waters. For example, even a slight change in pH can have an effect on metabolic activity (Seibel and Walsh 2003) and cause mortality in deep-sea benthic meiofauna (Thistle et al. 2005). Correlations can sometimes be made between species' occurrences and environmental factors, such as current flow and bottom-water oxygenation, suggesting a control through the environment. Disturbed areas and those characterized by organic enrichment often exhibit an overall suppressed diversity (Gage et al. 1994; Glover et al. 2001; Levin et al. 2001). Such areas include oxygen minima impinging on the benthic environment and areas of upwelling (Levin and Gage 1998), deep-ocean trenches (Jumars and Hessler 1976), canyons (Gage et al. 1995; Vetter and Dayton 1998), and bottom areas subjected to episodic erosive currents (benthic storms) driven by surface-originating vorticity that may increase food availability to benthic organisms (Thistle et al. 1985).

The structure and function of deep-sea benthic communities is strongly influenced by two particular factors, bottom-water oxygen concentrations and food availability. In both shallow and deep water, areas subject to periodic hypoxic events often display an initial mortality of certain sensitive organisms and large, long-lived equilibrium species and the succession to a pioneering community characterised by low diversity and high abundances of a few smaller, commonly epibenthic opportunistic species. If the hypoxia is relatively short-lived and not intense, the pre-hypoxic community is re-established and the populations shift again to mature equilibrium dominants (Diaz

and Rosenberg 1995). However, an area exposed to seasonal or persistent hypoxia often results in the elimination of long-lived equilibrium dominants (macrofaunal and megafaunal), as they succumb to the stresses associated with the persistently low-oxygen environment. This results in the reduction of species richness, the virtual absence of larger metazoans and a community dominated by a few highly specialised opportunistic ('pioneering') species able to tolerate the stressful environmental conditions (Pearson and Rosenberg 1978). The absence of many functionally important species represented by mature long-lived individuals, may have significant effects on geochemical and biological processes (Llansó and Diaz 1994). The low diversity, specialised community that is established will have a significantly lower energy utilisation and the ecosystem energy flow will be substantially altered.

2.2 Low Oxygen Environments

2.2.1 Terminology

The terminology and units used to define oxygen concentration values varies extensively between different scientific disciplines. I use the terms oxic, hypoxic and anoxic to define environments ranging from oxygenated to oxygen deficient. Following Diaz and Rosenberg (1995) and Pearson and Rosenberg (1978) these are defined as follows; oxic (O_2 = 2-10 mll^{-1}), hypoxic (O_2 < 2 mll^{-1}), severely hypoxic (O_2 < 0.2 mll^{-1}) and anoxic (O_2 = 0.0 mll^{-1}). In order to facilitate comparison with other oxygen units found in the literature, approximate equivalences are: 1 mll^{-1} = 1.4 mgl^{-1} = 1.4 ppm = 23.9 mm Hg = 23.9 torr = 3.18 kPa = 45.7 mM = 89.3 $mgatL^{-1}$ = 4.3% O_2 vol. = 14% air saturation at 20 psu (practical salinity units, equal to ‰), 25°C, 1 atmosphere pressure (Diaz and Rosenberg 1995).

2.2.2 Oxygen Minimum Zones (OMZs)

The modern global distribution of hypoxia in the World's oceans is shown in Figure 2.1 (from Kamykowski and Zentara 1990). Hypoxia may be anthropogenically

induced as a result of organic pollution leading to eutrophication. This is a growing problem in coastal areas and is prevalent in the Gulf of Mexico, Baltic Sea and Black Sea (Rabalais et al. 2001). In oceanic areas, however, hypoxia is usually associated with natural oxygen minimum zones. OMZs are mid-water features where O_2 is < $0.5 ml l^{-1}$ (Kamykowski and Zentara 1990; Helly and Levin 2004). They are typically associated with areas of high productivity where increased consumption of oxygen by the planktonic community creates an oxygen-deficient layer within the water column.

Figure 2.1 Map of areas of severe hypoxia in marine and estuarine regions of the worlds oceans. From Kamykowski and Zentara (1990).

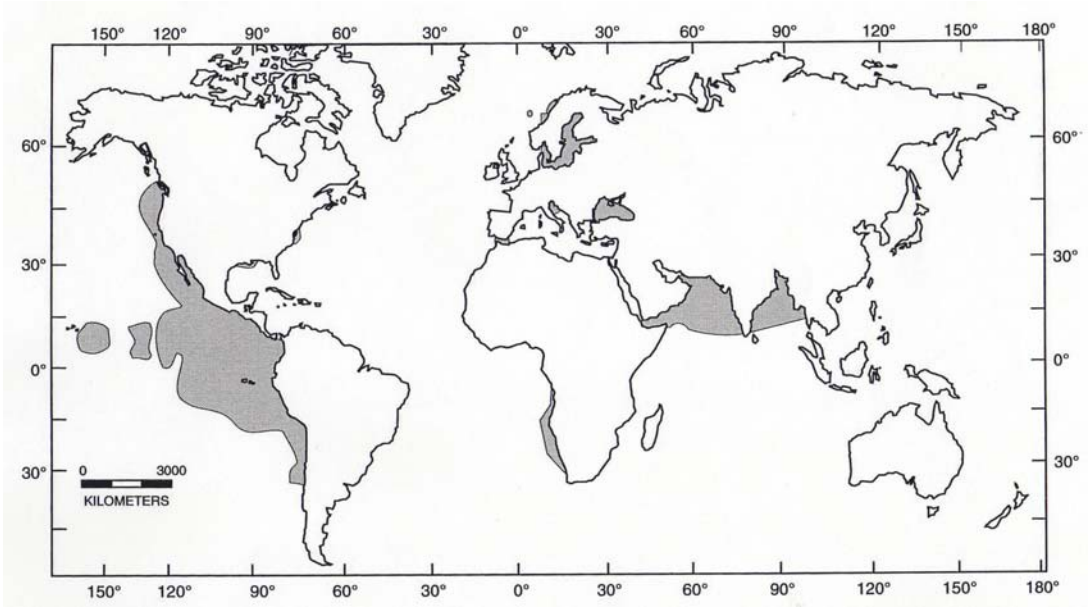
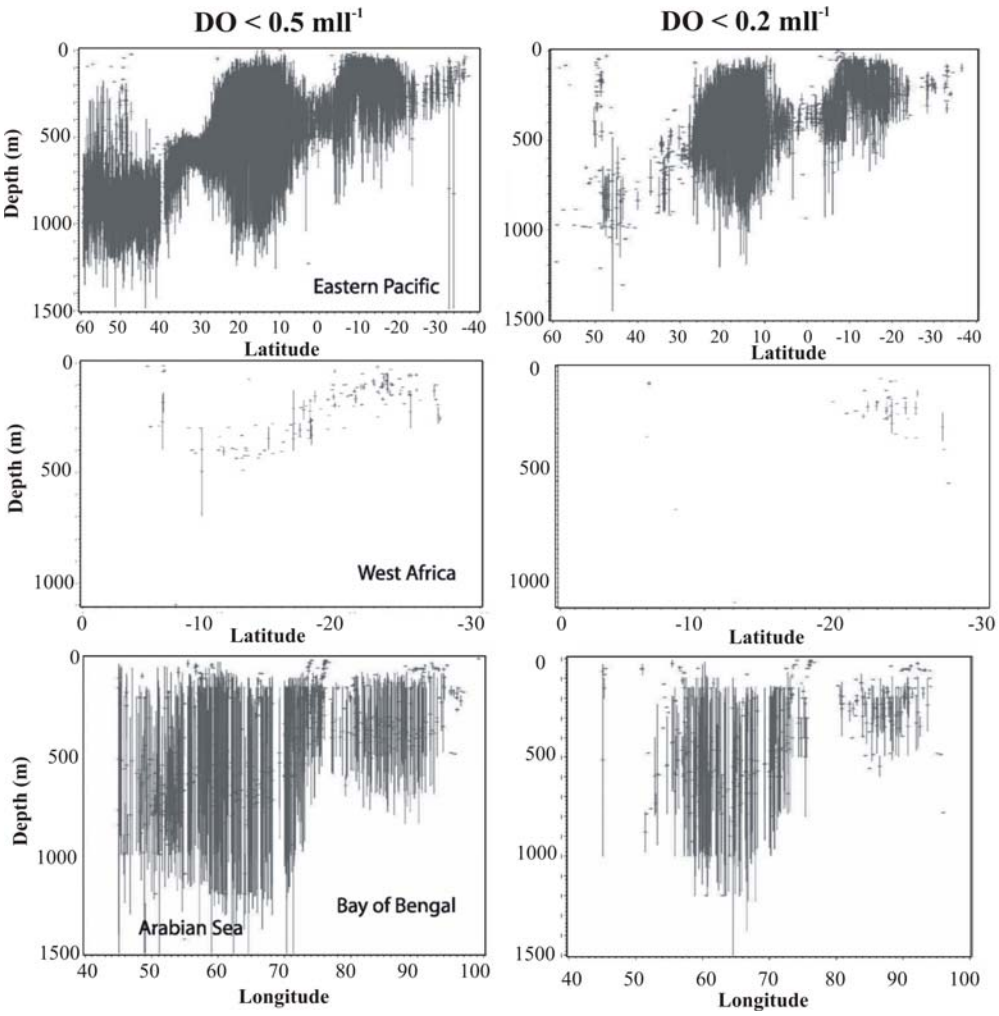


Figure 2.2 Depth distribution and intensity of the major OMZs in the modern ocean (adapted from Helly and Levin 2004).



OMZs are commonly found where the upwelling of nutrient-rich water stimulates high levels of surface primary production. Because of their association with upwelling regions, natural OMZs are particularly prevalent on the continental margins of the eastern Pacific, the Indian and western Atlantic Oceans (Helly and Levin 1994; Kamykowski and Zentara 1990). Other naturally hypoxic zones may form in areas of low circulation and in enclosed seas including silled basins and fjords (Alve 1995).

Natural OMZs commonly intercept the continental margin at shelf and upper bathyal depths, creating strong environmental gradients of bottom-water oxygen concentrations. Helly and Levin (2004) calculated that OMZs ($O_2 < 0.5$ ml^{-1}) cover 1,148,000 km^2 of the sea floor. Figure 2.2 shows the vertical and latitudinal extent of modern natural OMZs and illustrates the strong variation in their intensity (Helly and Levin 2004), with the northern Indian Ocean and particularly the Arabian Sea displaying the thickest and most intense levels of hypoxia. Despite representing only 2.2% of the ocean's continental margin, OMZs affect global biogeochemical cycling and support the largest reducing seafloor ecosystems in the World's oceans. These conditions have a profound influence on organic-matter degradation and burial, organism distributions, diversity and evolution (Rogers 2000). OMZs therefore have a great influence on global nutrient cycling, including the global oceanic carbon budget (Helly and Levin 2004).

2.2.3 Benthic faunas in oxygen-deficient environments

Where OMZs impinge on the seafloor, they create a stressful and hostile environment, in which only organisms adapted to the oxygen-depleted conditions can survive. This creates a benthic eukaryotic fauna of low diversity dominated by a few species among certain groups, notably protists, nematodes and in some cases polychaetes, which can exploit and utilize the large amounts of organic matter commonly associated with such areas. Bacteria associated with low oxygen include the filamentous genera *Thioploca* and *Beggiatoa,* both of which exhibit sulphide-oxidizing and nitrate-reducing capabilities (Gallardo et al. 1998; Jorgensen and Gallardo 1999). For example, in the northwestern Arabian Sea, (Oman margin), Jorgensen and Gallardo (1999) found *Thioploca* to be abundant in sediments at 400 m water depth within the core of the OMZ. Nematodes are the benthic metazoan meiofaunal taxon most tolerant of severe oxygen depletion (Moodley et al. 1997). Cook et al. (2000) analysed nematode abundance across down-slope bathymetric transect of the Oman margin OMZ and found that the abundance of nematodes was

not affected by bottom-water oxygen concentrations. Metazoan meiofaunal taxa, particularly nematodes, have developed various mechanisms to survive hypoxic conditions such as the ability to become facultative anaerobes (Levin et al. 1991) and also to develop symbiotic associations with bacteria (Bernhard and Sen Gupta 1999). This has allowed them to colonise stressful environments and to exploit organic matter with reduced competition or predation from other metazoans (Neira et al. 2001). Other metazoan meiofaunal taxa, including harpacticoid copepods and ostracods, decrease in abundance and diversity in low-oxygen environments (Neira et al. 2001). Macrofaunal and megafaunal metazoans are generally less tolerant and display trends of decreasing abundance and diversity and an increase in dominance with decreasing bottom-water oxygen concentration (Levin et al. 2000). Levin and Gage (1998) and Levin et al. (2000) suggested a threshold value for oxygen concentration of 0.45 $ml l^{-1}$, below which oxygen becomes a limiting factor and macrofaunal metazoan communities display changes in abundance and diversity. Annelids (polychaetes and oligochaetes) are generally the macrofaunal group most tolerant to low oxygen (Diaz and Rosenberg 1995; Gallardo et al. 1995; Levin and Edesa 1997; Levin and Gage 1998; Levin et al. 2000; Oliver 2001). Molluscs, including gastropods and bivalves, as well as ampeliscid amphipods are also found in hypoxic environments, whereas echinoderms are generally absent.

Macrofaunal communities of high biomass and low diversity were found where bottom-water oxygen concentrations were in the range 0.11-0.16 $ml l^{-1}$ on the flanks of Volcano 7 within the Pacific OMZ (Levin et al. 1991) and ~ 0.6 $ml l^{-1}$ off the Peruvian coast (Rosenberg et al. 1983). The Black Sea, in contrast, is not associated with high rates of organic production and there is therefore less competitive benefit for organisms to adapt tolerances to the hypoxic environment, resulting in a much reduced abundance and diversity of eukaryotic species where $O_2 < 0.7$ $ml l^{-1}$ (Bacesco 1963).

2.2.4 Benthic Foraminifera in oxygen-deficient environments

Oxygen concentration and organic carbon enrichment are closely related parameters (e.g. Altenbach and Sarnthein 1989; Van der Zwaan et al. 1999) and the distribution of benthic deep-sea Foraminifera is strongly associated with food supply and oxygen at both large (regional) and small (within sediment) spatial scales (Gooday and Turley 1990; Bernhard 1992; Jorissen et al. 1992; Rathburn and Corliss 1994; Alve and Bernhard 1995; Wollenburg and Mackensen 1998; Heinz et al. 2001; Gooday 2003).

2.2.4.1 Regional patterns

The importance of Foraminifera in oxygen-deficient benthic communities is reviewed by Sen Gupta and Machain-Castillo (1993), Bernhard (1992) and Bernhard and Sen Gupta (1999). Many authors have reported high densities of benthic Foraminifera in oxygen-deficient environments commonly associated with high organic enrichment (Phleger and Soutar 1973; Alve and Bernhard 1995; Bernhard et al. 1997; Bernhard and Bowser 1999). For example, Phleger and Soutar (1973) investigated the effects of oxygen concentration and food availability on the benthic foraminiferal standing stocks from OMZs in the eastern Pacific. Their conclusions were that in low oxygen/organic enriched environments, both factors played a considerable role in shaping the foraminiferal community, with low oxygen eliminating many metazoan groups and some foraminiferal groups, thus reducing predation and competition. High organic matter availability prompted a low diversity assemblage consisting of a few opportunistic species. Calcareous perforate Foraminifera (rotaliids and buliminids) usually have the highest tolerance to oxygen-deficient environments. Many authors have noted the dominance in modern and anoxic low-oxygen environments of "opportunistic", r-selected species, including those from the genera *Bolivina*, *Bulimina*, *Chilostomella*, and *Globobulimina* (Bernhard 1986; Mackensen and Douglas 1989; Koutsoukos et al. 1990; Alve and Bernhard 1995; Bernhard et al. 1997; Jorissen et al. 1998; Bernhard and Bowser

1999; Fontanier et al. 2002). These taxa also occur in deep-infaunal microhabitats in well-oxygenated settings and many have hyaline, calcareous tests with flattened, elongate, biserial or triserial morphologies and high surface to volume ratios. However, *Chilostomella* and *Globobulimina* have more rounded tests and therefore a lower surface to volume ratio and there seems to be no preferential test shape characterizing benthic Foraminifera from dysaerobic environments (Bernhard and Sen Gupta 1999). However, *Chilostomella* and *Globobulimina* have more rounded tests and therefore a lower surface to volume ratio.

In contrast to rotaliids and buliminids, miliolids are much more sensitive to low-oxygen conditions and they are largely absent from oxygen-deficient environments (Nolet and Corliss 1990; Moodley et al. 1998; Jannink et al. 1998; Jorissen 1999). There is evidence that some monothalamous agglutinated species such as *Psammosphaera bowmani* are capable of surviving anoxia for as long as an entire month (Bernhard and Alve 1996). There are also reports of soft-shelled monothalamous Foraminifera (allogromiids and saccamminids) from severely hypoxic settings (Gooday et al. 2005). In general, however, monothalamous Foraminifera are less tolerant of oxygen deficiency than calcareous Foraminifera (Moodley et al. 1998; Gooday et al. 2000).

Moodley and Hess (1992) found that calcareous foraminiferal species that were abundant in subtidal sediments in the southern North Sea, including *Ammonia beccarii, Elphidium excavatum, Quinqueloculina seminulum,* and *Eggerella scabra*, all had very low oxygen requirements. This is supported by the occurrence of living *A. beccarii* at a depth of 35cm in the sediment and the fact that the feeding behaviour and growth rates of these species were not affected when exposed to dysaerobic conditions (<12.5 μM). Bernhard (1987) reported similar results from shallow-water Antarctic sediments in which both calcareous and agglutinated Foraminifera were found living in anoxic layers. Corliss and Emerson (1990) and Bernhard (1992) also reported substantial numbers of living Foraminifera in completely anoxic

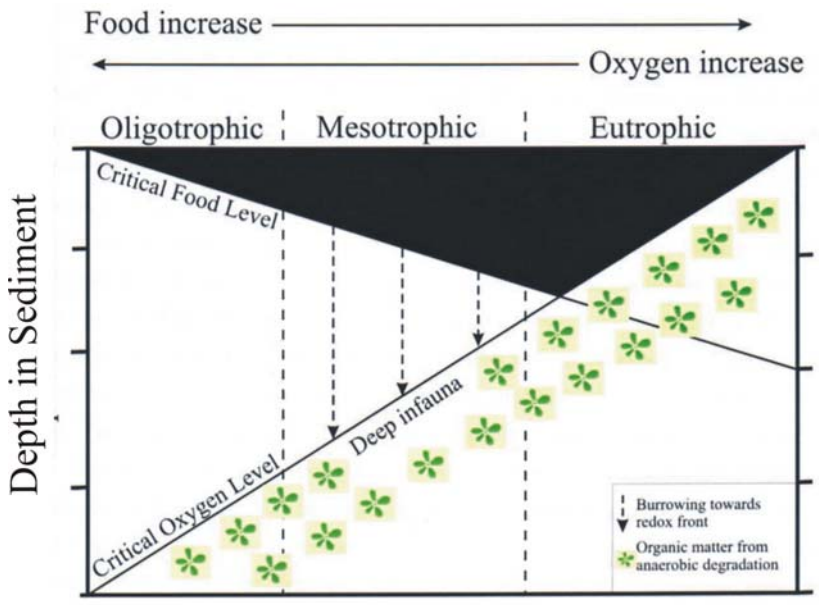
environments. This leads to the suggestion that Foraminifera may be facultative anaerobes (Bernhard 1989; Bernhard 1993; Moodley and Hess 1992; Sen Gupta and Machain-Castillo 1993). However, it is evident that Foraminifera cannot live in permanently anoxic environments (Schmiedl et al. 2000; Fontanier et al. 2002; Gupta and Srinivasan 1992). For example, they disappear entirely where anoxia is persistent on a regional scale (Alve and Nagy 1990). In experimental systems, species displaying a high tolerance of low oxygen have been observed living on surfaces elevated above the sediment-water interface when the sediment becomes anoxic; for instance, *Uvigerina vadescens* was observed climbing on top of a polychaete tube and extruding its pseudopodia in water (Kitazato 1994).

Symbiotic relationships in Foraminifera, including the sequestration of chloroplasts and the harbouring of bacteria, have been observed in a few species of deep-sea benthic Foraminifera. There appear to be adaptations to stressful environments such as cold seeps, hydrocarbon seeps and oxygen minimum zones, some of which may be accompanied by sulphidic conditions. For example, the retention of intact chloroplasts was observed in *Nonionella stella* from a hypoxic bathyal site (Santa Barbara Basin) (Bernhard and Bowser 1999). Other common foraminiferal inhabitants of hypoxic ($O_2 > 0.5$ mll^{-1}) and anoxic sites which sequester chloroplasts, include *Nonionella stella*, *Nonionella labradorica*, *Stainforthia fusiformis* and *Buliminella elegantissima* (Cedhagen 1991; Bernhard and Bowser 1999). *Virgulinella fragilis* from a sulphide-enriched bathyal site (Cariaco Basin, Venezuela) exhibited multiple symbiotic relationships, sequestering intact chloroplasts and harbouring sulphide-oxidising bacteria (Bernhard 2003). Symbiotic relationships with these bacteria is suggested to suppress sulphide concentrations in the surrounding pore waters around the Foraminifera, reducing stress caused by high levels of hydrogen sulphide. A white colouration of the protoplasm is an indication of Foraminifera harbouring sulphide-oxidising bacterial symbionts (Bernhard 2003).

2.2.4.2 Controls within the sediment profile

Food availability and oxygen concentrations also vary at smaller spatial scales within the vertical sediment profile. The occurrence of live Foraminifera in deeper sediment layers was first demonstrated by Basov and Khusid (1983), although it was the landmark paper of Corliss (1985) that first drew attention to the importance of this phenomenon. Many authors have suggested that the two key factors controlling the foraminiferal microhabitat are oxygen and food (e.g. Gooday 1986; Corliss and Chen 1988; Mackensen and Douglas 1989; Corliss and Emerson 1990; Barmawidjaja et al. 1992; Jorissen et al. 1992; Rosoff and Corliss 1992; Rathburn and Corliss 1994; Jorissen et al. 1995). Jorissen et al. (1995), explains the influence of these two factors in his TROX model (TROX model = Trophic-Oxygen-Microhabitat-Reaction) (Figure 2.3).

Figure 2.3 TROX model: a conceptual model explaining benthic Foraminifera living depth (black area) in terms of food availability and oxygen concentration. From Jorissen et al. (1995).



The TROX model encapsulates the idea that foraminiferal microhabitats are not static, but can change in order to optimise food acquisition, as also proposed by Linke and Lutze (1993). Jorissen et al. (1995) proposes that food and oxygen availability, which depend on the amount of organic flux to the seafloor, influence foraminiferal microhabitat preferences. In eutrophic conditions, where organic matter flux to the seafloor is high, food availability is not limiting and oxygen is the main factor controlling the depth of colonization in the sediment. In contrast, where organic matter flux is reduced and oligotrophic conditions prevail, food-limitation exerts the main control on microhabitats. Under such conditions, the vertical distribution of the Foraminifera is heavily dependent on the flux of organic matter to the seafloor. Jorissen (1999) considers competition, predation and bioturbation to be additional factors influencing microhabitats, but these are difficult to incorporate into the TROX model.

Previous studies have reported that Foraminifera migrate actively and change their microhabitat with changing oxygen conditions (Alve and Bernhard 1995; Moodley et al. 1998). In deep-sea oxic environments, a zonation of species within the sediment has been reported (Corliss 1985; Gooday 1986; Mackensen and Douglas 1989; Corliss 1991) and Foraminifera colonize down to depths between 10 and 15 cm in the sediment (Corliss and Emerson 1990). However, in low oxygen environments, such as OMZs, microhabitats of individual species are less apparent. Most living Foraminifera are restricted to the surface 1 cm of the sediment and even deep infaunal species move upwards towards the surface where oxygen is still available (Aranda da Silva 2005).

2.3 Organic matter availability in the deep sea

2.3.1 Benthic-pelagic coupling

The benthic food supply is largely controlled by organic matter flux from surface waters to the seafloor (Lampitt and Antia 1997). This was first proposed by Agassiz (1888) who suggested that organic detritus 'rained' down from overlying surface waters to the seafloor. For many years, it was thought that seasonal primary production was dampened out by the slow passage of tiny particles settling through the water column. However, observations of phytodetrital aggregates on the sea floor in the north Atlantic (Billett et al. 1983; Rice et al. 1986; Thiel et al. 1988; Campos-Creasey et al. 1994) provided evidence for benthic-pelagic coupling, linking surface-water primary productivity to seafloor deposits of phytodetritus. In temperate and high latitude benthic environments, surface productivity is seasonal and therefore episodic. This seasonally-pulsed organic-matter flux evokes a rapid response by benthic organisms – much faster than previously believed (Graf 1992). Many studies during the past two decades have investigated the response of the benthic fauna to the natural phytodetritus pulses (Tyler 1988; Gooday and Turley 1990; Gage and Tyler 1991; Sotwedel and Pfannkuche 1995; Smith and Druffel 1998; Gooday 2002). These observations have profound implications for nutrient cycling in benthic ecosystems and the role of the benthos in organic matter burial.

The flux of particulate organic matter is heavily influenced by water-column processes during the passage to the seafloor. The intensity of these processes may change seasonally. At smaller spatial scales, pelagic flux rate to the continental margin is affected by downslope transport by bottom nepheloid layers or lateral advection as a result of density gradients in the water column (Jahnke et al. 1990). This may result in a higher regional flux of particulate organic matter and higher organic burial rates at the sea floor on continental margins than in the oceanic abyss. In all areas, organic matter is reworked and decomposed by prokaryotes and small

protists (Lochte and Turley 1988; Turley et al. 1995) and grazed by zooplankton as it sinks through the water column. As a result, with increasing water depth, the particulate organic matter reaching the seafloor contains increasing amounts of refractory material. In areas of high zooplankton grazing activity, such as the Norwegian Sea, the seasonal pulses of organic matter to the benthic environment are substantially reduced. The resulting fluxes may not reflect the high surface productivity levels and may also be less labile owing to the increased recycling in surface waters (Bathmann et al. 1990; Bodungen et al. 1995).

Carbon fluxes transport some 1-2% of the photosynthetically fixed carbon from the surface waters to the seafloor, causing organic enrichment of the benthic environment. Once on the seafloor, the residence time and the quality of particulate organic matter is highly variable and dependent on the physical and chemical conditions of the benthic environment (Rice et al. 1986; Thiel et al. 1989). In oxygenated environments, the rate of decay by microbial activity will be high. Once the pore-water oxygenation is reduced, the decay of labile organic matter slows down, resulting in a higher concentration of food particles (Schönfeld and Altenbach 2005). In oxygenated settings, the lack of response by metazoans has been attributed to the degradation of phytodetritus by microbes (Turley and Lochte 1990; Poremba 1994). However, in oxygen-deficient environments, less degradation takes place and there is more organic matter available. If metazoans can tolerate the low oxygen conditions, they should be able to exploit the larger quantities of labile organic matter, in competition with Foraminifera.

2.3.2 The response of benthic Foraminifera to organic matter flux

Previous field studies have suggested that some species of Foraminifera are capable of a very rapid response to an organic flux event, resulting in the colonization of phytodetrital aggregates, an increase in population density, changes in the vertical distribution and the taxonomic composition of the assemblage (Gooday 1988;

Gooday 1993; Gooday and Lambshead 1989; Gooday and Turley 1990; Altenbach, 1992; Kitazato and Ohga 1995; Silva et al. 1996; Gooday and Rathburn 1999). Indeed, in many areas, a specific assemblage, including small species such as *Epistominella exigua*, develops in response to the phytodetritus flux (Gooday 1999; Gooday 1993; Gooday and Lambshead 1989). Experiments support these field observations. For example, in a shipboard microcosm experiment, Altenbach (1992) found a rapid response of the foraminiferan *Cribostomoides subglobosum* from 1240 m on the Vøring Plateau in the Norwegian Sea to a simulated pulse of organic matter. The positive responses recorded included a substantial increase in mean bodymass from 1.95 µg C to 3.68 µgC in only three days, primarily as a result of the packing of food vacuoles with food. More recent laboratory-based experiments by Moodley et al. (2002), Heinz et al. (2002, 2003), Kitazato et al. (2003), Nomaki et al. (2002, 2005a, 2005b and 2006), and Witte et al. (2003a, 2003b) have demonstrated population and species level foraminiferal responses to inputs of artificial phytodetritus.

Underlying the response of Foraminifera to pulsed food inputs is their highly efficient system for gathering food. A mobile network of granuloreticulose pseudopodia (Travis and Bowser 1991; Bernhard and Bowser 1992; Bowser et al. 1992) is able to rapidly collect organic particles. This is advantageous when Foraminifera are in competition for food with metazoans (Cedhagen 1993) and allows Foraminifera to exploit the increase in labile organic matter before most metazoans can utilize it.

Smaller size groups of benthic organisms such as bacteria and protists (including Foraminifera) have much shorter generation times than metazoans and can respond faster than larger metazoans to food pulses (reviewed by Gooday 2002). Unlike larger multicellular organisms, they display a higher rate of somatic growth and require less energy for reproduction (Gooday et al. 1996). There is also evidence that some species of Foraminifera are capable of closing down their cell metabolism at

times of low food availability and remaining dormant until reawakened by renewed food availability (McGee-Russell 1974; Linke 1992, Soltwedel et al. 1996) while others exhibit a decrease in cell size during periods of starvation (Myers 1942; Lee 1974; Lipps 1983; Linke 1989) and an ability to respond rapidly to high levels of food.

Foraminifera often display a more obvious response in terms of population growth to organic enrichment from the sublittoral zone to the abyss. However, the apparent lack of response by metazoan meiofauna at the higher taxon level, may mask a species-level response (Fleeger and Shirley 1990; Gooday et al. 1996). It is possible that the reproductive cycles of nematode and harpacticoid species are linked to phytodetrital deposition, since the increased food availability allows more energy to be allocated to gametogenesis and reproduction (Moore and Bett 1989). Although nematodes are not known to exploit phytodetritus directly, they may display an increase in abundance linked to the consumption of microbes, which increase in density following a flux of labile organic matter to the seafloor (Poremba 1994). Moreover, some polychaetes are able to rapidly ingest labile organic matter (Levin et al. 1997) and may be more active in the short term processing of this material than either Foraminifera or bacteria (Aberle and Witte 2003; Witte et al. 2003a, 2003b).

2.4 Nutrition of benthic Foraminifera

2.4.1 Food sources and feeding preferences

Ultimately, all deep-sea benthic organisms, apart from those associated with chemosynthetic systems, are dependent on food particles derived from surface water productivity to meet their nutritional demands. Foraminifera are no exception. Many previous studies have investigated the diets and feeding behaviour of benthic species (Lee et al. 1966; Lee and Muller 1973; Lee 1974; Lipps and Valentine 1979; Lee 1980; Lipps 1983; Goldstein and Corliss 1994; Goldstein 1999; Gooday et al. 2002a;

Suhr et al. 2003; Ward et al. 2002, 2003; Kitazato et al. 2003; Nomaki et al. 2005a; 2005b; 2006; Topping et al. 2006). These studies have documented a high trophic versatility in Foraminifera, enabling them to feed on a wide range of nutritional sources available in the benthic environment, including algae, bacteria and detritus.

Resource partitioning has also been recognised in foraminiferal feeding. For example, in shallow-water settings, labile organic matter is relatively abundant and many foraminiferal species select specific food sources such as diatoms, flagellates and bacteria (Lee et al. 1966). Lee et al. (1966) observed that saltmarsh Foraminifera feed preferentially on diatoms, followed by the unicellular alga *Dunaliella parva*. Whilst algae are the main food source for many species of benthic Foraminifera, particularly those living in coastal settings, bacteria and undifferentiated detritus are also ingested. There is evidence that a bacterial component to the diet is essential for reproduction in some species (Muller and Lee 1969). In ^{14}C tracer experiments, littoral Foraminifera selected a bacterial food source (Lee et al. 1966). In a laboratory-based feeding experiment, *Ammonia beccarii* actively ingested the bacterium *Vibrio alginolyticus* when all other food sources were absent (Larkin, unpubl. data). Langezaal et al. (2005) also observed *Allogromia laticollaris* and *Ammonia beccarii* actively ingesting bacteria. The allogromiid *Allogromia laticollaris* is able to consume bacterial biofilms (Bernhard and Bowser 1992). In a series of laboratory experiments using radiolabelled substrates (amino acids, glucose and adenine), DeLaca (1981) and DeLaca et al. (1982) observed some agglutinated species, e.g. *Notodendrodes antarctikos* from a shallow water site in Antarctica, capturing suspended particulate organic material as well as utilizing dissolved organic matter (DOC). An additional feeding mechanism termed 'bacteria farming' was suggested by Langer and Gehring (1993). They observed some small epiphytic, non-symbiont-bearing, motile Foraminifera, e.g. *Textularia bocki* and *Quinqueloculina ungeriana*, secreting glycosaminoglycan, an energy-rich substrate which is thought to stimulate bateria and fungi and therefore optimize these food sources for the Foraminifera.

In the more oligotrophic deep sea, food availability is usually an important limiting factor. This has led to the suggestion that all deep-sea Foraminifera are unselective detrital feeders (Lipps and Valentine 1979). This idea is supported by the study of Heeger (1990) who found that the food vacuoles of deep-sea foraminifera from 1240 m water depth in the Greenland-Norwegian Sea contained a wide range of organic matter sources including phytoplankton and bacteria, indicating a deposit-feeding and scavenging trophic strategy. However, there is also evidence for selective feeding among deep-sea Foraminifera. Certain epifaunal to shallow-infaunal species have been found to consume labile material such as phytodetritus as indicated by their green-coloured cytoplasm (Gooday 1988; Gooday and Turley 1990). Evidence of selective feeding by other individual species includes transmission electron microscope observations of *Uvigerina peregrina* from the San Pedro Basin (California, USA), which demonstrate the consumption of diatoms, whilst *Globobulimina pacifica* from the same locality did not (Goldstein and Corliss 1994). In an *in situ* feeding experiment in Sagami Bay, Japan, Nomaki et al. (2005a, 2006) found that many species of deep-sea shallow and deep-infaunal species, selectively ingested algae. In laboratory-feeding experiments, shallow-infaunal calcareous species displayed the highest rates of carbon assimilation and selection of algal food sources (Nomaki et al. 2005b). However, Nomaki (2005a) also observed differences in the feeding preferences of two deep-infaunal species, *Globobulimina affinis* and *Chilostomella ovoidea*, with *Globobulimina* sp. ingesting fresh organic matter transported to deeper sediment layers through bioturbation and *Chilostomella* sp. displaying no uptake despite occupying a similar microhabitat.

As mentioned above, there is evidence that bacteria are a vital dietary component for some coastal foraminiferal species (Muller and Lee 1969). It has been suggested that in bathyal settings, deep infaunal species consume bacteria associated with sediment redox boundaries (Jorissen et al. 1998; Fontanier et al. 2002). Based on features of the test and cytoplasm, Gooday (2003) speculated that some deep-sea monothalamous Foraminifera (particularly allogromiids with tubular apertural

extension) feed mainly on bacteria. However, direct evidence for consumption of bacteria by deep-sea Foraminifera is slight. Thiel et al. (1988) observed very few bacteria, except cyanobacteria, in TEM micrographs of live stained Foraminifera from the abyssal BIOTRANS site. Gooday et al. (2002c) reported a substantial bacterial component in the diet of *Bathysiphon capillare* de Folin from a 950-m site on the northern Rockall Trough, but concluded that this was a result of unselective feeding on sediment, detritus and associated bacteria. Nomaki et al. (2006) found that many species of bathyal Foraminifera from Sagami Bay assimilated few if any bacteria and no species preferentially selected bacteria. This suggests that bacteria are not an optimum nutritional source for most Foraminifera. Given the choice, many deep-sea species seem to prefer other organic matter sources and only ingest bacteria incidentally when it is associated with other organic matter particles.

Most of the evidence for feeding in deep-sea Foraminifera comes from bathyal environments. However in highly oligotrophic central oceanic settings, monothalamous Foraminifera that accumulate stercomata predominate. We know little about the trophic ecology of these taxa but it seems likely that they are deposit feeders that ingest sediment and associated bacteria (Gooday et al. in press; Nozawa et al. in press).

2.4.2 Foraminiferal feeding mechanisms

A fundamental feature of Foraminifera is the complex network of granuloreticulose pseudopodia (Bowser and Travis 2002). These are extensions of the cell that form a mobile network, creating a highly efficient mechanism for gathering food particles (Travis and Bowser 1991; Bernhard and Bowser 1992; Bowser et al. 1992). This feeding mechanism is similar in all species of Foraminifera from shallow- and deep-waters (see Figure 2.4 for pseudopodial activity in *Ammonia beccarii* from intertidal sediments in Nojima bay, Japan). Foraminifera are able to use their pseudopodia to select different food particles under laboratory conditions (Bradshaw 1955; 1961;

Lee 1966; Muller 1975; Lee 1980; Lee et al. 1988; Kitazato and Ohga 1995). For example, in laboratory experiments, Langezaal et al. (2005) used a cell-permanent fluorescent nucleic acid stain to show that *Allogromia laticollaris* and *Ammonia beccarii* actively ingested bacteria, selecting these from inorganic polystyrene particles. Whilst some food particles such as bacteria are easily captured, digested and incorporated into the cytoplasm, others, such as diatoms, are large resilient structures and are consequently more difficult to utilise. Nevertheless, some coastal calcareous species, e.g. *Haynesina germanica*, have been observed to fracture diatom frustules in order to feed on the diatom cell (Banner and Culver 1978; Austin et al. 2005). This behaviour may be similar to the mechanisms used by some shallow-water Foraminifera to extract intact chloroplasts from algae using small teeth or tubercles around the aperture and on other parts of the test (Bernhard and Bowser 1999).

Figure 2.4 Pseudopodia radiating from the single aperture in the benthic foraminiferan *Ammonia beccarii* from an intertidal mudflat, Nojima Bay, Japan. x 250. (photo by K. Larkin)

Once captured by pseudopodia, extracellular food particles are conveyed into the foraminiferal cell body by pseudopodial surface transport (Travis and Bowser 1991). It has been hypothesized that nutrients may be stored in pseudopodia within the intratest space as lipid droplets in order to protect food resources from predators and to segregate food reserves from the cell body (Bowser et al. 1995).

Bowser et al. (1985) showed that the lacunary system described by Lengsfeld (1969) in *Allogromia laticollaris* is a fixation artefact and that the reticulopodial network of allogromiids plays no direct role in the digestion of prey. However, extracellular spaces bounded by cell membranes but enclosed almost entirely within the cytoplasm have been observed in the komokiacean *Rhizammina algaeformis* (Cartwright et al. 1989) and three xenophyophore species (*Aschemonella ramuliformis, Reticulammina labyrinthica* and *Galatheammina lamina*) (Hopwood et al. 1997). These spaces may form a kind of "gut" that allows Foraminifera to use hydrolytic enzymes to digest extracellular food particles (Tendal 1979; Lee et al. 1991; Bowser et al. 1995).

2.4.3 The use of fatty acids as biomarkers

Lipids are hydrocarbon macromolecules that are present in all living organisms. They form structural components of the cell such as membranes and organelles and may also be used as chemical storage reserves (Harwood and Russell 1984). All groups of organisms have specific lipid compositions and certain fatty acids are only synthesised by particular groups of organisms, meaning that these can be used as indicators for a particular carbon (food) source (Boschker et al. 1999; Moodley et al. 2000). Lipids, in particular fatty acids, are therefore useful biochemical markers for investigating trophic pathways and diets (Boschker et al. 1998; Moodley et al. 2000) and as tracers in the marine food chain. Lipid analysis examines the total cellular contents of the organism. Hence a limitation of lipid analysis is the inability to distinguish between food items that have been simply ingested and those that have been assimilated. Therefore in Foraminifera, there is no way to detect fatty acids that

derive from ingested food material stored in the food vacuoles and fatty acids that have been incorporated into the foraminiferal membranes and organelles. In addition, lipids derived from symbionts and host organisms cannot be distinguished.

Fatty acids (carboxylic acids) occur in many molecular forms and can be subdivided into well-defined families according to their structure. The fatty acids most useful as biomarkers are the polyunsaturated fatty acids (PUFAs). These polyenoic compounds contain multiple double bonds that are most commonly separated by a single methylene group (CH_2) (Gunstone 1967). Many PUFAs are unique to plants and cannot be synthesised by animals or protists. Foraminifera are no exception and any PUFAs that they contain must be derived from plant material either ingested directly, or indirectly through bacteria that have themselves consumed dissolved organic matter (DOM) derived from plants (Anderson and Pond 2000). Polyenoic acids are described in the literature by their shorthand designation using the formula x: z(*n*-b), where x is the number of carbons in the chain, z is the number of double bonds (degree of unsaturation), n is the terminal methyl group at the end of the chain and b indicates the location of the last double bond in terms of the number of carbons from the methyl group (Christie 1982). For example, eicosapentaenoic acid (EPA), with the chemical formula $H_2C(CH_2)_{18}COOH$, is an example of a PUFA unique to plants and more specifically to algae. Its shorthand designation is 20:5(*n*-3), which refers to a chain of 20 carbons with 5 double bonds, the last of which is located 3 carbons from the terminal methyl group. PUFAs are considered as an indication of the freshness of organic matter, with high amounts of PUFA indicating a higher lability and a more recent deposition (Wakeham et al. 1997a; Fileman et al. 1998). Table 1 in Appendix B lists some key biomarker fatty acids, their sources and references in the literature.

The most important nutritional fatty acids are the long-chain *n*-3 polyunsaturated fatty acids (LC*n*-3PUFAs), such as eicosapentaenoic acid [EPA; 20:5(*n*-3)] and docosahexaenoic acid [DHA; 22:6(*n*-3)]. These appear to be especially important in

the nutrition of organisms at higher trophic levels such as zooplankton and fish (Muller-Navarra et al. 2004). For example, a lack of (*n*-3) polyunsaturated fatty acids has been linked to growth retardation and reduced reproduction potential in copepods (Marsh and Tenore 1990). In some cases, these *n*-3 polyunsaturated fatty acids may also be produced via cellular biochemical pathways involving the elongation and desaturation of precursor fatty acids such as 18:3(*n*-3), 18:4(*n*-3) and 18:5(*n*-3) (Veloza et al. 2006). However, long-chain (*n*-3) polyunsaturated fatty acids are termed essential fatty acids as bioconversion in the higher organism is often too slow to meet physiological demands and the organism relies on acquisition of these fatty acids by bioaccumulation from ingestion of algae that have themselves synthesized these fatty acids (Smith and Morris 1980). At present, there is no conclusive evidence that Foraminifera can synthesize any lipid biomarkers *de novo*. However, Ward et al. (2003) speculated that the foraminiferan *Haynesina germanica* may be able to synthesize the fatty acid 18:2(*n*-6) in the foraminiferal cell and other authors have suggested that other marine benthic protists may be synthesizing *n*-6 PUFA fatty acids (Bell et al. 1986, Bowles et al. 1999).

Fatty acid biomarkers have been used as a biochemical technique to assess the diets and reproduction of many shallow-water and pelagic organisms including fish (e.g. Bell et al. 1996), antarctic krill (Pond et al. 1995; 2005), the copepod *Calanus finmarchicus* (Mayor 2005) and the coccolithophore *Emiliana huxleyi* (Pond and Harris 1996). Previous studies on the diets of deep-sea benthic eukaryotic organisms mostly focus on megafauna including echinoderms (Bell et al. 2001; Howell et al. 2003) and holothurians (Hudson et al. 2003; 2004). Some attention has also been given to organisms from hydrothermal vent sites, such as hydrothermal vent mussels (Pond et al. 1998), the bresiliolid shrimp *Rimicaris exoculata* (Pond et al. 1997; 2000a; 2000b) and *Alvinocaris markensis* (Pond et al. 1997) and hydrothermal vent worms *Ridgea piscesae* and *Protis hydrothermica* (Pond et al. 2002) all on a Mid Atlantic Ridge hydrothermal vent.

A few previous studies have analysed the fatty acids in protist groups such as the thraustochytrids (e.g. Bowles et al. 1999) and the flagellated heterotrophic protist *Chilomonas paramecium* (Boëchat et al. 2005) but few studies have focused on Foraminifera. The first comprehensive analysis of fatty acids in a foraminiferal species was conducted on *Bathysiphon capillare* de Folin from a 950 m site on the northern Rockall Trough (Gooday et al. 2002c). Gooday et al. (2002c) reported for the first time in a protist, the presence of non-methylene diene-interrupted fatty acids (NMIDS), particularly 22:2Δ7,13 and 22:2Δ7,15. These bacterial biomarkers were present among a diverse spectrum of fatty acids and this deep infaunal species was therefore inferred to be a deposit feeder consuming sediment, detritus and associated bacteria.

Suhr et al. (2003) used fatty acid biomarkers to assess the affect of a seasonal phytoplankton bloom and associated organic matter deposition on the diets of three dominant species on the western Antarctic Peninsula Shelf, *Globocassidulina subglobosa*, *Thurammina albicans*, and *Quinqueloculina seminulum*. They reported that *Globocassidulina subglobosa* displayed a significant short-term increase in polyunsaturated fatty acids (PUFAs) (indicators of fresh phytodetritus) following a deposition event of organic matter (phytodetritus) to the seafloor associated with the summer bloom. In addition, Suhr and Pond (2006) found evidence from fatty acid analysis for selective feeding on high quality phytodetritus by *Cassidulina crassa* from 55-m water depth in Arthur Harbor, Anvers Island, Antarctica.

Other studies on the diets of foraminifera have addressed experimental techniques. Ward et al. (2002, 2003) used fatty acids to analyse the uptake of algae and sewage by the shallow-water foraminiferan *Haynesina germanica*, in a series of laboratory microcosm experiments conducted on intertidal sediments from the Hamble estuary, UK. Whilst Foraminifera were reported to have consumed diatoms (seen from the substantial increases in diatom biomarkers such as 20:5(*n*-3) and 16:1(*n*-7), there was no conclusive evidence that *H. germanica* was consuming sewage, although Topping

et al. (2006) suggest that this result may be influenced by the time (season) of sampling.

3 The study area in the Arabian Sea

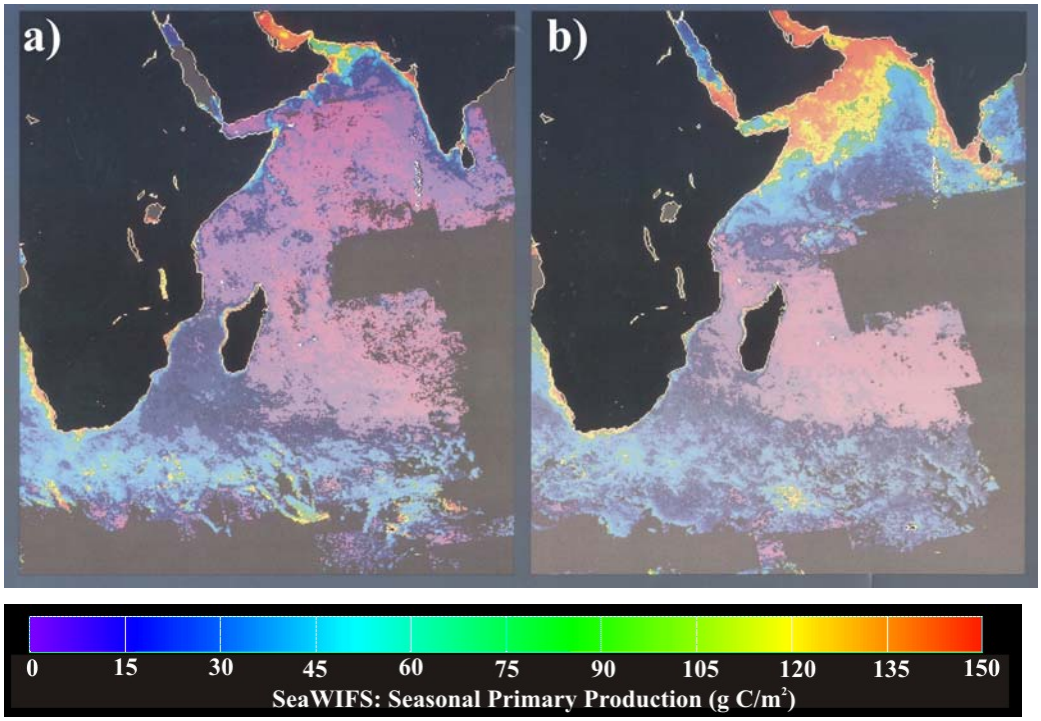
3.1 The Arabian Sea OMZ

Despite its comparatively small size, covering an area of 6.2×10^6 km^2 or approximately 1 % of the global ocean surface (Pfannkuche and Lochte 2000), the Arabian Sea is one of the most biogeochemically active oceanic regions of the World's oceans and responsible for approximately 5% of the world's annual productivity. As a result, it is believed to play an important role in the carbon cycle (Cowie et al. 2005). The key feature of the present-day northern Arabian Sea is an intense, mid-water Oxygen Minimum Zone (OMZ) extending from the bottom of the euphotic zone (100-150 m) to depths greater than 1 km. This represents one of the thickest low-oxygen layers in the modern ocean (Wyrtki 1971; 1973; Deuser et al. 1978; Olson 1993; You and Tomczak 1993) and constitutes 59% of the area covered by OMZs in the world oceans (based on $O_2 < 0.5 ml l^{-1}$) (Helly and Levin 2004). It is closely linked to the seasonally oscillating monsoonal wind regime.

3.1.1 Monsoonal winds and primary productivity

The prevailing monsoonal wind forces nutrient-rich waters from the deep ocean to the surface, stimulating surface productivity (Summerhayes et al. 1992). As a result, the northern Arabian Sea exhibits some of the highest productivity in the open ocean with values of between 200 and 400 $gC.m^{-2}.yr^{-1}$ (Qasim 1982; Codispoti et al. 1991; Antoine et al. 1996). Two maxima in biological production occur during the SW and NE monsoon (Ryther and Menzel 1965; Qasim 1982; Caron and Dennett 1999; Rixen et al. 2000) (Figure 3.1). Productivity is highest during the summer, when the strong southwest monsoonal winds create an anticyclonic surface circulation driven by the Findlater Jet (Rixon et al. 2000) and drive intense coastal upwelling of nutrient rich water off the coasts of Somalia, Oman and southwestern India (Wyrtki 1973; Burkill et al. 1993b). In contrast, the winter monsoonal winds are cold, dry and

Figure 3.1 Surface productivity in the Indian Ocean during a) spring intermonsoon, b) SW monsoon (2003). Satellite images from NASA. The brighter colours indicate higher surface productivity (see scale below).



blow from the northeast, initiating an annual reversal from anticyclonic surface circulation during the SW monsoon (May to September) to a cyclonic surface circulation pattern during the NW (November to March) monsoon. The winter monsoonal winds are typically less intense and productivity across the Arabian Sea basin is lower than during the SW monsoon, except off Pakistan where there is localised high productivity stimulated by surface water cooling creating convective overturn (Wyrtki 1973; Banse 1987; Bauer et al. 1991; Madhupratap et al. 1996).

Whilst the open Arabian Sea resembles the stereotypic, unperturbed tropical ocean, with a thin oligotrophic mixed layer and a pronounced subsurface chlorophyll maximum, the interannual northeast and southwest monsoons disrupt this typical tropical hydrography causing mixed-layer deepening and eutrophication in the central and northern Arabian Sea (Brock et al. 1993). Based on analysis of the

nitrogen/phosphorus (N/P) ratios during the SW monsoon and autumn intermonsoon seasons during 1994, Woodward et al. (1999) suggested that phytoplankton production was potentially nitrogen-limited in all the surface waters of the Arabian Sea, with the greatest nitrogen limitation during the intermonsoon period. Previous studies of the phytoplankton community of the Arabian Sea have reported a dominance (in some cases up to 40 %; Burkill et al. 1993a) of prokaryote taxa, especially the cyanobacterium *Synechococcus* spp. and a high percentage of diatoms especially in near-shore upwelling areas (Burkill et al. 1993a; Jochem 1995; Barlow et al. 1999; Tarran et al. 1999).

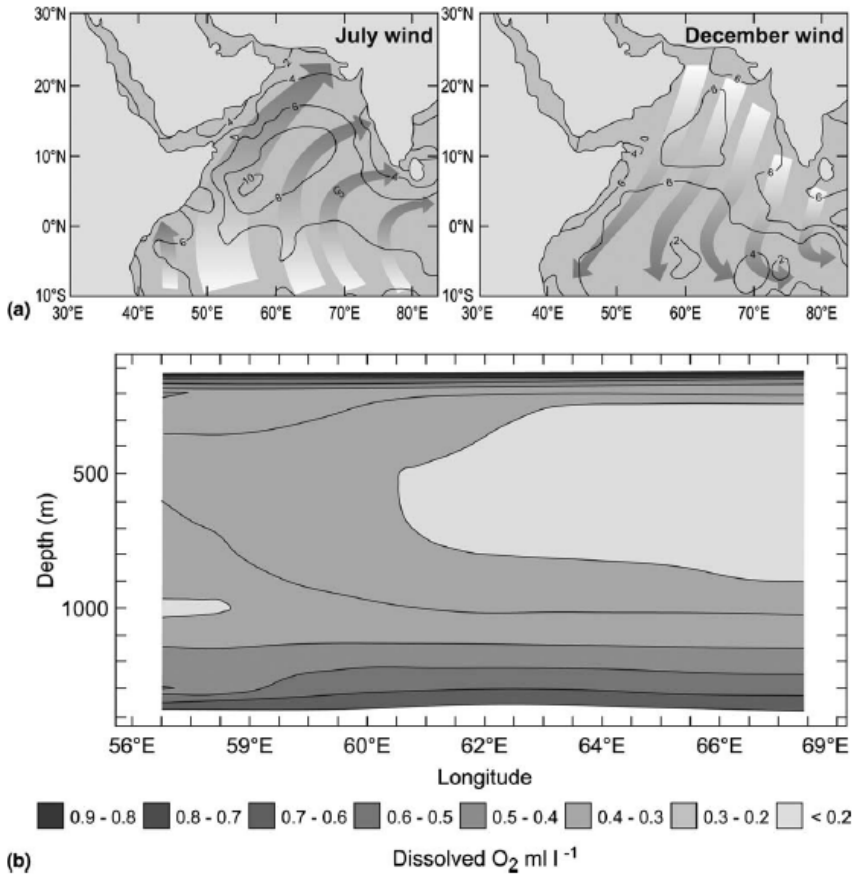
3.1.2 Development of the OMZ

The northern Arabian Sea OMZ is a basin-wide feature that maintains its intensity from the Oman margin to the Pakistan margin (Wyrtki 1971; Deuser et al. 1978; Olson et al. 1993; Reichart et al. 2002). It is a persistent feature, encompassing water masses with oxygen concentrations ≤ 0.5 mll^{-1}, and with oxygen concentrations as low as 0.1 mll^{-1} in its core (Reichart et al. 2002). The driving force behind the formation of the OMZ, and the unique biogeochemical conditions associated with it, is the seasonally oscillating monsoonal wind regime; the summer southwestern monsoonal winds from May to September and the winter northeastern monsoonal winds from November to March (Figure 3.2). As explained above, these drive the surface circulation of the Arabian Sea and create upwelling leading to intensely seasonal surface productivity rates in the region. The development of the OMZ is linked to these processes (Wyrtki 1973).

The high surface productivity leads to high rates of upper and mid-water biological activity which starve the upper oceanic water masses of oxygen. However, the mid-water layer of oxygen-deficient water is also developed and maintained by a number of other factors. The stability of the OMZ results largely from the land-locked setting of the northern Arabian Sea, which limits circulation. High surface temperatures lead to a pronounced thermohaline stratification, which isolates deeper waters from the

atmosphere, resulting in limited mixing between water masses and modest rates of thermocline ventilation (You and Tomczak 1993; Cowie et al. 1999). Finally, the inflow of low-oxygen water from the Persian Gulf into the northwestern Arabian Sea basin also adds to the hypoxic nature of the mid-water masses.

Figure 3.2 a) The Arabian Sea monsoonal wind regime showing the annual reversal of the prevailing winds and the average mixed layer depths during the SW (July) and NE (December) monsoons. From Cowie (2005) adapted from Honjo and Weller (1997). b) A schematic of the cross – section of the water-column in the Arabian Sea showing water – column dissolved oxygen concentrations at 17.5°N. From Cowie (2005) adapted from Levitus and Boyer (1994).



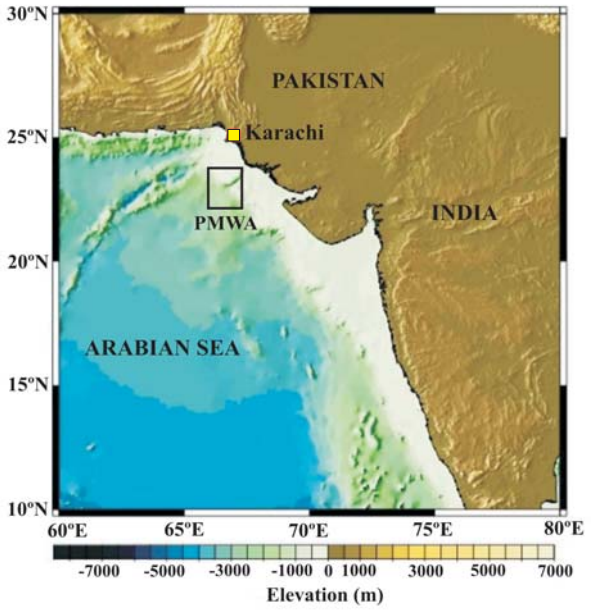
Bottom water oxygen levels in the core of the Pakistan Margin OMZ (300-900 m) are approximately 0.1mll^{-1}. Over geological time scales, the OMZ core has remained stable and strongly dysoxic conditions have prevailed. However, there is evidence that fluctuations in the intensity of the NADW circulation and changes in surface water productivity over time periods of 1000 to 10,000 years have reduced the stability of the lower part of the OMZ (Den Dulk et al. 1998). The upper part of the OMZ seems to have been more stable over geological time scales but exhibits a much greater degree of seasonal variability than the lower boundary.

3.2 The Pakistan Margin OMZ during 2003

As part of the large NERC-funded project '*Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling'*, two pairs of cruises were carried out by the RRS *Charles Darwin* to the Pakistan margin, an area where the sediment geochemistry and benthic fauna are poorly described. The first pair of cruises (March-May 2003, CD145 and CD146) preceded the SW summer monsoon and was followed by the two post-monsoon cruises from August-October 2003 (CD150 and CD151). This allowed a study of interannual variations in the fate and utilisation of organic carbon by the benthic community and sediments. The main sampling area covered a region between 22º40' and 23º30' N latitude and 65º45' and 67º0' E longitude, NW of the Indus Canyon and SE of the tectonically active Makran continental margin (Figure 3.3a). Five main coring sites were chosen across a bathymetric transect of the Pakistan Margin OMZ at depths of 140 m, 300 m, 940 m, 1200 m and 1850 m (Figure 3.3b). This study focuses on the two sites within the upper part of the OMZ transect, A140 (c.140 m) and A300 (c. 300 m).

Figure 3.3 Locality maps. a) The NE Arabian Sea, highlighting the Pakistan margin working area (PMWA), b) Detailed locality map of the study site, showing the five main coring sites, including the sites investigated in this study; A140 (c. 140 m), A300 (c. 300 m). ▲ = Coring site

a)



b)

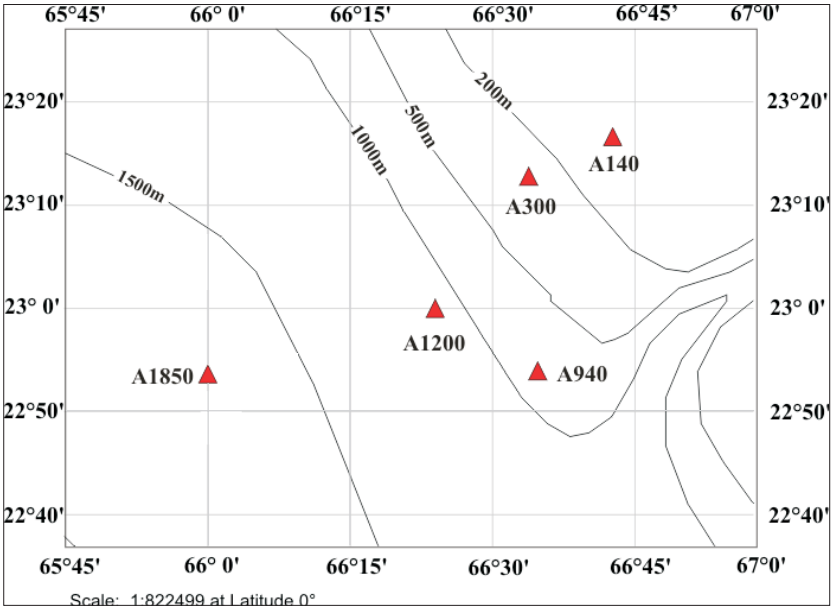
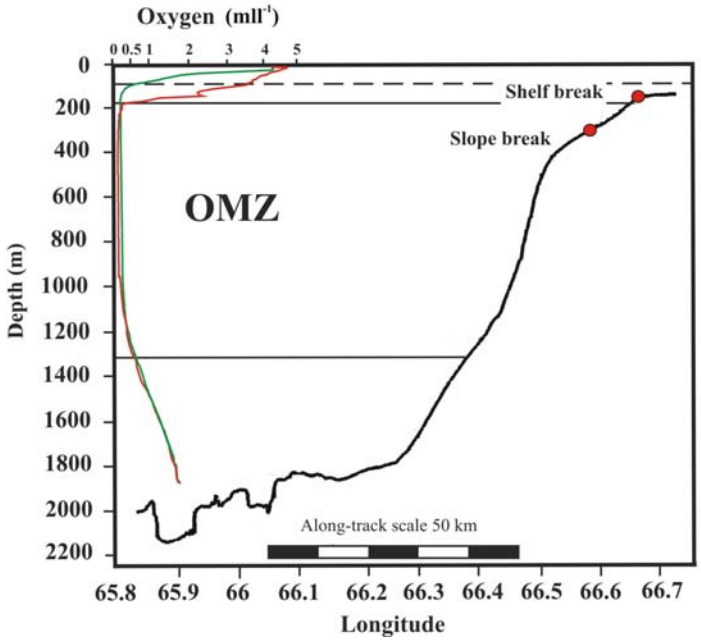
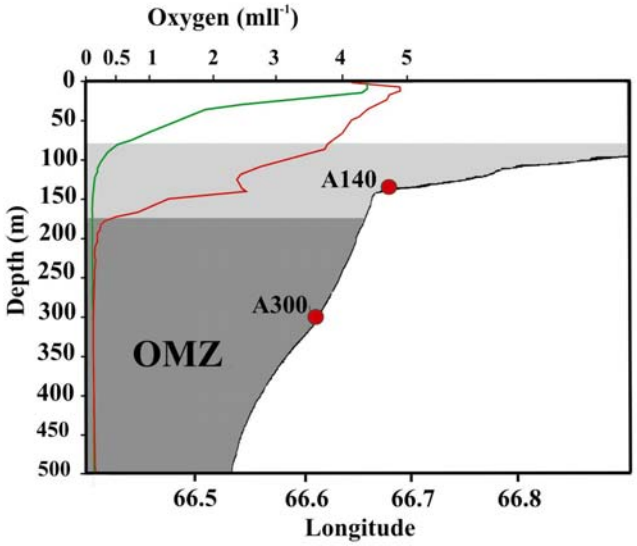


Figure 3.4 Pakistan continental margin primary transect sampled in 2003 with full oxygen profiles for the two seasons sampled; spring intermonsoon (April 2003) (red line) and SW monsoon (October 2003) (green line). The two sites at 140 m and 300 m are shown by red dots in both figures. a) Full profile of OMZ. b) The upper part of the OMZ (0 to 500 m water depth) showing the upward shift in the upper OMZ boundary following the SW monsoon. The seasonal OMZ (c. 80-180 m) following the SW monsoon is shown by a) dashed lines b) light grey area. (Adapted from Bett et al. 2003a. Oxygen values are CTD data from Bett et al. 2003a; 2003b).

a)



b)



3.2.1 General trends

The following section describes general environmental and faunal trends observed across the Pakistan Margin OMZ during the spring intermonsoon and the SW monsoon season of 2003.

3.2.1.1 The pelagic environment

Spring intermonsoon (March-May)
During the spring intermonsoon season, the OMZ encompassed the water column between c. 180-1300 m depth. The surface 180 m of the water column was fully oxygenated, warm and saline. This upper water layer was relatively low in nutrients ($PO_4 < 0.5$, $SiO_3 < 2.0$ and $NO_3 < 1.0$ μM), probably a result of active sequestration of water-column nutrients in the photic zone by phytoplankton communities during the low-intensity NE winter monsoon which preceded the spring intermonsoon season (Bett et al. 2003a; 2003b). Below 180 m during the spring intermonsoon, water masses displayed strong gradients in oxygen and nutrient concentrations, resulting in a layer of hypoxic ($O_2 < 0.5 ml l^{-1}$, $1 mg l^{-1}$), cooler, fresher water with increased nutrient concentrations ($PO_4 > 2$, $SiO_3 > 10$ and $NO_3 > 10$ μM). The oxygen concentration increased steadily at depths below 1000 m, reaching 0.5 $ml l^{-1}$ at approximately 1300m (lower boundary of the OMZ), but remaining less oxygenated than the upper water layer (above 180 m) until at least 3km depth.

SW monsoon (August-October)
Following the SW summer monsoon, there was a shallowing of the upper boundary of the OMZ from c. 180m (spring intermonsoon) to c. 80m (SW monsoon) (Figure 3.4b). The expansion of the OMZ onto the continental shelf led to a much greater area of the seafloor experiencing bottom-water oxygen concentrations of $\leq$ 0.5 $ml l^{-1}$ following the SW monsoon. In addition, the intensity of the OMZ increased on the upper slope because of a shallowing of the 'core' of the OMZ where bottom water oxygen concentrations were $\leq$ 0.1 $ml l^{-1}$ (Bett et al. 2003a; Bett et al. 2003b).

The lower boundary of the OMZ (c. 1300m) was relatively stable between the two seasons, with only a slight shallowing following the SW monsoon. The main cause of the upwards shift of the OMZ was probably the monsoon, which caused wind - driven upwelling and increased primary productivity and biological oxygen demand in surface waters, resulting in oxygen depletion at shallower depths during the monsoon season. A thinning of the mixed layer to the surface 50 m, probably as a result of upwelling of nutrient–rich deep-water, also occurred. This phenomenon was previously recorded in the western Arabian Sea (Weller et al. 2002). The hypoxic, colder, fresher layer extended from 50m to approximately 1200m. Nutrient concentrations increased in the surface waters following the SW monsoon as a direct result of monsoon driven upwelling of nutrient–rich, deep-water masses.

3.2.1.2 Evidence for a phytodetrital flux

The Arabian Sea is characterised by seasonal productivity maxima (Figure 3.2) and consequently pulsed inputs of organic matter from the euphotic zone to the seafloor. Maximum particle flux during the monsoon has been recorded at 180-190 mg m^{-2} day^{-1}, compared to 0.1-60 mg m^{-2} day^{-1} during the intermonsoon (Haake et al. 1993). This suggests that the seasonal deposition of phytodetritus is inevitable and that a flux event occurred at some point during the SW monsoon of 2003, prior to the second sampling campaign (CD150/151). Unfortunately, there is no direct evidence for a depositional event occurring during the SW monsoon, since there were no sediment traps to record the levels of organic matter flux to the seafloor. However, a range of data, including analyses of the sediment biochemistry during each season, provide evidence supporting the idea that phytodetritus was deposited on the seafloor as a result of high productivity associated with the SW monsoon.

Although there was no measurable change in the percentage of organic carbon in the sediments (% Corg) between seasons (Table 3.1), carbohydrates and lipids did show an increase in concentrations after the SW monsoon (R. Jeffreys, C. Woulds, pers.

comm.). During the spring intermonsoon, the average sediment surface lipid concentrations (and the proportion of polyunsaturated fatty acids) at 140 m and 300 m were low. Lipids and in particular PUFAs serve as bioindicators for the quality and freshness of organic matter (Suhr and Pond 2006). Therefore the low concentrations during the spring intermonsoon indicate that organic matter at the sediment surface was relatively refractory (degraded) (R. Jeffreys, pers. comm.). Following the SW monsoon, an increase in the average quantity of surface sediment lipids and polyunsaturated fatty acids (PUFAs) was observed at 140 m and 300 m (R. Jeffreys unpub. data), reflecting an increase of labile organic matter on the sediment surface. In addition, pigment concentration (µg / g dry sediment) increased substantially at the 300-m site following the SW monsoon (Table 3.1). Both of these observations are consistent with the recent deposition of phytodetritus on the seafloor.

3.2.1.3 The benthic environment

The following section describes the benthic environment and fauna at the two main sites (140 m and 300 m) in the upper part of the Pakistan Margin OMZ during the spring intermonoson (March-May 2003) and SW monsoon (August-October 2003) seasons. Table 3.1 summarises some environmental conditions and faunal trends across the OMZ during 2003.

140 m

During the spring intermonsoon, the 140-m station was positioned above the OMZ and bottom water was fully oxygenated with oxygen concentrations of 2.05 mll^{-1}. Following the SW monsoon, bottom-water oxygen concentrations at the 140-m site were substantially reduced to 0.11mll^{-1} as a result of the upward expansion of the OMZ. As a result, the continental shelf between c. 80 m and c. 150 m experienced an extreme seasonal shift of bottom-water oxygen concentration from an oxygenated environment (O_2 = 2.05 mll^{-1}) to a hypoxic environment (O_2 = 0.11 mll^{-1})

between the spring intermonsoon (March – May 2003) and the SW monsoon (August – October 2003) seasons. Bottom water temperature decreased from 23ºC to 18.5ºC over the same period, probably a result of surface water cooling resulting from monsoonal winds (Bett et al. 2003a; 2003b). Salinity was relatively stable between the seasons sampled (36.6 and 36.1 during the spring intermonsoon and following the SW monsoon respectively) (CD145, CD150 data, Bett 2003a; Bett 2003b). The slightly higher values during the spring intermonsoon were probably the result of the deepening of the warm, saline mixed layer to c. 180 m during this season. However, salinity levels did not drop at 140 m following the SW monsoon, despite an upwards shift of cooler, fresher waters impinging on the 140 m site and the consequent thinning of the mixed layer (T. Brand, pers. comm.).

Table 3.1 A summary of environmental features of sampled sites along the Pakistan continental margin at four sites during the spring intermonsoon (March-May 2003) and following the SW monsoon (August-October 2003). Laminations (a) = irregular, Laminations (b) = faint. Sites marked with an asterisk (140 m and 300 m) are investigated in this study. ND = No data. Adapted from Woulds et al. (in prep).

Station Depth (m)	Temp. (ºC)	Dissolved O_2	% Corg	OM Quality (DI)	Pigment Concentration (μg / g dry sed)	Macrofaunal Biomass g(wet) m-2	Sediment
Spring intermonsoon (2003)							
*140m	22.5	2.05	1.4 ± 0.0	ND	7.7 ± 0.7	9.2 ± n/a	bioturbated
*300m	15.5	0.1	2.3 ± 0.1	ND	29.0 ± 6.2	0.02 ± 0.02	laminations (a)
940m	9	0.13	3.2 ± 0.1	ND	25.5 ± 3.5	62 ± 45	laminations (b)
1850m	3.5	1.78	1.1 ± 0.2	ND	0.8 ± 0.5	9 ± 15	bioturbated
SW monsoon (2003)							
*140m	18.2	0.11	1.4 ± 0.0	-0.74 ± 0.03	6.2 ± 1.1	4.6 ± 2.2	bioturbated
*300m	14.8	0.11	2.5 ± 0.1	-0.17 ± 0.10	40.4 ± 17.8	0.01 ± 0.02	laminations (a)
940m	9.3	0.17	3.2 ± 0.2	-0.21 ± 0.05	28.1 ± 2.6	45.7 ± 0.02	laminations (b)
1850m	3.7	1.65	1.0 ± 0.1	-0.8 ± 0.14	1.2 ± 1.0	1.8 ± 0.9	bioturbated

300 m

The 300-m site exhibited a much more stable bottom-water chemistry over the two seasons sampled compared to 140m. Bottom-water oxygen concentrations were consistently ~ 0.11 mll^{-1}. Bottom-water temperature and salinity were lower than at 140 m and, in contrast to the 140-m site, remained relatively constant with temperature ranging between 14 and 14.5ºC and salinity at c. 36.0 over both seasons (data from CD145, Bett et al. 2003a).

3.2.1.4 Sediments and fauna at 140 m and 300 m: a seasonal comparison

140 m

Sediments at 140 m were muddy and fully bioturbated but with a fine burrow network present to 7.5 cm depth and some tube structures up to 1.5 mm in diameter visible in X-radiographs, reflecting the presence of sediment–dwelling benthos (Figure 3.5). Little change was observed in the overall sediment appearance between the seasons and sediments remained relatively well-burrowed and homogeneous.

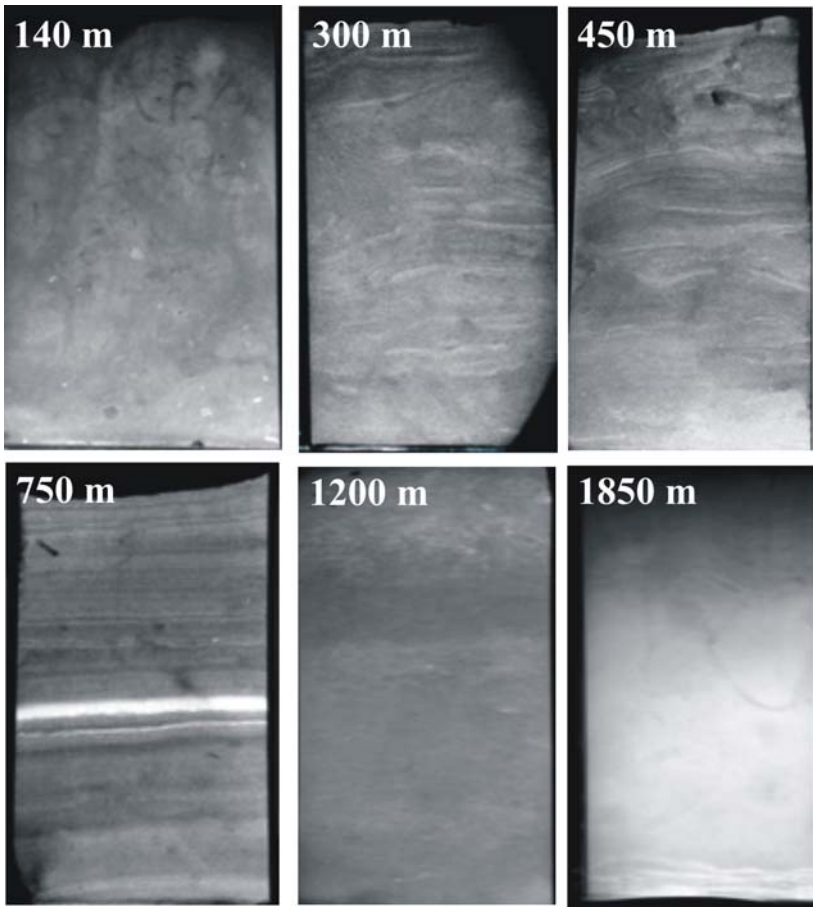
Few metazoan meiofauna were observed in the > 300 µm residues at 140 m. Metazoan macrofauna were relatively abundant at 140 m (biomass = 9.2 g(wet) m^{-2}) during the spring intermonsoon season when bottom-water oxygen levels were high (O_2 = 2.05 mll^{-1}) (Levin 2003a; 2003b) (Table 3.1). Following the SW monsoon and the associated drop in bottom-water oxygen concentration to 0.11 mll^{-1}, metazoan macrofauna declined in abundance (biomass = 4.6 g (wet) m^{-2}) (Table 3.1). The metazoan macrofauna at 140 m during both seasons was dominated by polychaetes. Foraminifera were also abundant at this site during both seasons sampled.

300 m

X-radiographs of cores from 300 m exhibited fine, irregular, and curved (concave downwards) sediment laminations to at least 12 cm depth (Figure 3.5) during both seasons. Clear colour zonation was evident in cores, with an upper 1-2 cm layer of flocculent, brown, soupy sediment present above olive homogeneous sediment.

There was a single or double layer of orange Fe/Mn oxide within a few mm of the sediment surface. In contrast to the 140-m site, metazoan macrofauna were nearly absent at the 300-m site (biomass = 0.02 g(wet)m^{-2} during the spring intermonsoon and 0.01 g(wet)m^{-2} during the SW monsoon). (Levin 2003a) (Table 3.1). Foraminifera dominated the eukaryotic biomass in the > 300 μm residues.

Figure 3.5 X-radiographs (courtesy of Lisa Levin) of sediments across the Pakistan continental margin OMZ (c. 180 – 1300 m) during the spring intermonsoon (April 2003). During both seasons, fully bioturbated sediments are found above at 140 m and below 1000 m. Laminations were present between 300 m and 1000 m. At 300 m, the laminations were irregular and curved but between 600 m and 800 m, laminations were uniform and unbroken with very few biogenic features. (Levin 2003a, Whitcraft 2003)



4 The impact of the Pakistan Margin OMZ upper boundary on live macrofaunal (> 300 µm) benthic Foraminifera and metazoans: a seasonal comparison

4.1 Introduction

The Arabian Sea is as an area of unusually high biogeochemical activity extending from the air-sea interface to water column fluxes and the benthic environment. The magnitude of these processes establish the Arabian Sea as having a global significance for major elemental cycles such as carbon, nitrogen and phosphorous. The monsoonal regime and the associated development of a basin-wide mid-water (approx. 150 – 1200 m) oxygen minimum zone (OMZ) have created an area with highly dynamic biogeochemical processes, many of which display a unique semiannual cycle. The continental margins form a natural laboratory where biological and geological processes can be investigated across strong environmental gradients, for example, of oxygen and organic matter flux (see Chapter 3 for a more detailed account of the locality). Assessing seafloor processes within the Arabian Sea OMZ is integral to our understanding of the role of the Arabian Sea in the global carbon cycle and the importance of this relatively small, but biogeochemically active oceanic region. However, few studies have focused primarily on the benthic environment of the Arabian Sea.

Previous studies of the living (Rose Bengal stained) foraminiferal faunas from the Arabian Sea include those of Zobel (1973), Burmistrova (1969; 1976; 1977), Gupta (1994) and Kurbjeweit et al. (2000). In a recent study, Heinz and Hemleben (2006) compared the influence of the northeast monsoon on the living benthic foraminiferal assemblage from the western and southern parts of the Arabian Sea. Studies focusing on the northwestern Arabian Sea (Oman margin) include Stubbings (1939), Hermelin and Shimmield (1990), Naidu and Malmgren (1995) and Gooday et al. (2000a). The benthic foraminiferal assemblages from the northeast Arabian Sea (Pakistan margin)

are less well known. The only studies are those of Jannink et al. (1998), Maas (2000), Erbacher and Nelskamp (2006), and Schumacher et al. (2006). Many of the studies mentioned above have focused on single sample transects across the OMZ, or on the mid-lower parts of the OMZ and abyssal regions of the Arabian Sea. There has been little emphasis to date on the benthic fauna in the upper part and upper boundary of the OMZ (≤ 300 m).

The aim of this study was to analyse "complete" (i.e. including all taxonomic components) rose-Bengal-stained ('live') benthic foraminiferal assemblages in low-oxygen habitats on the Pakistan margin and to compare the abundance of foraminiferans and metazoans. Soft-walled monothalamous (allogromiid and saccamminid) taxa may be an important constituent of benthic communities, but are frequently overlooked (Larkin and Gooday 2004). The assemblages come from sites within the core (300-m water depth) and at the upper border (140 m) of the OMZ.

4.2 Materials and Methods

4.2.1 Sample collection

To assess the influence of oxygen and organic enrichment on the diversity and abundance of the macrofaunal (>300 μm) benthic community (Foraminifera and Metazoa), two contrasting sites (c.140 m and c.300 m) within the upper part of the Pakistan margin OMZ were sampled in 2003 during two different seasons; the spring intermonsoon (March-May 2003, cruises CD145 and CD146) and the period directly following the SW summer monsoon (August-October 2003, cruises CD150 and CD151). I refer to the two seasons as spring intermonsoon and SW monsoon. Chapter 3 describes the Pakistan margin locality in more detail (Figure 3.3a,b). The two sites were chosen because they exhibit contrasting oxygen regimes. The 140-m site was seasonally oxygenated with bottom-water oxygen concentrations = 2.05 ml^{-1} during the spring intermonsoon (April 2003), but it became hypoxic (O_2 = 0.11 ml^{-1}) during the SW monsoon (October 2003) as a result of an upward expansion of the

OMZ across the continental shelf. In comparison, the 300-m site was permanently hypoxic, with bottom water oxygen concentrations consistently ~ 0.11 ml^{-1}. I focus on the > 300 μm fraction for two reasons. First, because this coarse fraction can be analysed relatively quickly, making it possible to study replicate samples to 5 cm depth in the sediment in order to obtain an accurate estimate of species numbers and abundances, allowing for spatial variability and patchy distributions. Second, to facilitate comparison with the metazoan macrofauna.

Sediment cores for the analysis of foraminiferal community abundance and diversity were obtained using a hydraulically-dampened Barnett-Watson multicorer (Barnett et al. 1984), which is able to recover cores (25.5 cm^2 cross-sectional area) in which the sediment surface is virtually undisturbed. Four replicate multicores were collected from each site during each season (Table 4.1). The top 0-1 cm of the core was sliced into 0.5 cm thick layers and then the core was sliced into 1–cm thick layers to a depth of 5 cm. Each layer was fixed in 10% formalin (= 4 % formaldehyde solution) buffered with sodium borate (borax) for optimum preservation. Replicate samples from separate multicore deployments were taken at each site in order to quantify small-scale variability.

4.2.2 Laboratory processing

Sediment was sieved wet on a 300 μm screen and the sieved residue stained overnight using rose Bengal, following the recipe described by Thiel (1966) (1g rose Bengal in 1L of tap water containing 10g of phenol). Samples were then sorted in filtered (25 μm mesh) water for 'live' (stained) foraminiferans and metazoans using water under a low-power binocular dissecting microscope. The commonly used criterion for judging if a species is 'live' when using the rose-Bengal staining, is that at least one chamber should contain brightened cytoplasm (Walton 1952). However, in this study, stricter criteria were adopted. Only those individuals in which most of the test, and its constituent chambers (if present) were full of rose Bengal stained or unstained green cytoplasm were regarded as having been alive when collected.

Table 4.1 List of samples from sites A140 (c. 140 m water depth) and A300 (c. 300 m water depth) analysed from the Pakistan margin in 2003 for macrofaunal (>300 μm) Foraminifera and Metazoa (in chronological order of collection).

Cruise	Station	Series	Date	Water depth (m)	Latitude °N	Longitude °E
CD145	55803	#5	21.03.03	306	23°20.88'	66°56.78'
CD146	55901	#5	21.04.03	134	23°27.75'	66°71.25'
CD146		#7	21.04.03	134	23°28.11'	66°70.91'
CD146		#11	22.04.03	135.5	23°27.68'	66°70.50'
CD146		#13	23.04.03	133	23°27.85'	66°71.56'
CD146	55902	#5	25.04.03	304	23°20.53'	66°56.63'
CD146		#12	27.04.03	298.5	23°21.23'	66°56.50'
CD146		#26	01.05.03	309	23°21.01'	66°56.75'
CD150	56033	#1	01.09.03	134	23°28.06'	66°71.26'
CD150	56036	#4	02.09.03	137	23°26.60'	66°70.96'
CD150	56037	#1	02.09.03	306	23°20.70'	66°56.88'
CD151	56101	#7	20.09.03	132.5	23°28.01'	66°71.18'
CD151	56101	#27	24.09.03	133	23°28.00'	66°71.18'
CD151	56105	#7	28.09.03	302.5	23°20.76'	66°56.69'
CD151	56107	#6	30.09.03	298	23°20.80'	66°56.68'
CD151	56115	#2	04.10.03	299	23°20.80'	66°56.63'

This strict 'live recognition' criterion was particularly important in the Pakistan margin study area since low-oxygen environments are believed to display lower rates of cytoplasmic decay than well-oxygenated settings (Jorissen 1999). This could result in the cytoplasm of some dead individuals persisting and staining after death, leading to the overestimation of 'live' individuals (Lutze and Altenbach 1991; Murray and Bowser 2000).

The adoption of this strict criterion was also important in the case of calcareous taxa with a good preservation potential. The tests of dead, calcareous individuals containing cytoplasm, are more likely to persist in the sediment than agglutinated

taxa such as *Reophax* spp. and soft-shelled forms such as saccamminids and allogromiids which are particularly delicate and prone to decay at a faster rate once dead. Therefore, different criteria were used for assessing these delicate groups. In *Reophax* spp., the cytoplasm was more dispersed, even in individuals that were judged to be 'live'. The criteron for assessing 'live' individuals was therefore adjusted to include those individuals with one or more chambers containing a clearly-stained cytoplasmic body. In species where no stain was visible from the exterior, even at the aperture, the test was carefully broken open in order to establish the presence or absence of stained cytoplasm. In soft-shelled taxa such as allogromiids, the protoplasm often contained numerous stercomata (waste pellets) and sediment grains. These did not stain as clearly as calcareous species. However, because of the delicate nature of the organic or agglutinated wall, any intact soft-shelled individual that displayed some degree of staining, was recorded as live. In some instances, stained specimens were inspected more closely by placing them in anhydrous glycerol on a cavity slide and observing the cytoplasm under an Olympus BH-2 compound microscope.

Specimens were identified to the lowest possible taxon, and where necessary described, and then stored using one of two methods. 'Live' calcareous and agglutinated species were mounted dry on micropalaeontological slides and soft-walled monothalamous foraminiferans were stored in glycerol on open cavity slides. Metazoa and larger Foraminifera such as *Pelosina* sp. and some delicate soft-walled forms were stored in glass vials in 10% formalin.

4.2.3 Species documentation

Taxonomic notes and light or SEM photographs of the species recognised in this study are given in Appendix A of this thesis.

4.2.3.1 Photography

Photographs of live specimens were taken at sea, using a Nikon Coolpix MH-53 digital camera and a Nikon Coolpix microcam relay lens 22-701 attached to a Leica MZ75 microscope. In the laboratory, digital photographs were taken of stained specimens, using the same camera attached to an Olympus BH-2 compound microscope, equipped with Nomarski interference and Phase contrast optics.

4.2.3.2 Scanning Electron Microscopy

Scanning Electron Microscopy (SEM) was conducted on representative specimens of the most common species and other selected species. Specimens were cleaned with filtered water and a brush under a binocular microscope, air dried, mounted on adhesive carbon films on aluminium stubs and then gold coated using a Hummer VI-A Sputter Coater. Once prepared, the stubs with gold-coated specimens were inserted into a LEO 1450 VP SEM and images were obtained of whole specimens and of particular features of interest, such as the wall, the pores, or the aperture.

4.2.4 Vertical distribution analysis

The vertical distribution of the live Foraminifera between 0-5 cm was assessed using the Average Living Depth (ALDx) formula as shown below (Jorissen et al. 1995). For both A140 and A300 sites, ALD_5 was calculated for the entire live assemblage and for the top 5 ranking species in both seasons.

$$ALD_x = \sum_{I = 0,x} (n_i \text{ x } D_i) / N$$

x = lower boundary of the deepest sample (5cm in this present study)

n_i = number of individuals in interval i

D_i = midpoint of sample interval I

N = total number of individuals for all levels

4.2.5 Statistical Analyses

The PRIMER statistical software package (v.5.2.1) (Carr 2001; Clarke and Warwick 1994) was used to calculate diversity measures including species richness (S), the Fisher Alpha Index (α) (Fisher et al. 1943), Shannon–Wiener Index ($H'\log_e$) (Shannon 1948) and Pielou's eveness (J') indices, Rank 1 Dominance (R1D) and rarefied species numbers ($ES_{(n)}$). Multivariate statistics were used to analyse the faunal data in a number of ways; Bray-Curtis percentage similarity and 1-way analysis of similarity (ANOSIM) were applied to compare the total foraminiferal abundance between replicate samples from the two seasons and sites. Non-metric Multi-Dimensional scaling (MDS) ordination and 1-way analysis of similarity (ANOSIM) were used to determine the similarity (patterns and significance respectively) of the foraminiferal species composition of the topmost two sediment layers (0-0.5 and 0.5-1 cm) at the two sites and seasons sampled (Clarke and Warwick 1994). The ANOSIM test was not carried out on all deeper sediment layers (1-5 cm) because the lack of live Foraminifera in some replicate samples resulted in too few permutations for the tests to be powerful enough. All multivariate statistics were based on similarity matrices calculated as Bray-Curtis similarity on square-root transformed data. Results of statistical analyses are displayed in Appendix D.

4.3 Results and Discussion

Environmental data for the Pakistan margin study sites are summarised in Table 3.1, Chapter 3. Results and discussion in this chapter are presented in three main sections. Firstly, a faunal analysis of the macrofaunal (> 300 μm) Foraminifera is presented for the 140-m site followed by the 300-m site. Secondly, a seasonal comparison of the foraminiferal assemblage at these two sites is presented. Thirdly, metazoan macrofauna (both meiofaunal and macrofaunal taxa) data are presented for the 140-m and 300-m sites. In all sections, abundance data for Foraminifera and Metazoa are presented as counts of complete (unfragmented) live individuals from the actual sample (25.5 cm^2) and normalised to live individuals per 10 cm^2 for comparison with previous benthic foraminiferal studies and with metazoan data. Total live abundance data are presented as individual vertical sediment layers.

4.3.1 The 140-m site

4.3.1.1 Abundance

The abundance of live macrofaunal (> 300 μm) benthic Foraminifera at 140 m in the total sample (0-5 cm) is shown in Table 4.2 (see Appendix C for full abundance data, all vertical sediment layers). Live abundances increased from the intermonsoon season to the SW monsoon season. The number of mean live Foraminifera increased significantly ($P<0.05$, 2-sample t-test) from 189 individuals per 25.5 cm^2 (74 per 10 cm^2) to 390 individuals per 25.5 cm^2 (153 per 10 cm^2) following the SW summer monsoon. Abundance of live macrofaunal Foraminifera at 140 m in the upper 0-1cm of the sediment is shown in Table 4.3. Over 89% of all living Foraminifera were present in the surface 1 cm of the sediment during both seasons and the total number of live individuals in the 0-1 cm fraction was therefore very similar to the 0-5 cm, with 169 individuals per 25.5cm^2 (66 per 10 cm^2) during the spring intermonsoon season and 377 per 25.5cm^2 (148 per 10 cm^2) during the SW monsoon season.

Table 4.2 140-m site. Abundances of complete (unfragmented) living macrofaunal (>300µm) Foraminifera in the 0-5 cm sediment layer. Data are presented for 4 replicates in each season sampled; spring intermonsoon (April 2003) and SW monsoon (October 2003). *Mean = average of 4 replicates. Data are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2.

	spring intermonsoon					SW monsoon				
	55901					56		56101		
	#5	#7	#11	#13	*Mean	033#1	036#4	#7	#27	*Mean
monothalamous										
Allogromiid sp. 1	2	0	0	1	0.8	3	1	0	0	1.0
Allogromiid sp. 5	0	1	0	0	0.3	1	0	0	0	0.3
Bathysiphon sp. nov. 1	1	3	0	3	1.8	0	0	0	0	0.0
Hyperammina sp. nov. 1	1	3	3	0	1.8	1	4	3	3	2.8
Lagenammina arenulata	2	0	5	0	1.8	0	2	0	7	2.3
Psammosphaerid sp. 1	1	1	0	3	1.3	1	0	0	0	0.3
Pelosina sp. 1	5	2	1	1	2.3	0	2	5	0	1.8
Saccamminid sp. 1	0	2	0	1	0.8	0	4	0	0	1.0
other agglutinated										
Ammodiscus aff. *cretaceus*	1	1	2	0	1.0	0	1	0	0	0.3
Reophax bilocularis	8	7	2	6	5.8	1	2	1	1	1.3
Reophax sp.1	6	1	0	1	2.0	0	0	1	3	1.0
calcareous										
Amphicoryna aff. *scalaris*	0	0	1	4	1.3	0	0	0	0	0.0
Baggina philippinensis	2	0	0	0	0.5	0	0	0	0	0.0
Bolivina aff. *dilatata*	0	1	3	6	2.5	15	23	31	29	24.5
Cancris auriculus	28	9	8	11	14.0	40	20	70	36	41.5
Cassidulina laevigata	0	1	0	5	1.5	0	0	0	2	0.5
Cibicides sp. 1	2	3	10	4	4.8	0	0	6	0	1.5
Dentalina aff. *flintii*	0	0	1	0	0.3	0	0	1	0	0.3
Globobulimina cf. *G. pyrula*	8	2	3	10	5.8	1	0	11	2	3.5
Laevidentalina aphelis	0	1	1	0	0.5	0	1	2	0	0.8
Lenticulina aff. *iota*	1	0	0	2	0.8	0	2	0	0	0.5
Neolenticulina variabilis	1	1	0	0	0.5	0	1	0	0	0.3
Nodosaria aff. *pyrula*	1	0	0	0	0.3	0	0	0	0	0.0
Quinqueloculina aff. *venusta*	0	0	0	0	0.0	0	1	0	2	0.8
Saidovina amygdalaeformis	0	0	0	0	0.0	0	1	10	1	3.0
Saracenaria italica	0	0	1	0	0.3	0	0	1	0	0.3
Uvigerina ex. gr. *semiornata*	178	120	89	161	137	239	265	306	395	301
Indeterminate attached	0	0	1	0	0.3	0	0	0	0	0.0
% *Uvigerina*	72	75	68	74	72	79	80	68	82	77
Total monothalamous	12	12	9	9	10.5	6	13	8	10	9.3
Total other agglutinated	15	9	4	7	8.8	1	3	2	4	2.5
Total calcareous	221	138	118	203	170	295	314	438	467	378.5
Total live species	15	16	14	15	-	9	14	14	11	-
[1]Total inds. per 25.5 cm^2	248	159	131	219	189	302	330	448	481	390
[2]Total inds. per 10 cm^2	97	62	51	86	74	118	129	176	189	153

Table 4.3 140-m site. Abundances of complete (unfragmented) living macrofaunal (>300µm) Foraminifera in the 0-1 cm sediment layer. Data are presented for 4 replicates in each season sampled; spring intermonsoon (April 2003) and SW monsoon (October 2003). *Mean = average of 4 replicates. Data are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2.

	spring intermonsoon					SW monsoon				
	55901					56		56101		
	#5	#7	#11	#13	*Mean	033#1	036#4	#7	#27	*Mean
monothalamous										
Allogromiid sp. 1	2	0	0	1	0.8	3	1	0	0	1.0
Allogromiid sp. 5	0	1	0	0	0.3	1	0	0	0	0.3
Bathysiphon sp. nov. 1	1	3	0	3	1.8	0	0	0	0	0.0
Hyperammina sp. nov. 1	1	3	3	0	1.8	1	4	3	3	2.8
Lagenammina arenulata	2	0	5	0	1.8	0	2	0	7	2.3
Psammosphaerid sp. 1	1	1	0	3	1.3	1	0	0	0	0.3
Pelosina sp. 1	5	2	1	1	2.3	0	2	5	0	1.8
Saccamminid sp. 1	0	2	0	1	0.8	0	3	0	0	0.8
other agglutinated										
Ammodiscus aff. *cretaceus*	1	1	2	0	1.0	0	1	0	0	0.3
Reophax bilocularis	5	5	2	6	4.5	1	2	1	1	1.3
Reophax sp.1	6	1	0	1	2.0	0	0	1	3	1.0
calcareous										
Amphicoryna aff. *scalaris*	0	0	1	4	1.3	0	0	0	0	0.0
Baggina philippinensis	2	0	0	0	0.5	0	0	0	0	0.0
Bolivina aff. *dilatata*	0	1	3	6	2.5	15	23	31	29	24.5
Cancris auriculus	24	8	3	11	11.5	40	20	59	36	38.8
Cassidulina laevigata	0	1	0	5	1.5	0	0	0	2	0.5
Cibicides sp. 1	2	3	9	4	4.5	0	0	6	0	1.5
Dentalina aff. *flintii*	0	0	1	0	0.3	0	0	1	0	0.3
Globobulimina cf. *G. pyrula*	7	2	2	8	4.8	1	0	6	2	2.3
Laevidentalina aphelis	0	1	1	0	0.5	0	1	2	0	0.8
Lenticulina aff. *iota*	1	0	0	2	0.8	0	2	0	0	0.5
Neolenticulina variabilis	1	1	0	0	0.5	0	1	0	0	0.3
Nodosaria aff. *pyrula*	1	0	0	0	0.3	0	0	0	0	0.0
Quinqueloculina aff. *venusta*	0	0	0	0	0.0	0	1	0	2	0.8
Saidovina amygdalaeformis	0	0	0	0	0.0	0	1	8	1	2.5
Saracenaria italica	0	0	1	0	0.3	0	0	1	0	0.3
Uvigerina ex. gr. *semiornata*	154	104	78	149	121	239	263	273	394	292
Indeterminate attached	0	0	1	0	0.3	0	0	0	0	0.0
% *Uvigerina*	71	74	69	73	72	79	80	69	82	77
Total monothalamous	12	12	9	9	10.5	6	12	8	10	9.0
Total other agglutinated	12	7	4	7	7.5	1	3	2	4	2.5
Total calcareous	192	121	100	189	151	295	312	387	466	365
Total live species	15	16	15	15	-	9	15	13	11	-
[1]Total inds. per 25.5 cm^2	216	140	113	205	169	302	327	397	480	377
[2]Total inds. per 10 cm^2	85	55	44	80	66	118	128	156	188	148

4.3.1.2 Taxonomic composition

Major taxa

The foraminiferal assemblage at 140 m was dominated by calcareous taxa in both the 0-5 cm and the 0-1 cm sediment layers (Figure 4.1). The percentage of calcareous forms in the 0-5 cm live assemblage increased from 89% during the intermonsoon to 97% following the SW monsoon. Buliminids were the dominant group, comprising 76% (spring intermonsoon) and 85% (SW monsoon) of live individuals in the 0-5 cm layer. The increase in abundance following the SW monsoon was unique to the buliminids and all other foraminiferal groups declined in abundance from the intermonsoon to the monsoon- influenced seasons.

Within the 0-1 cm layer, the dominance of calcareous forms, was even more pronounced. Between the intermonsoon and SW monsoon seasons, the percentage increased from 89% to 96%, of which buliminids comprised 83% to 95% respectively. The remaining assemblage during the intermonsoon season included other calcareous Foraminifera (6%), monothalamous (6%) and other agglutinated (5%) taxa. Following the SW summer monsoon, the dominance of buliminids was even more apparent in the 0-1cm sediment layer, with 95% of the live foraminiferal individuals belonging to this group. The other groups together composed only 5% of the assemblage (Figure 4.1).

Species

A total of 29 species (>300 μm) was recognized at 140 m; 26 occurred in samples collected during the spring intermonsoon season and 23 species occurred in samples collected following the SW monsoon (see Plates 1-7, Appendix A for SEM and light photographs of all species). In each case, the majority, 15 and 13 species respectively, were calcareous. The top 10 ranked species from both seasons were also dominated by calcareous forms (Table 4.4), with 5 calcareous species in the top-10-ranked species during the intermonsoon and 6 during the monsoon season. Five species were ranked in the top 10 in both seasons and 3 of these species, *Uvigerina* ex. gr. *semiornata*, *Cancris auriculus,* and *Bolivina* aff. *dilatata*, increased

significantly (P<0.05, 2-sample t-test) in absolute and percentage abundance following the SW summer monsoon.

Figure 4.1 140-m site. Percentage abundance of major foraminiferal groups in the 0-5 cm and 0-1 cm sediment layers (live assemblage; > 300µm fraction). Data are mean percentage abundances (4 replicate samples per season). N = Mean live abundance in each sediment layer shown.

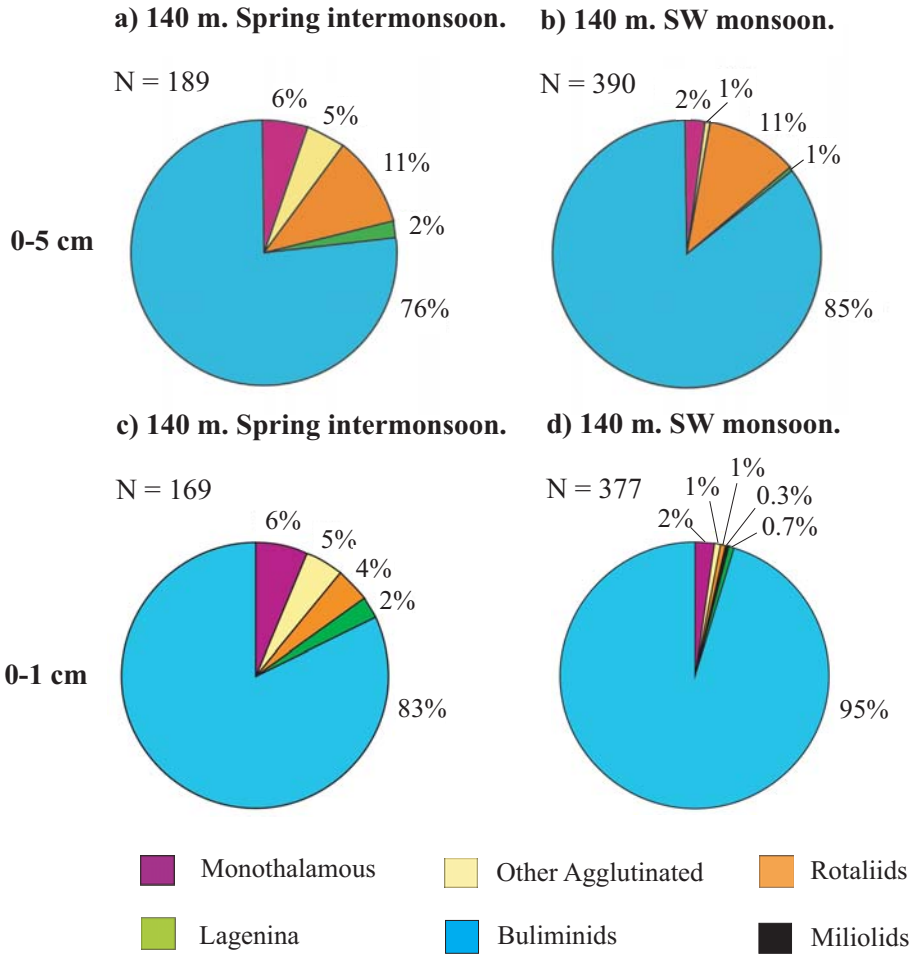


Table 4.4 140-m site. Abundance of the top-10-ranked macrofaunal (>300µm) foraminiferal species in the 0-5 cm sediment layer during a) spring intermonsoon (April 2003), b) SW monsoon (October 2003). Data are given as *Mean = Average total live individuals from 4 replicate samples (25.5 cm^2) and as percentage abundance based on mean data. Species occurring in the top 10 in both seasons are marked with an *. Note the dominance of calcareous forms (underlined) in both seasons sampled.

a) 140 m. Spring intermonsoon.

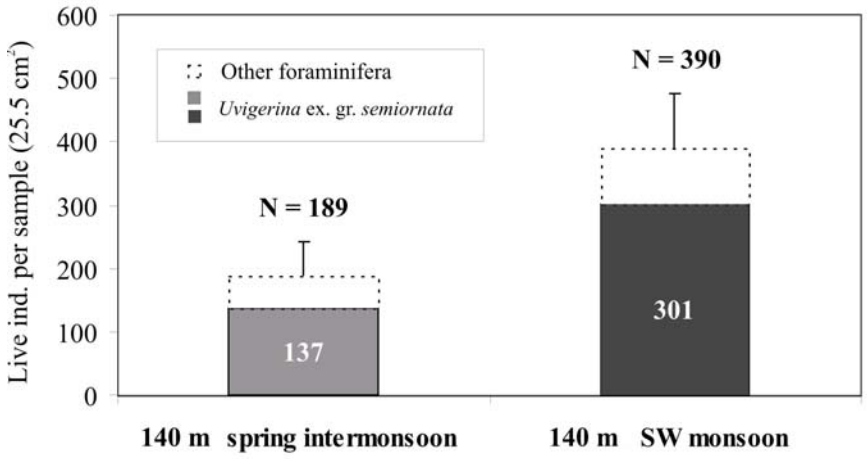
Rank	Top 10 ranked Foraminifera (> 300 µm)	*Mean	Abundance (%)
1	*Uvigerina* ex. gr. *semiornata**	137	72.4
2	*Cancris auriculus**	14	7.4
3	*Reophax bilocularis* *	6	3.0
4	*Globobulimina* cf. *G. pyrula**	6	3.0
5	*Cibicides* sp. 1*	5	2.5
6	*Bolivina* aff. *dilatata**	3	1.3
7	*Pelosina* sp. 1*	2	1.2
8	*Reophax* sp.1	2	1.1
9	*Bathysiphon* sp. nov. 1*	2	0.9
10	*Hyperammina* sp. nov. 1*	2	0.9
	Total live top 10 ranked species (sample^{-1})	178	93.8
	Total live Foraminifera (sample^{-1})	189	-
	Total live species	26	-

b) 140 m. SW monsoon.

Rank	Top 10 ranked Foraminifera (> 300 µm)	*2Mean	Abundance (%)
1	*Uvigerina* ex. gr. *semiornata**	301	77.2
2	*Cancris auriculus**	42	10.6
3	*Bolivina* aff. *dilatata**	25	6.3
4	*Globobulimina* cf. *G. pyrula**	4	0.9
5	*Saidovina amygdalaeformis*	3	0.8
6	*Hyperammina* sp. nov. 1*	3	0.7
7	*Lagenammina arenulata*	2	0.6
8	*Pelosina* sp. 1*	2	0.4
9	*Cibicides* sp. 1*	2	0.4
10	*Reophax bilocularis**	1	0.3
	Total live top 10 ranked species (sample^{-1})	383	98.1
	Total live Foraminifera (sample^{-1})	390	-
	Total live species	23	-

The buliminid *Uvigerina* ex. gr. *semiornata* was the dominant foraminiferal species in the live assemblage at 140 m (72.4% of all live specimens in the intermonsoon samples and 77.2% in the monsoon samples). This species displayed the largest increase in standing stock between the two seasons sampled, rising from a mean of 137 individuals during the spring intermonsoon, to 301 individuals following the SW monsoon (Figure 4.2).

Figure 4.2 140-m site. Abundances of live *Uvigerina* ex. gr. *semiornata* (white numbers in bars) and other Foraminifera in the 0-5 cm sediment layer during the spring intermonsoon (April 2003) and SW monsoon (October 2003). Data are averages of four replicate samples per season. N = Mean total live individuals (all species) shown for each season sampled. 95% Confidence Intervals are shown.



The rotaliid *Cancris auriculus* was the second-ranked species in both seasons, comprising 7.4% of all live specimens in samples collected from the spring intermonsoon and 10.6% in samples collected following the SW monsoon. The buliminid *Bolivina* aff. *dilatata* was the sixth–ranked species during the intermonsoon season (1.3%), but increased in abundance to become the third–ranked species in the monsoon–influenced season (6.3%). Two other calcareous species, *Globobulimina* cf. *G pyrula* and *Cibicides* sp. 1, were present in the top-10-ranked

species in both seasons, but, unlike the more abundant calcareous forms, both declined in relative abundance from 3% to 0.9% (*Globobulimina* cf. *G. pyrula*) and 2.5% to 0.4% (*Cibicides* sp.1) in the intermonsoon and monsoon samples respectively. Other calcareous species present in the live assemblage were large multichambered lagenina (nodosariids and lenticulinids), the buliminid *Saidovina amydalaeformis*, the rotaliids *Cassidulina laevigata* and *Baggina philippinensis*, a single miliolid species *Quinqueloculina* aff. *venusta* (3 live specimens in the monsoon - influenced season only) and an indeterminate species attached to a live specimen of *Uvigerina* ex. gr *semiornata*.

Soft-shelled Foraminifera (including monothalamous allogromiids and saccamminids) were uncommon, but relatively diverse. Eight species (6 of them undescribed) were recognized in the live assemblage including Psammosphaerid sp. 1, *Lagenammina arenulata*, *Bathysiphon* sp. nov. 1 (found protruding from core surfaces following the SW monsoon), *Hyperammina* sp. nov. 1, two organic-walled allogromiid species, one soft-walled saccamminid species and *Pelosina* sp. (present on core surfaces). *Pelosina* sp. 1 and *Hyperammina* sp. nov. 1 were among the top-10 species during both seasons, comprising between 0.4% and 1.2% of the live assemblage in all samples analysed. Other monothalmous species within the top 10 were *Bathysiphon* sp. nov. 1 (intermonsoon only, 0.9% abundance), and *Lagenammina arenulata* (monsoon only, 0.6% abundance). Two species of the multichambered agglutinated genus *Reophax* were also relatively abundant; *Reophax bilocularis* (abundance; intermonsoon 3%, monsoon 0.3%) and *Reophax* sp. (intermonsoon only, 1.1% abundance). An ammodiscacean, *Ammodiscus* aff. *cretaceus* was also present (4 specimens from the intermonsoon season and 1 specimen from the monsoon season). Despite a slight increase in the mean absolute abundance of some monothalamous forms (e.g. *Hyperammina* sp. nov. 1) between the intermonsoon and monsoon–influenced seasons, all monothalamous and other agglutinated species present among the top-10 ranked species declined in percentage

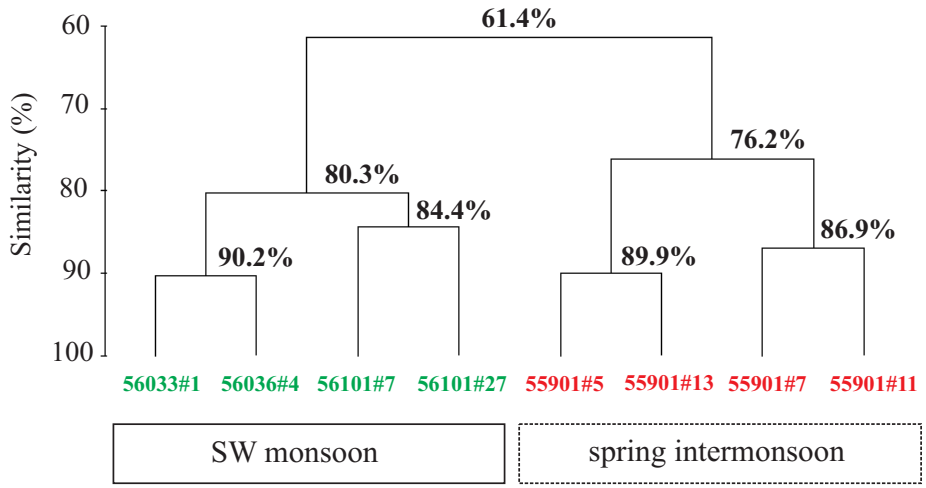
abundance following the SW summer monsoon in both the 0-5 cm and 0-1 cm sediment layers.

4.3.1.3 Multivariate analysis

Cluster analysis

Samples were only 61.4 % similar between the two seasons sampled (cluster analysis) (Figure 4.3), indicating a clear seasonal difference in the foraminiferal standing crop at the 140-m site. Replicate samples from each season displayed clear groupings, with replicate samples from the SW monsoon season displaying a higher percentage of similarity (80.3%) compared to the similarity shared between the spring intermonsoon replicate samples (76.2%).

Figure 4.3 140-m. Cluster analysis (dendrogram) of 0-5 cm. 4 replicate cores per season; spring intermonsoon (red), SW monsoon (green). Based on similarity matrix (Bray-Curtis Similarity) calculated from square-root transformed data (live individuals per sample (25.5 cm^2)).



Multidimensional scaling

Multidimensional scaling (Figure 4.4) calculated on the entire foraminiferal assemblage (0-5 cm layer) and the upper 1 cm layer revealed a clear, significant

(P<3, ANOSIM) seasonal difference between replicate samples. However, there was no clear grouping between the two sediment layers (0-5 cm and 0-1 cm) within each season, indicating a high degree of similarity between the entire foraminiferal assemblage (0-5 cm) and the upper 1 cm layer. Multidimensional scaling was also conducted on the uppermost sediment layers, 0-0.5 cm and 0.5-1 cm (Figure 4.5). During the spring intermonsoon, there was no significant (P > 3, ANOSIM) difference between the foraminiferal assemblage in the 0-0.5 cm layer and the 0.5-1 cm layer, indicating that the Foraminifera within the 0-1 cm layer was relatively homogeneous. This was possibly a result of the oxygenated bottom water at 140 m during the intermonsoon season allowing oxygen to penetrate deeper in the sediment pore water and enabling many foraminiferal species to colonise the entire upper 1cm of the sediment. In contrast, the topmost (0-0.5 and 0.5-1 cm) sediment layers displayed a much clearer separation following the SW monsoon (green symbols), reflecting a significant difference (P < 3, ANOSIM) in the foraminiferal assemblage between the two sediment layers (Figure 4.5). This is likely to be a result of the shift in bottom-water oxygen concentration between the spring intermonsoon (oxic, O_2 = 2.05 mll^{-1}) and the SW monsoon (hypoxic, O_2 = 0.11 mll^{-1}) seasons and resulting changes in the foraminiferal community, including the upwards migration of many species into the upper 0-0.5 cm layer and the corresponding decline in numbers of foraminiferal individuals in the 0.5-1 cm layer.

Replicate samples of the 0-0.5 cm sediment layer grouped together according to season, indicating a difference (although not significant) in the foraminiferal assemblage in the upper 0-0.5 cm layer between the two seasons sampled. In contrast, replicate samples from the 0.5-1 cm sediment layer were much more scattered, indicating greater heterogeneity in the foraminiferal assemblage at this depth, possibly a result of localised differences in oxygen penetration of the sediment controlling the abundance of live Foraminifera below 0.5 cm. There was no significant difference (P > 3, ANOSIM) between the foraminiferal assemblage in the 0.5-1 cm layer between the spring intermonsoon and following the SW monsoon.

Figure 4.4 Multidimensional scaling (MDS) of live Foraminifera (> 300 µm) in 0-5 cm and 0-1 cm sediment layers at 140 m during spring intermonsoon and SW monsoon seasons. SW monsoon samples are circled. Based on a Bray-Curtis Similarity matrix of square-root transformed data (live abundance). Stress = 0.08.

◆ = 0-5 cm, spring intermonsoon ◇ = 0-1 cm, spring intermonsoon

◆ = 0-5 cm, SW monsoon ◇ = 0-1 cm, SW monsoon

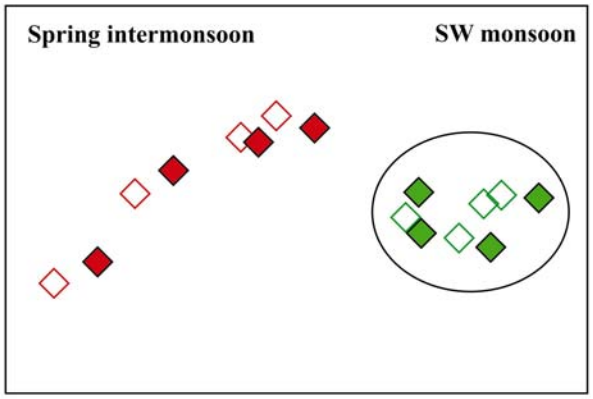
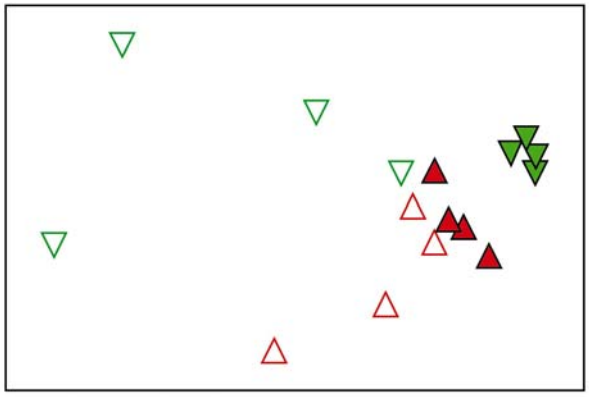


Figure 4.5 Multidimensional scaling (MDS) of live Foraminifera (> 300 µm) in 0-0.5 cm and 0.5–1 cm sediment layers at 140 m during spring intermonsoon and SW monsoon seasons. Based on a Bray-Curtis Similarity matrix of square-root transformed data (live abundance). Stress = 0.08.

▲ = 0-0.5 cm layer, spring intermonsoon; △ = 0.5-1 cm layer, spring intermonsoon;

▼= 0-0.5 cm layer, SW monsoon ▽= 0.5-1 cm layer, SW monsoon



4.3.1.4 Diversity

Diversity parameters and the total number of individuals recognized in all replicate samples from each season are shown in Table 4.5. Within each season, diversity values displayed considerable variation between replicates. Species richness (S) was higher in spring intermonsoon samples (15 to 17 species recognized in each of 4 replicate samples; 26 species total) than in those collected during the SW monsoon season (9-15 species recognized in each of 4 replicate samples; 23 species total). Fisher's α and H' values were also highest in intermonsoon samples and varied between replicates; for example Fisher's α values for the four intermonsoon sample were 4.1, 4.8, 4.4, 3.6 compared to 1.7, 3.2, 2.5, 2.0 for the four monsoon samples.

Table 4.5 140-m site. Diversity data for complete individuals (excluding indeterminate specimens) in the 0-5 cm sediment layer for spring intermonsoon (April 2003) and SW monsoon (October 2003). Data are presented for each of 4 replicates in each season. N = number of live individuals (per 25.5cm^2 sample and per 10cm^2), S = Species richness, Fisher α = Fisher alpha diversity index, H'(loge) = Shannon-Wiener diversity index, $ES_{(n)}$ = expected number of species for n individuals, R1D = Rank 1 dominance, J' = Pielou's evenness.

Station - series	Abundance (N) sample^{-1}	Abundance (N) 10 cm^{-2}	S	Fisher α	H'(loge)	R1D (%)	ES(40)	ES(100)	J'
140 m. Spring intermonsoon.									
55901#5	248	97	17	4.1	1.2	71.8	7.1	11.9	0.4
55901#7	159	62	17	4.8	1.2	75.5	7.9	11.3	0.4
55901#11	131	51	15	4.4	1.4	67.9	8.6	13.5	0.5
55901#13	219	86	15	3.6	1.2	73.5	7.9	13.4	0.4
140 m. SW monsoon.									
56033#1	302	118	9	1.7	0.7	79.1	3.9	5.4	0.3
56036#4	330	129	15	3.2	0.9	80.3	5.3	8.4	0.3
56101#7	448	176	13	2.5	1.1	68.3	5.8	8.2	0.4
56101#27	481	189	11	2.0	0.7	82.1	4.4	6.3	0.3

The values for ES(40) also indicate that diversity was more variable in samples taken during the monsoon–influenced season. Rank 1 dominance ranged from 67.9% to 75.5% during the intermonsoon and 68.3% to 82.1% during the monsoon. The increase in R1D values from intermonsoon to monsoon–influenced seasons, reflected the increased abundance of *Uvigerina* ex. gr. *semiornata*.

4.3.1.5 Vertical distribution patterns

Total live assemblage

The decrease in bottom-water oxygen concentrations at 140m following the SW monsoon was reflected in the vertical distribution of live macrofaunal Foraminifera in a number of ways. During the 2003 spring intermonsoon, the 140-m site was situated above the OMZ and bottom-water oxygen concentrations were 2.05mll^{-1}. Despite this, the ALD_5 was relatively shallow (0.57 cm). Only 11% of all live Foraminifera were found in sediment layers between 1 and 5 cm (Table 4.6 and Figure 4.6). Following the SW summer monsoon and the associated upward expansion of the OMZ to c.80m water depth, bottom-water oxygen concentrations at the 140-m site dropped to 0.11mll^{-1}. The proportion of live Foraminifera found between 1 and 5 cm decreased to only 3.5 % and the ALD_5 decreased to 0.31 cm. The seasonal increase in percentage of live Foraminifera found in the 0-1 cm layer was most apparent in the topmost layer (0-0.5 cm) where it rose from 60.4% to 89.4% after the SW monsoon. The 0.5-1 cm sediment layer actually showed a decline in percentage abundance from 28.7% to 7%.

The main foraminiferal groups

The three main foraminiferal groups, calcareous, monothalamous and other agglutinated forms, displayed different vertical distribution patterns and responses to the seasonal changes in bottom-water oxygen concentration (Table 4.6; Figure 4.6). Calcareous Foraminifera were present in all layers down to 5 cm depth during the spring intermonsoon. However, following the SW monsoon, calcareous forms were found only to a depth of 3 cm. In both seasons, most of the calcareous Foraminifera were found within the upper 1cm of the sediment, increasing from 89.2% of the total

live assemblage in the spring intermonsoon to 97.0% after the SW monsoon. The remaining 3% of live calcareous Foraminifera colonised sediment layers between 1 and 3 cm. The proportion of non-calcareous Foraminifera (monothalamous and other agglutinated) declined in all sediment layers following the SW monsoon. Other agglutinated taxa (multilocular agglutinated forms and ammodiscaceans) displayed a similar trend to calcareous forms. There was a reduction of the maximum colonisation depth from 3 cm during the intermonsoon to 2 cm during the monsoon – influenced seasons. Monothalamous forms maintained a relatively stable vertical distribution pattern between the two seasons, with live specimens found only within the 0-1cm sediment layer and only 1 specimen (of Saccamminid sp. 1) found below the upper 1cm sediment layer (1-2 cm layer, monsoon season).

Table 4.6 140-m site. Mean percentage abundance of live macrofaunal (>300µm) foraminiferal groups at 140m. a) All vertical layers analysed, b) Σ of vertical layers 0-1cm, 1-5cm, 0-5cm. Data are mean values of 4 replicates per season ± 95% Confidence Interval. Underlined data show a significant increase in percentage abundance from intermonsoon to monsoon ($P < 0.05$, student t-test assuming unequal variances). Grey boxes highlight layers where no live Foraminifera are present.

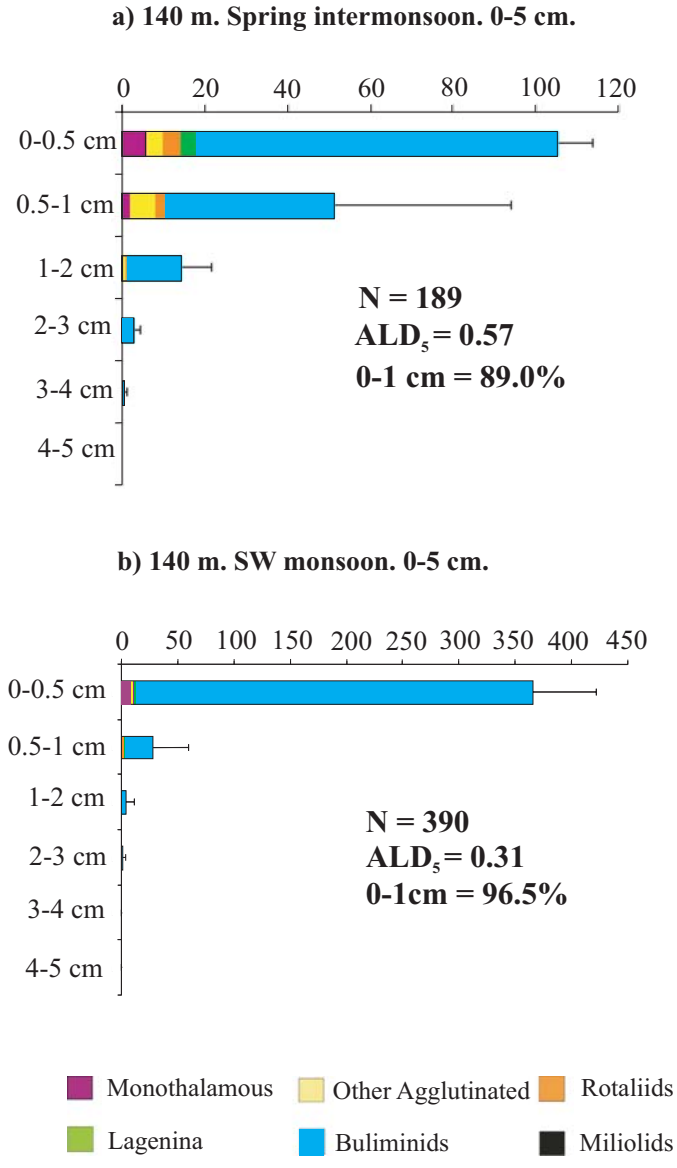
a)

140 m	Mean % Total Live		Mean % calcareous		Mean % other agglutinated		Mean % monothalamous	
	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon
0-0.5	60.4 ± 14.3	89.4 ± 12.2	55.2 ± 11.3	86.7 ± 11.9	1.2 ± 0.7	0.6 ± 0.3	4.0 ± 2.5	2.1 ± 0.6
0.5-1	28.7 ± 15.8	7.0 ± 7.0	24.3 ± 13.9	6.9 ± 7.2	2.8 ± 1.4	0.0 ± 0.0	1.6 ± 1.2	0.2 ± 0.3
1-2	8.7 ± 2.3	1.2 ± 1.6	8.3 ± 2.1	1.0 ± 1.4	0.4 ± 0.6	0.4 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
2-3	1.5 ± 0.6	0.4 ± 0.6	1.2 ± 0.5	0.4 ± 0.6	0.3 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
3-4	0.3 ± 0.4	0.0 ± 0.0	0.3 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
4-5	0.5 ± 1.5	0.0 ± 0.0	0.5 ± 1.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

b)

140 m	Mean % Total Live		Mean % calcareous		Mean % other agglutinated		Mean % monothalamous	
	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon
0-1	89.0 ± 3.3	96.5 ± 5.5	89.2 ± 4.9	97.0 ± 5.2	5.0 ± 0.9	0.6 ± 0.3	5.5 ± 1.6	2.3 ± 0.9
1-5	11.0 ± 3.3	3.5 ± 5.5	10.3 ± 3.1	3.5 ± 5.6	1.7 ± 0.7	0.4 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
0-5	100	100	89.8 ± 2.4	97.0 ± 1.2	4.6 ± 1.6	0.6 ± 0.3	5.5 ± 1.6	2.4 ± 1.0

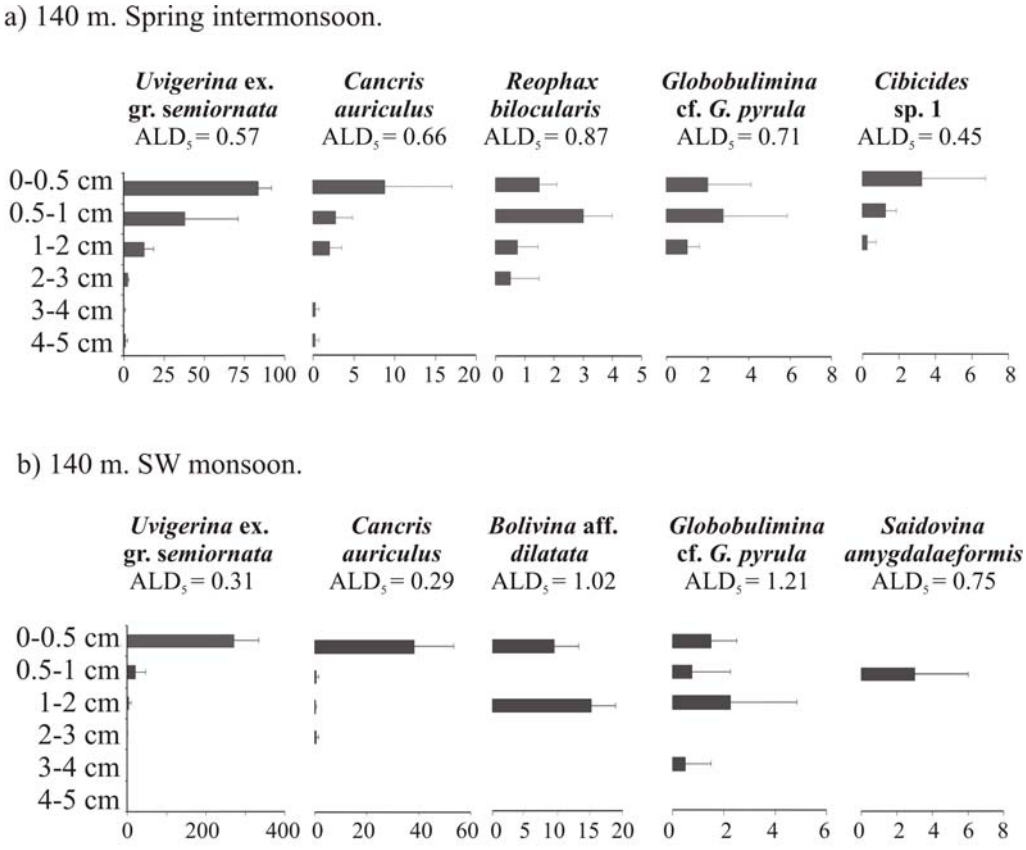
Figure 4.6 140-m site. Vertical distribution of live macrofaunal (>300 µm) Foraminifera within the 0-5 cm layer during both seasons sampled: a) spring intermonsoon (April 2003), b) SW monsoon (October 2003). Data are mean values of total live individuals from 4 replicates (25.5 cm^2) per season and are presented for major foraminiferal groups. 95% Confidence Intervals are shown. N = Mean live individuals (average of 4 replicate samples of 25.5 cm^2). ALD_5 = Average Living Depth in 0-5 cm. Mean percentage abundance of live individuals in the 0-1 cm layer is also shown.



Top-5-ranked species

The vertical distributions of the top-5-ranked species at 140 m during both seasons are shown in Figure 4.7. During the spring intermonsoon, the five most abundant species all displayed an Average Living Depth of < 1 (Figure 4.7). Three calcareous species, *Uvigerina* ex. gr. *semiornata*, *Cancris auriculus* and *Cibicides* sp. 1, displayed relatively shallow ALD_5 (0.57, 0.66 and 0.45 cm respectively) and all three species displayed a peak in abundance in the upper 0-0.5 cm sediment layer. A few individuals of *U*. ex. gr. *semiornata* and *C. auriculus* were found in the 2 to 5 cm sediment layer. Possibly, this was a result of either contamination with surface layers during laboratory sampling procedure or redistribution by bioturbation, rather than the true living position of these individuals. The deep-infaunal species *Globobulimina* cf. *G. pyrula* and *Reophax bilocularis* displayed a deeper colonization of the sediment (ALD_5 = 0.71 cm and 0.87 cm respectively) during the spring intermonsoon compared to the other most abundant species, with a peak in abundance within the 0.5-1 cm sediment layer. Following the SW monsoon, *U*. ex gr. *semiornata* and *C. auriculus* displayed a decrease in the Average Living Depth (ALD_5 = 0.31, ALD_5 = 0.29 cm respectively) following the SW monsoon and a substantially higher peak in abundance within the upper 0-0.5 cm sediment layer than seen during the spring intermonsoon season. In contrast, *Globobulimina* cf. *G. pyrula* displayed an increase in Average Living Depth following the SW monsoon (ALD_5 = 1.21). *Bolivina* aff. *dilatata* was found between 0-2 cm sediment depth (ALD_5 = 1.02) and *Saidovina amygdalaeformis* was found in the 0.5-1 cm sediment layer only (3 individuals).

Figure 4.7 140-m site. Vertical distribution of the top-5-ranked live macrofaunal (>300µm) foraminiferal species in the 0-5 cm sediment layer a) spring intermonsoon (April 2003) b) SW monsoon (October 2003). Data are mean values of 4 replicates per season. 95% Confidence Intervals are shown. Average Living Depth in the 0-5 cm sediment layer (ALD_5) is shown for each species.



4.3.2 The 300-m site

4.3.2.1 Abundance

The abundance of live macrofaunal Foraminifera from the 0-5 cm layer of the sediment is shown in Table 4.7 (see Appendix C for full abundance data, all vertical sediment layers). Abundances increased from the intermonsoon season to the monsoon season. In the 0-5 cm sediment layer, the mean total was 218 individuals per 25.5 cm^2 (86 per 10 cm^2), rising to 311 (122 per 10 cm^2) following the SW

summer monsoon. The abundance of live macrofaunal Foraminifera from the upper 0-1 cm layer of the sediment is shown in Table 4.8. Abundance is presented as actual counts of complete (unfragmented) individuals per sample (25.5cm^2) and also normalised to individuals per 10cm^2 for comparison with previous benthic foraminiferal studies. 93.6 % of all live Foraminifera were present in the surface 1 cm of the sediment during the spring intermonsoon season, rising to 96.1 % during the SW monsoon season. Therefore, total numbers in the 0-1 cm layer were very similar to the 0-5 cm, with 202 individuals per 25.5 cm^2 (79 per 10 cm^2) during the spring intermonsoon season and 299 per 25.5 cm^2 (117 per 10 cm^2) during the SW monsoon season.

4.3.1.2. Taxonomic composition

Major taxa

The foraminiferal assemblage was dominated by calcareous taxa in both the 0-5 cm and the upper 0-1 cm sediment layers (Figure 4.8). The percentage of calcareous forms in the 0-5 cm live assemblage increased from 60% during the intermonsoon to 71% following the SW summer monsoon. Buliminids were the dominant group, comprising 57% of the live assemblage during the intermonsoon and 68% following the SW monsoon. The increase in abundance following the SW monsoon was unique to the buliminids and all other foraminiferal groups either declined in percentage abundance or remained stable between the two seasons. Agglutinated Foraminifera remained the second most abundant group, comprising 31% during the intermonsoon, declining to 25% following the monsoon. Monothalamous forms were far less abundant, comprising 9% in the intermonsoon assembage, and declining to 4% in the monsoon assemblage. Within the 0-1 cm layer, the percentage of calcareous Foraminifera increased slightly from the spring intermonsoon (62%) to the SW monsoon (73%). The dominance of buliminids was slightly more pronounced, whereas the rotaliids maintained a low percentage abundance during both seasons (3% to 4% from the spring intermonsoon to the SW monsoon respectively).

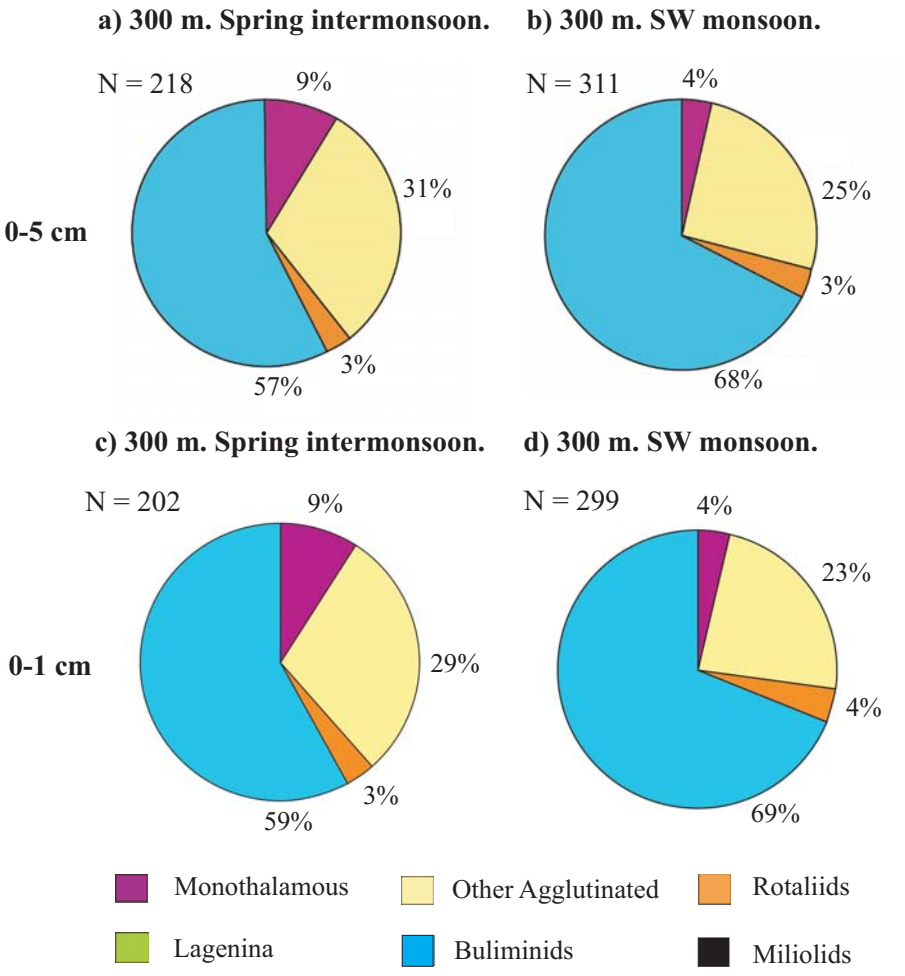
Table 4.7 300-m site. Abundances of complete (unfragmented) living macrofaunal (>300µm) Foraminifera in the 0-5 cm sediment layer. Data are presented for 4 replicates in each season sampled; spring intermonsoon (April 2003) and SW monsoon (October 2003). *Mean = average of 4 replicates. Data are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2.

	spring intermonsoon					SW monsoon				
	55803	55902				56037	561			
	#5	#5	#12	#26	*Mean	#1	05#7	07#6	15#2	*Mean
monothalamous										
Allogromiid sp. 2	0	0	4	0	1.0	4	4	1	0	2.3
Allogromiid sp. 3	0	3	0	1	1.0	0	0	1	0	0.3
Allogromiid sp. 4	0	0	1	0	0.3	1	0	1	0	0.5
Bathysiphon sp. nov. 1	5	14	0	18	9.3	4	11	1	5	5.3
Bathysiphon sp. nov. 2	6	3	1	0	2.5	0	0	0	0	0.0
Hyperammina sp. nov. 1	2	0	1	5	2.0	0	0	0	0	0.0
Saccamminid sp. 1	1	1	0	2	1.0	1	0	0	0	0.3
Saccamminid sp. 2	1	0	0	0	0.3	1	2	0	0	0.8
Saccamminid sp. 3	4	2	1	2	2.3	2	6	3	2	3.3
other agglutinated										
Ammodiscus aff. *cretaceus*	15	20	22	8	16.3	2	7	16	5	7.5
Reophax bilocularis	0	0	0	2	0.5	0	0	0	0	0.0
Reophax dentaliniformis	37	44	33	47	40.3	65	68	49	29	52.8
Reophax sp.2	9	5	8	2	6.0	7	8	21	3	9.8
Veleroninoides crassimargo	4	0	5	1	2.5	3	9	8	6	6.5
Veleroninoides wiesneri	2	1	2	0	1.3	1	1	4	2	2.0
calcareous										
Baggina philippinensis	0	1	0	0	0.3	0	0	0	0	0.0
Bolivina aff. *dilatata*	1	3	14	2	5.0	29	10	18	8	16.3
Cancris auriculus	2	9	0	3	3.5	6	4	6	2	4.5
Cassidulina laevigata	6	3	2	0	2.8	1	16	0	6	5.8
Cibicides sp. 1	0	0	1	0	0.3	0	0	2	0	0.5
Globobulimina cf. *G. pyrula*	15	11	14	24	16.0	18	14	19	11	15.5
Saidovina amygdalaeformis	0	0	0	0	0.0	0	0	2	0	0.5
Uvigerina ex. gr. *semiornata*	74	84	152	107	104	138	151	205	213	177
% *Uvigerina*	40	42	58	48	45	49	49	57	73	57
Total monothalamous	19	23	8	28	19.5	13	23	7	7	12.5
Total other agglutinated	67	70	70	60	66.8	78	93	98	45	78.5
Total calcareous	98	111	183	136	132	192	195	252	240	220
Total live species	15	14	14	13	-	15	13	15	11	-
[1]Total inds. per 25.5 cm^2	184	204	261	224	218	283	311	357	292	311
[2]Total inds. per 10 cm^2	72	80	102	88	86	111	122	140	115	122

Table 4.8 300-m site. Abundances of complete (unfragmented) living macrofaunal (>300µm) Foraminifera in the 0-1 cm sediment layer. Data are presented for 4 replicates in each season sampled; spring intermonsoon (April 2003) and SW monsoon (October 2003). *Mean = average of 4 replicates. Data are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2.

	spring intermonsoon					SW monsoon				
	55803	55902				56037	561			
	#5	#5	#12	#26	*Mean	#1	05#7	07#6	15#2	*Mean
monothalamous										
Allogromiid sp. 1	0	0	4	0	1.0	4	4	1	0	2.0
Allogromiid sp. 3	0	3	0	1	1.0	0	0	1	0	0.0
Allogromiid sp. 4	0	0	1	0	0.0	1	0	1	0	1.0
Bathysiphon sp. nov. 1	5	13	0	16	9.0	3	11	1	5	5.0
Bathysiphon sp. nov. 2	6	3	1	0	3.0	0	0	0	0	0.0
Hyperammina sp. nov. 1	2	0	1	5	2.0	0	0	0	0	0.0
Saccamminid sp. 1	1	1	0	2	1.0	1	0	0	0	0.0
Saccamminid sp. 2	1	0	0	0	0.0	1	2	0	0	1.0
Saccamminid sp. 3	4	2	1	2	2.0	2	6	3	2	3.0
other agglutinated										
Ammodiscus aff. *cretaceus*	4	0	5	1	3.0	3	9	8	6	7.0
Reophax bilocularis	2	1	2	0	1.0	1	1	4	2	2.0
Reophax dentaliniformis	14	20	22	7	16.0	2	7	14	5	7.0
Reophax sp. 2	0	0	0	0	0.0	0	0	0	0	0.0
Veleroninoides crassimargo	28	40	31	39	35.0	46	60	47	25	45.0
Veleroninoides wiesneri	7	4	8	2	5.0	4	8	21	3	9.0
calcareous										
Baggina philippinensis	1	3	14	2	5.0	29	10	18	8	16.0
Bolivina aff. *dilatata*	0	0	0	0	0.0	0	0	2	0	1.0
Cancris auriculus	2	9	0	3	4.0	6	4	6	2	5.0
Cassidulina laevigata	0	1	0	0	0.0	0	0	0	0	0.0
Cibicides sp. 1	6	3	2	0	3.0	1	16	0	6	6.0
Globobulimina cf. *G. pyrula*	0	0	1	0	0.0	0	0	2	0	1.0
Saidovina amygdalaeformis	12	9	14	13	12.0	18	13	18	8	14.0
Uvigerina ex. gr. *semiornata*	69	83	152	105	102	137	150	204	213	176
% *Uvigerina*	42	43	59	53	50	53	50	58	75	59
Total monothalamous	19	22	8	26	17.0	12	23	7	7	12.3
Total other agglutinated	55	65	68	49	59.0	56	85	94	41	69.0
Total calcareous	90	108	183	123	126	191	193	250	237	218
Total live species	15	14	14	12	-	15	13	15	12	-
[1]Total inds. per 25.5 cm^2	164	195	259	198	202	259	301	351	285	299
[2]Total inds. per 10 cm^2	64	76	102	78	79	102	118	138	112	117

Figure 4.8 300-m site. Percentage abundance of major foraminiferal groups in the 0-5 cm and 0-1 cm sediment layers (live assemblage; > 300µm fraction). Data are mean percentage abundances (4 replicate samples per season). N = Total live abundance



Agglutinated Foraminifera remained the second-ranked group, comprising 29% during the spring intermonsoon, declining to 23% following the SW monsoon. Monothalamous forms again comprised 9% in the spring intermonsoon assembage and 4% in the SW monsoon assemblage.

Species

A total of 23 macrofaunal (>300 μm) species was recognized at 300 m; 22 species occurred in the 0-5 cm samples collected during the intermonsoon season and 19 in 0-5 cm samples collected during the monsoon-influenced season. Eighteen species were found in both seasons. Seven calcareous species were present in each season and 6 of these (*Cancris auriculus*, *Cassidulina laevigata*, *Cibicides* sp. 1, *Bolivina* aff. *dilatata, Globobulimina* cf. *G. pyrula* and *Uvigerina* ex. gr. *semiornata*) were found in both seasons. The top-10-ranked species from both seasons comprised 5 of these calcareous species, 2 monothalamous species (*Bathysiphon* sp. nov. 1, *Bathysiphon* sp. nov. 2), 2 multilocular agglutinated species (*Reophax dentaliniformis*, *Reophax* sp. 2) and 1 ammodiscacean (*Ammodiscus* aff. *cretaceus*) (Table 4.9). Nine of these species appeared in the top 10 in both seasons; they were joined by the monothalamous *Bathysiphon* sp. nov. 2 in the spring intermonsoon samples and the multilocular agglutinated species *Veleroninoides crassimargo* in samples collected during the SW monsoon. *Uvigerina* ex. gr. *semiornata* was the dominant species and increased significantly in standing stock ($P<0.05$, 2-sample t-test) from 104 individuals per multicore sample (25.5cm^2 surface area) during the spring intermonsoon, to 177 individuals per sample following the SW monsoon (Figure 4.9). The percentage abundance of *Uvigerina* ex. gr. *semiornata* also increased from the spring intermonsoon (47.8%) to the SW monsoon (56.9%).

Monothalamous Foraminifera were relatively diverse with 9 undescribed species recognised over the two seasons; all 9 species occurred in the intermonsoon season and 7 in the monsoon season. Some species, such as *Bathysiphon* sp. nov. 1, *Bathysiphon* sp. nov. 2, *Hyperammina* sp. nov. 1 and Saccamminid sp. 3, were relatively abundant. Other agglutinated forms (*Reophax* and ammodiscaceans) were represented by 6 species over the two seasons, all 6 being present in the intermonsoon season and 5 in the monsoon season.

Table 4.9 300-m site. Abundance of the top-10-ranked macrofaunal (>300µm) foraminiferal species in the 0-5 cm sediment layer during a) spring intermonsoon, b) SW monsoon. Data are given as *[1]Mean = Average total live individuals from 4 replicate samples (25.5 cm^2) and as % abundance based on Mean data. Species occurring among the top 10 ranked in both seasons as marked with an *. Note the dominance of calcareous forms (underlined) in both seasons sampled.

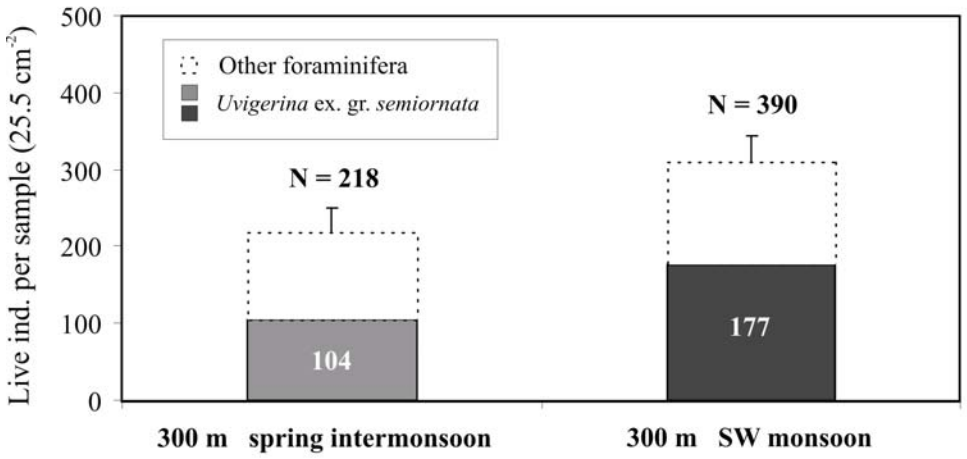
a) 300 m – spring intermonsoon

Rank	Top 10 ranked species	*[1]Mean	Abundance (%)
1	*Uvigerina* ex. gr. *semiornata**	104	47.8
2	*Reophax dentaliniformis**	40	18.4
3	*Ammodiscus* cf. *cretaceus**	16	7.4
4	*Globobulimina* cf. *G. pyrula**	16	7.3
5	*Bathysiphon* sp. nov. 1*	9	4.2
6	*Reophax* sp.2*	6	2.7
7	*Bolivina* aff. *dilatata**	5	2.3
8	*Cancris auriculus**	4	1.6
9	*Cassidulina laevigata**	3	1.3
10	*Bathysiphon* sp. nov. 2	3	1.1
	Total live Top 10 ranked species (sample^{-1})	206	94.3
	Total live Foraminifera (sample^{-1})	218	-
	Total live species	21	-

b) 300 m – SW monsoon

Rank	Top 10 ranked species	*Mean	Abundance (%)
1	*Uvigerina* ex. gr. *semiornata**	177	56.9
2	*Reophax dentaliniformis**	53	17.0
3	*Bolivina* aff. *dilatata**	16	5.2
4	*Globobulimina* cf. *G. pyrula**	16	5.0
5	*Reophax* sp.2*	10	3.1
6	*Ammodiscus* aff. *cretaceus**	8	2.4
7	*Veleroninoides crassimargo*	7	2.1
8	*Cassidulina laevigata**	6	1.9
9	*Bathysiphon* sp. nov. 1*	5	1.7
10	*Cancris auriculus**	5	1.4
	Total live Top 10 ranked species (sample^{-1})	301	96.7
	Total live Foraminifera (sample^{-1})	311	-
	Total live species	18	-

Figure 4.9 300-m site. Abundances of live *Uvigerina* ex. gr. *semiornata* (white numbers) and other Foraminifera in the 0-5 cm sediment layer during the spring intermonsoon (April 2003) and SW monsoon (October 2003). Data are averages of four replicate samples per season. N = Mean live individuals during each season. 95% Confidence Intervals are shown.

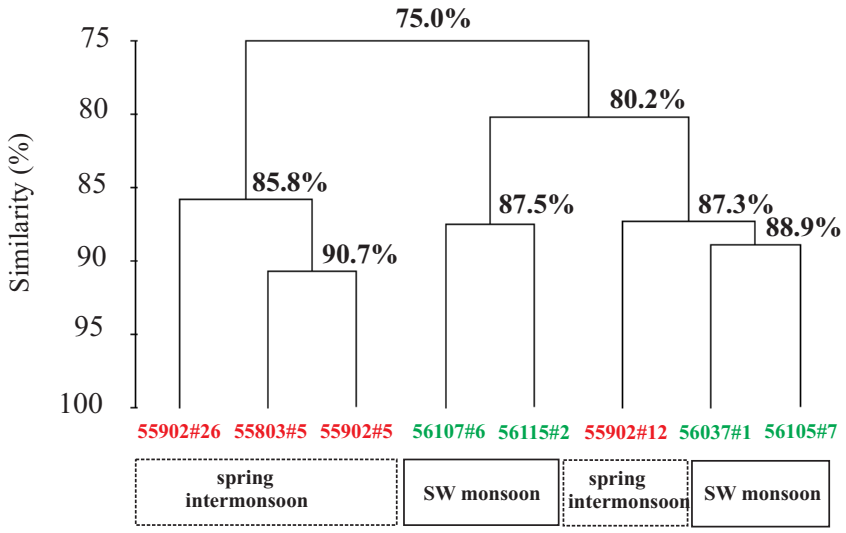


4.3.1.3 Multivariate analysis

Cluster analysis

A cluster-analysis of abundances in replicate samples from the 300-m site illustrated a high degree of similarity (75%) between all samples from both seasons sampled (Figure 4.10). There was less grouping of samples within each season, with one sample from the intermonsoon (55902#12) displaying an 87.3% similarity with two samples from the monsoon season (56037#1 and 56105#7). This indicates little change in the live foraminiferal abundance from the spring intermonsoon to the SW monsoon.

Figure 4.10 300-m. Cluster analysis (dendrogram) of 0-5cm. 4 replicate samples (25.5 cm^2) per season; Green = spring intermonsoon, samples in red = SW monsoon. Based on similarity matrix (Bray-Curtis Similarity) calculated from square-root transformed data (live individuals per 25.5cm^2).



Multidimensional Scaling

Multidimensional Scaling based on a similarity matrix (Bray-Curtis) calculated on replicate samples of the entire foraminiferal assemblage (live abundance) in the 0-5 cm and 0-1 cm layers revealed a clear grouping of statistical significance ($P < 3$, ANOSIM) between the assemblages in the two sediment layers (0-5 cm and 0-1 cm) from both seasons sampled (Figure 4.11). Samples from each season also grouped together, although there was no significant difference because of one outlier in each season. Multidimensional scaling was also used to analyse the similarity between the foraminiferal assemblage in the topmost sediment layers 0-0.5 cm and 0.5-1 cm layers (Figure 4.12). The MDS plot (Figure 4.12) shows a clear separation, of statistical significance ($P<3$, ANOSIM) between samples from these two sediment layers. A particularly tight grouping was seen by replicate samples from the 0-0.5 cm layers. However, there was no significant difference between samples of the same vertical sediment layer in either of the seasons sampled.

Figure 4. 11 Multidimensional scaling (MDS) of total live Foraminifera (> 300 µm) in the 0-5 cm and 0-1 cm sediment layers at 300 m during spring intermonsoon and SW monsoon seasons. Based on a Bray-Curtis Similarity matrix on square-root transformed data (live abundance). Stress = 0.09.

● = 0-5 cm layer, spring intermonsoon ● = 0-5 cm layer, SW monsoon
○ = 0-1 cm layer, spring intermonsoon ○ = 0-1 cm layer, SW monsoon

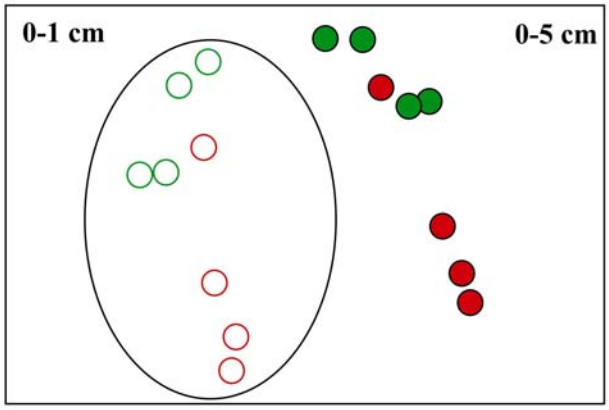
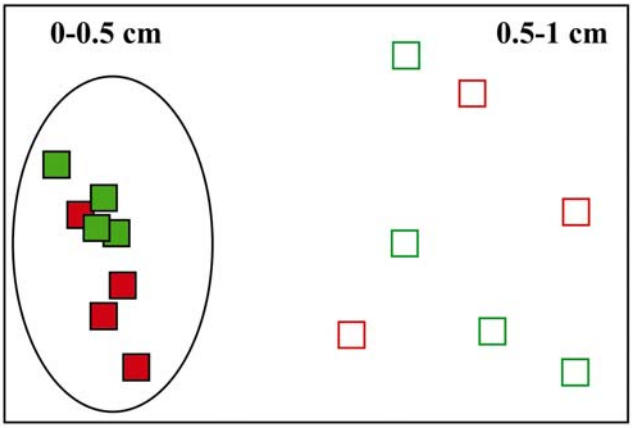


Figure 4.12 Multidimensional scaling (MDS) of total live Foraminifera (> 300 µm) in the upper 1 cm (0-0.5 cm and 0.5–1 cm sediment layers) at 300 m during spring intermonsoon and SW monsoon seasons. Based on a Bray-Curtis Similarity matrix on square-root transformed data (live abundance). Stress = 0.08.
■ = 0-0.5 cm layer, spring intermonsoon; □ = 0.5-1 cm layer, spring intermonsoon; ■ = 0-0.5 cm layer, SW monsoon; □ = 0.5-1 cm layer, SW monsoon



4.3.2.4 Diversity

Diversity parameters for all replicate samples, and the total number of individuals recognized from each season, are shown in Table 4.10. Within each season, diversity values displayed some variation between replicates. There was little seasonal change in the species richness (S) in samples from the intermonsoon (14 - 15 species; 16 species total) and the SW monsoon seasons (12 - 15 species; 16 species total). All measure of species diversity were higher in intermonsoon samples. Rank 1 dominance (R1D) showed a corresponding increase from between 40.2% and 58.2% during the spring intermonsoon to between 48.6% and 72.9% during the SW monsoon. These changes in diversity and dominance values from the spring intermonsoon to the SW monsoon season reflected the increased abundance of *Uvigerina* ex. gr. *semiornata*.

Table 4.10 300-m site. Diversity data for complete (unfragmented) individuals (excluding indeterminate specimens) in the 0-5 cm sediment layer for both seasons sampled; spring intermonsoon and SW monsoon. Data are presented for 4 replicates in each season. N = number of individuals (per 25.5cm^2 sample and per 10cm^2), S = Species richness, Fisher α = Fisher alpha diversity index, H'($\log_e$) = Shannon-Wiener diversity index, $ES_{(n)}$ = expected number of species for n individuals, R1D = Rank 1 dominance, J' = Pielou's evenness.

Station - series	Abundance (N) sample^{-1}	Abundance (N) 10 cm^{-2}	S	Fisher α	H'(loge)	R1D (%)	ES(40)	ES(100)	J'
300 m. Spring intermonsoon.									
55803#5	224	88	14	3.3	1.6	47.8	7.8	11.1	0.6
55902#5	183	72	15	3.9	1.9	40.2	10.0	13.4	0.7
55902#12	204	80	15	3.7	1.9	41.2	9.3	12.7	0.7
55902#26	261	102	15	3.5	1.5	58.2	7.9	10.9	0.6
300 m. SW monsoon.									
56037#1	282	111	15	3.4	1.6	48.8	7.6	10.9	0.6
56115#2	311	122	14	3.0	1.7	48.6	9.1	12.2	0.7
56105#7	356	140	15	3.2	1.6	57.4	8.1	11.0	0.6
56107#6	292	115	12	2.5	1.1	72.9	6.8	10.0	0.5

4.3.2.5 Vertical distribution patterns

Total live assemblage

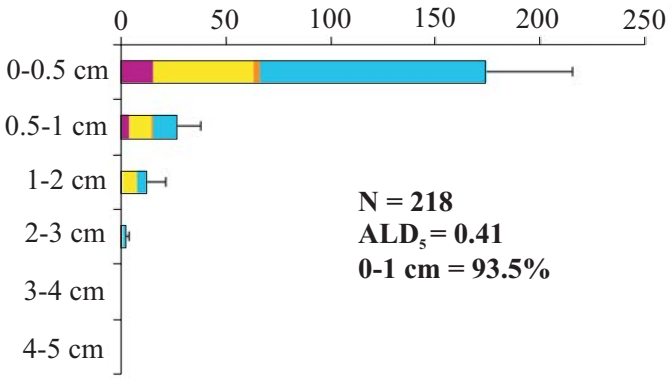
The persistent severely hypoxic environment at 300 m was reflected in the vertical distribution of live macrofaunal Foraminifera (Table 4.11 and Figure 4.13). In both seasons sampled, bottom-water oxygen was less than 0.5 mll^{-1} and the ALD_5 was < 0.5 cm, with over 93% of all live Foraminifera found in the upper 1 cm sediment layer. Following the SW monsoon, the ALD_5 decreased slightly from 0.41 (intermonsoon) to 0.33 (monsoon) and the concentration of live Foraminifera in the upper 1 cm sediment layer increased correspondingly from 93.5% to 97.6% respectively. Less than 7% of all live Foraminifera were found in sediment layers between 1 and 5 cm during each of the seasons sampled.

The main foraminiferal groups

There was little seasonal change in the vertical distribution patterns of the three main foraminiferal groups, calcareous, monothalamous and other agglutinated at the 300-m site (Table 4.11 and Figure 4.13). Calcareous forms maintained a relatively stable vertical distribution pattern between the two seasons. They were restricted to the upper 3 cm of sediment, but were mainly found in the upper 1 cm, increasing from 58.3% of the total live assemblage in the intermonsoon season to 70.8% after the SW summer monsoon. The proportion of non-calcareous Foraminifera (monothalamous and other agglutinated) declined in all sediment layers following the SW monsoon. The colonization depth of other agglutinated forms (multilocular agglutinated forms and ammodiscaceans) decreased from 0-3 cm during the intermonsoon, to 0-2 cm following the SW monsoon. The colonization depth of monothalamous forms displayed a similar trend to the agglutinated forms, decreasing from 0-3 cm preceding the monsoon to 0-2 cm following the monsoon. All live monothalamous forms were found in the upper 0-1 cm sediment layer, unlike calcareous and agglutinated forms, which also occurred in deeper sediment layers.

Figure 4.13 300-m site. Vertical distribution of live macrofaunal (>300 µm) Foraminifera within the 0-5 cm sediment vertical fraction during both seasons sampled: a) spring intermonsoon, b) SW monsoon. Data are mean values of total live individuals from 4 replicates (25.5 cm^2) per season and are presented for major foraminiferal groups. 95% Confidence Intervals are shown. N = Mean live individuals (average of 4 replicate samples of 25.5 cm^2). ALD_5 = Average Living Depth in 0-5 cm. Mean percentage abundance of live individuals in the 0-1 cm layer is also shown.

a) 300 m. Spring intermonsoon. 0-5 cm.



b) 300 m. SW monsoon. 0-5 cm.

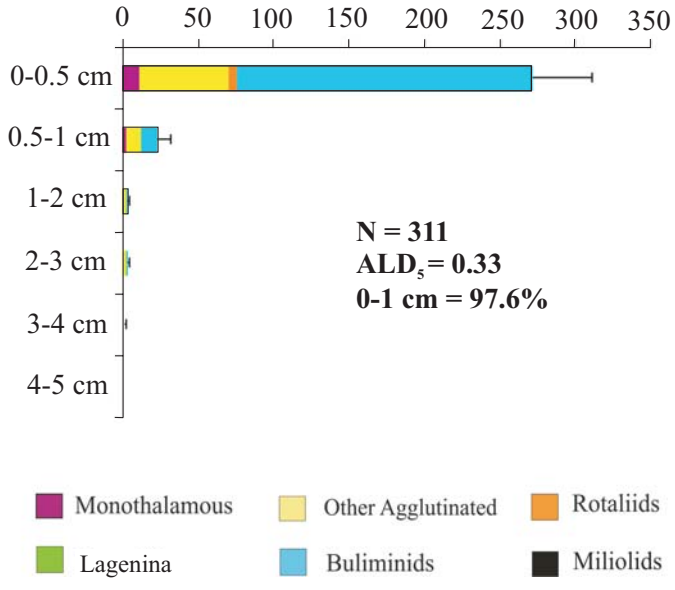


Table 4.11 300-m site. Mean percentage abundance of live macrofaunal (>300µm) foraminiferal groups at 140m. a) All vertical layers analysed, b) Σ of vertical layers 0-1cm, 1-5cm, 0-5cm. Data are mean values of 4 replicates per season ± 95% Confidence Interval. Underlined data show a significant increase in percentage abundance from intermonsoon to monsoon ($P < 0.05$, student t-test assuming unequal variances). Grey boxes highlight layers where no live Foraminifera are present. Note the increase in mean percentage abundance of total Foraminifera and calcareous Foraminifera in monsoon samples and a corresponding decline in monothalamous and other agglutinated forms.

a)

300 m	Mean % Total Live		Mean % calcareous		Mean % other agglutinated		Mean % monothalamous	
	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon
0-0.5	80.8 ± 8.7	88.5 ± 3.4	52.5 ± 10.6	66.8 ± 5.5	22.2 ± 4.2	19.3 ± 5.9	7.1 ± 3.4	3.5 ± 2.0
0.5-1	12.6 ± 4.9	7.7 ± 3.2	5.8 ± 3.9	4.0 ± 2.6	5.2 ± 0.6	3.2 ± 2.1	1.6 ± 1.3	0.6 ± 0.4
1-2	5.7 ± 4.4	1.5 ± 0.5	2.3 ± 2.2	0.5 ± 0.3	3.0 ± 2.2	0.6 ± 0.4	0.3 ± 0.4	0.1 ± 0.2
2-3	0.9 ± 1.0	2.0 ± 2.9	0.5 ± 0.6	0.2 ± 0.2	0.5 ± 0.5	0.0 ± 0.0	0.7 ± 0.5	0.0 ± 0.0
3-4	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
4-5	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

b)

300 m	Mean % Total Live		Mean % calcareous		Mean % other agglutinated		Mean % monothalamous	
	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon	intermonsoon	monsoon
0-1	93.4 ± 5.3	96.3 ± 3.2	58.3 ± 9.0	70.8 ± 7.8	27.4 ± 4.3	22.4 ± 6.4	8.1 ± 3.3	3.0 ± 1.9
1-5	4.9 ± 4.3	4.5 ± 3.1	1.9 ± 1.9	0.7 ± 0.3	2.9 ± 2.5	3.1 ± 3.1	0.1 ± 0.2	0.1 ± 0.2
0-5	100	100	61.1 ± 7.4	71.5 ± 8.0	30.9 ± 5.3	25.5 ± 6.7	9.0 ± 4.1	4.1 ± 2.0

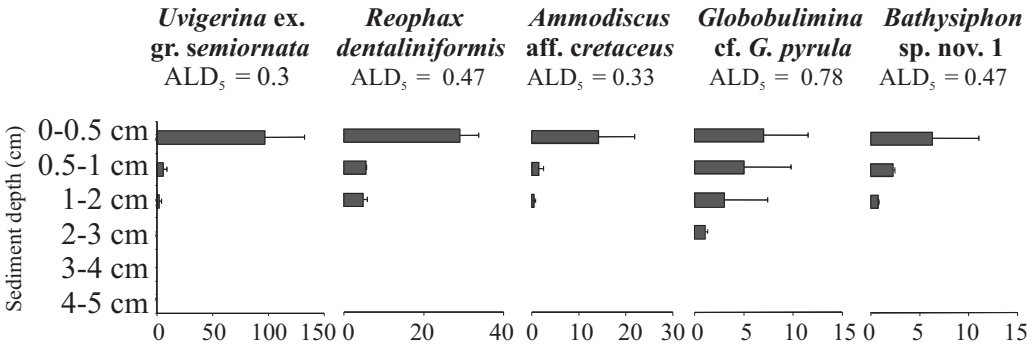
Top-5-ranked species

The top-5-ranked species at 300 m were represented by both calcareous and agglutinated species (Figure 4.14). During the spring intermonsoon season, two calcareous species (*Uvigerina* ex. gr. *semiornata* and *Globobulimina* cf. *G. pyrula*) and three agglutinated species (*Reophax dentaliniformis*, *Ammodiscus* aff. *cretaceus* and *Bathysiphon* sp. nov. 1) comprised the top 5 ranked species. The most abundant species *U.* ex. gr. *semiornata*, displayed a shallow Average Living Depth (ALD_5 = 0.3), with a substantial peak in abundance within the upper 0-0.5 cm sediment layer. All other species displayed a similar trend with the maximum number of individuals in the upper 0-0.5 cm layer. *Reophax dentaliniformis*, *A.* aff. *cretaceus* and *B.* sp. nov. 1 all had an Average Living Depth of < 0.5 cm (ALD_5 = 0.47 cm, 0.33 cm, 0.47 cm

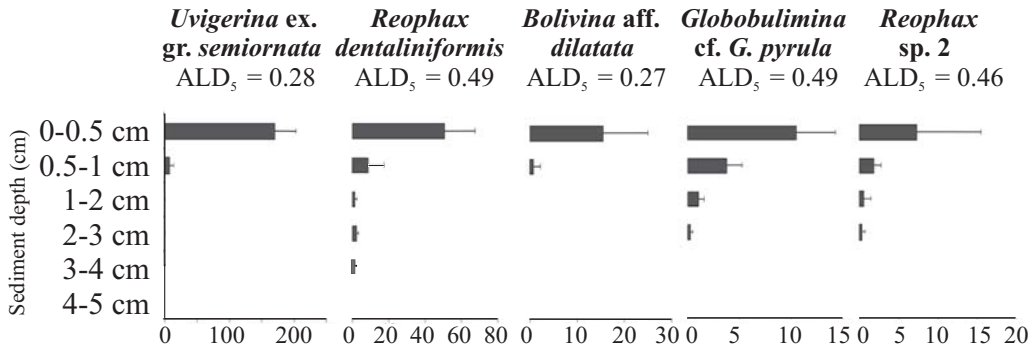
respectively). However, *G*. cf. *G. pyrula* penetrated the deepest, with an Average Living Depth of 0.78 cm; live individuals were found between 0-3 cm sediment depth. Following the SW monsoon, the five most abundant species (again three calcareous and two agglutinated) all displayed a shallow Average Living Depth of < 0.5 cm. *Uvigerina* ex. gr. *semiornata* displayed a slight decrease in Average Living Depth (ALD_5 = 0.28) following the SW monsoon and all individuals were restricted to the upper 0-0.5 cm sediment layer.

Figure 4.14 300-m site. Vertical distribution of the top-5-ranked live macrofaunal (>300µm) foraminiferal species in the 0-5 cm sediment layer: a) spring intermonsoon (April 2003), b) SW monsoon (October 2003). Data are mean values of 4 replicates per season. 95% Confidence Intervals are shown. Average Living Depth in the 0-5 cm sediment layer (ALD_5) is shown for each species.

a) 300 m. Spring intermonsoon.



b) 300 m. SW monsoon.



Bolivina aff. *dilatata* displayed a similar trend to *Uvigerina* ex. gr. *semiornata* with an Average Living Depth of 0.27. The third calcareous species in the top 5, *Globobulimina* cf. *G. pyrula*, displayed a deeper Average Living Depth (ALD_5 = 0.49), although this was based on a few individuals found below 0-1 cm. Two species of *Reophax* (*Reophax dentaliniformis* and *Reophax* sp. 2 were present in the top 5 in the monsoonal samples. Both displayed a very similar trend, penetrating fairly deep into the sediment with live individuals found between 0-3 cm sediment depth (*Reophax* sp. 2, ALD_5 = 0.46) and 0-4 cm sediment depth (*Reophax dentaliniformis*, ALD_5 = 0.49).

4.4 Seasonal changes in the live foraminiferal assemblages at the 140-m and 300-m sites

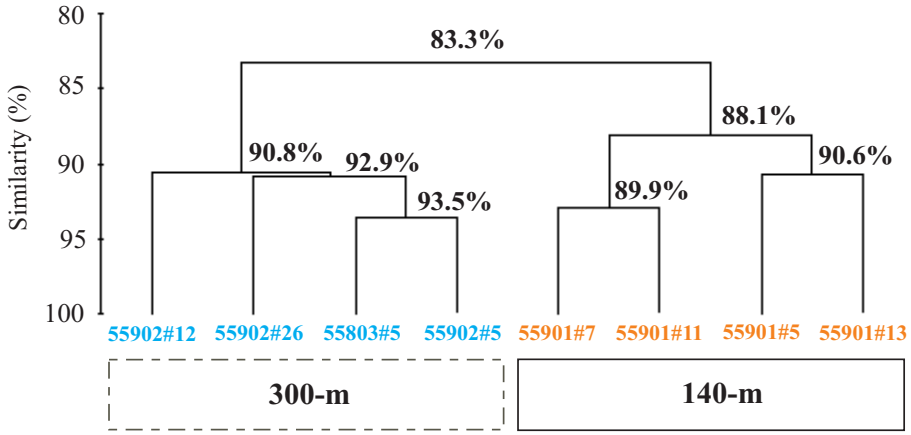
4.4.1 Multivariate analysis

4.4.1.1 Cluster analysis

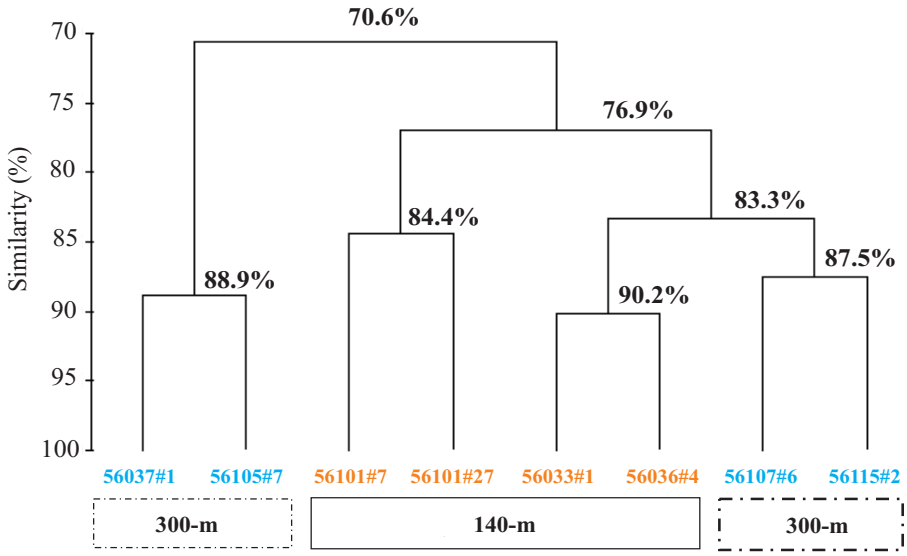
During the spring intermonsoon, the two sites experienced very different oxygen regimes. The benthic environment at 140 m was fully oxygenated (O_2 = 2.05 $ml l^{-1}$) and at 300 m it was hypoxic (O_2 = 0.11 $ml l^{-1}$). Many species were common to both sites and in both cases *Uvigerina* ex. gr. *semiornata* dominated the live assemblage. This is reflected in an 83.3% similarity between all samples from both sites (Figure 4.15a). However, despite this bathymetric proximity, the foraminiferal assemblages were different, as reflected in the distinct grouping of replicate samples. The four replicate cores at 140m shared 88.1% similarity. At 300 m, the four replicate cores were less variable with a 90.8% similarity. During the SW monsoon a different pattern was evident (Figure 4.15b). Both sites were now hypoxic (bottom-water O_2 < 0.5 $ml l^{-1}$) and therefore their abiotic characteristics were more similar than during the intermonsoon season. This was reflected in the less distinct grouping of samples between sites. The overall similarity between the samples was less (70.6%).

Figure 4.15 Cluster analysis (dendrogram) of total (0-5cm) samples from 140 m and 300 m during the two seasons sampled; a) spring intermonsoon, b) SW monsoon. Four replicate cores per site; Samples in blue = 300 m, samples in orange = 140 m. Based on similarity matrix (Bray-Curtis Similarity) calculated from square-root transformed data (live individuals per 25.5cm^2).

a) Spring intermonsoon. Similarity between the live macrofaunal Foraminifera at 140 m and 300 m.



b) SW Monsoon: Similarity between the live macrofaunal Foraminifera at 140 m and 300 m.



All 140-m site samples were grouped together, reflecting the relative homogeneity of the foraminiferal assemblages following the SW monsoon. Moreover, the four samples from 140 m form two groups corresponding to their collection dates. Samples 56033#1 and 56036#4 were collected in September 2003 during CD150 wheras samples 56101#7 and 56101#27 were collected in October 2003 during CD151. The grouping of samples from different time points within the same season may reflect a short time scale for temporal change in the foraminiferal assemblage at the 140-m site. At the 300-m site, the samples were not grouped according to time of collection, but in two pairs according to the total number of live individuals and in particular the total number of live *Uvigerina* ex. gr. *semiornata*. This suggests that the variability in the 4 replicates colleted at 300m during the Monsoon season was a result of localised patchiness rather than a temporal shift in the foraminiferal assemblage. This idea is consistent with the relatively constant environmental conditions during different seasons at the 300-m site.

4.4.1.2 Multidimensional Scaling

Multidimensional scaling was used to compare the entire foraminiferal assemblage (0-5 cm layer) and the upper 1 cm layer from the 140 m and 300 m sites during the spring intermonsoon and SW monsoon (Figure 4. 16). The MDS plot revealed a clear grouping and significant ($P < 3$, ANOSIM) difference between replicate samples from each site. Replicate samples from each site were also clearly grouped by season (except for one outlier; one replicate sample of 0-5 cm, spring intermonsoon, red closed circle, Figure 4.16). There was no clear grouping or significant difference between replicate samples from the two sediment layers (0-5 cm and 0-1 cm), indicating a high degree of similarity between the entire foraminiferal assemblage and the surface 1 cm layer. Multidimensional scaling was also conducted on the two upper sediment layers (0-0.5 and 0.5-1 cm) (live foraminiferal abundance data) at 140 m and 300 m during the spring intermonsoon and SW monsoon-influenced seasons (Figure 4.17). The MDS plot revealed clear differences in the foraminiferal

Figure 4.16 Multidimensional scaling (MDS) of total live Foraminifera (> 300 µm) in 0-5 cm and 0-1 cm sediment layers at 140 m and 300 m during spring intermonsoon and SW monsoon seasons. Samples from the 300-m site are circled. Based on a Bray-Curtis Similarity matrix on square-root transformed data (total live abundance). Stress = 0.06.

140 m: ◆ = 0-5 cm, spring intermonsoon ◇ = 0-1 cm, spring intermonsoon
◆ = 0-5 cm, SW monsoon ◇ = 0-1 cm, SW monsoon
300 m: ● = 0-5 cm, spring intermonsoon ○ = 0-1 cm, spring intermonsoon
● = 0-5 cm, SW monsoon ○ = 0-1 cm, SW monsoon

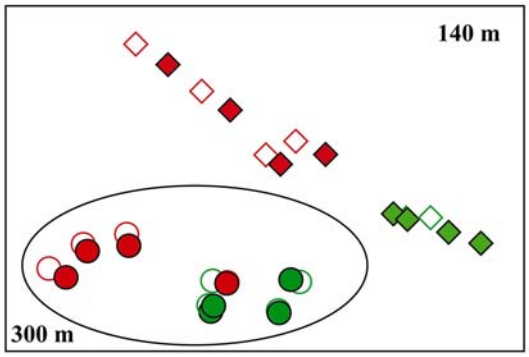
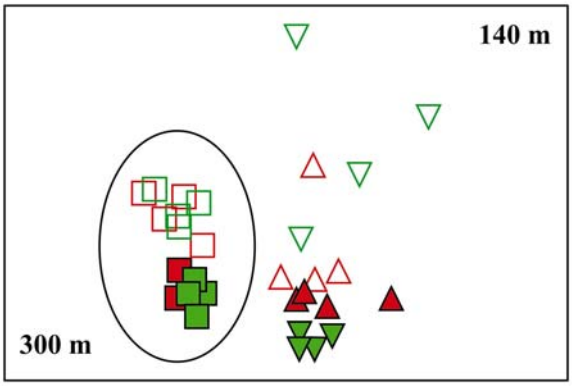


Figure 4.17 Multidimensional scaling (MDS) of total live Foraminifera (> 300 µm) in 0-0.5 cm and 0.5–1 cm sediment layers at 140 m and 300 m during spring intermonsoon and SW monsoon seasons. Samples from the 300-m site are circled. Based on a Bray-Curtis Similarity matrix on square-root transformed data (total live abundance). Stress = 0.15.

140 m: ▲ = 0-0.5 cm, spring intermonsoon; △ = 0.5-1 cm, spring intermonsoon;
▼ = 0-0.5 cm, SW monsoon ▽ = 0.5-1 cm, SW monsoon
300 m: ■ = 0-0.5 cm, spring intermonsoon; □ = 0.5-1 cm, spring intermonsoon;
■ = 0-0.5 cm, SW monsoon; □ = 0.5-1 cm, SW monsoon



assemblage response to the SW monsoon between the two sites. This was illustrated by a clear grouping of samples from each site and a significant difference (P<3, ANOSIM) between both sediment layers and seasons sampled at both sites (Figure 4.17). However, replicate samples from 140 m were generally more scattered in the MDS plot, indicating a higher degree of variability in the foraminiferal assemblage of each sample.

4.5 Metazoan macrofauna

The macrofauna is interpreted here in a broad sense to include all metazoan organisms retained on a 300 μm mesh. I therefore include meiofaunal taxa (copepods, nematodes ostracods) in addition to strictly macrofaunal groups (amphipods, bivalves, small echinoderms, gastropods and polychaetes). All metazoan organisms were assumed to have been alive when sampled.

4.5.1 The 140-m site

4.5.1.1 Abundance

Abundance of metazoan macrofauna (> 300 μm) at the 140-m site in the total sample (0-5cm) and the upper 0-1 cm sediment layer are shown in Tables 4.12 and 4.13. (see Appendix C for full abundance data, all vertical sediment layers). Abundance is presented as counts of individuals from the actual sample (25.5cm^2) and normalised to individuals per 10cm^2 for comparison with the foraminiferal data. Mean abundances of macrofaunal metazoa were low in both seasons sampled and there was considerable variability between samples. Total abundances decreased from the spring intermonsoon to the SW monsoon. In the 0-5 cm sediment layer, the mean for the total macrofauna was 53 individuals per 25.5 cm^2 (21 per 10 cm^2), reducing to 28 individuals per 25.5 cm^2 (11 per 10 cm^2) following the SW summer monsoon. The values in the 0-1 cm sediment layer followed a similar trend, with the mean total abundances decreasing from 33 individuals per 25.5 cm^2 (13 per 10 cm^2), reducing to 18 individuals per 25.5 cm^2 (7 per 10 cm^2) following the SW summer monsoon.

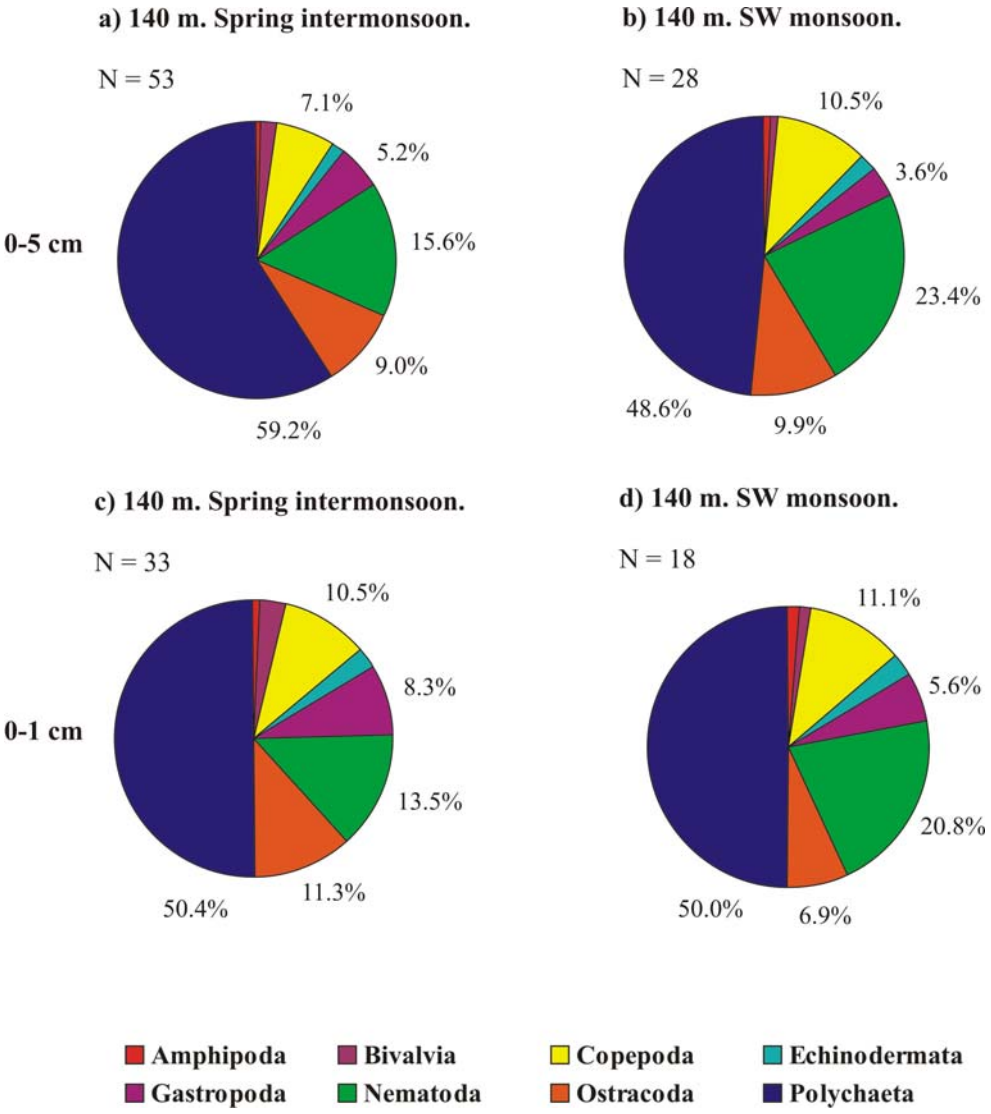
Table 4.12 140-m site. Abundances of macrofaunal (>300 µm) Metazoa in the 0-5 cm sediment layer. Data are presented for 4 replicates in each season sampled. Total metazoans are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2. *Mean = Average of 4 replicates.

	spring intermonsoon					SW monsoon				
	55901					56		56101		
	#5	#7	#11	#13	*Mean	033#1	036#4	#7	#27	*Mean
Amphipoda	0	0	1	0	0.3	0	1	0	0	0.3
Bivalvia	1	2	0	1	1.0	0	1	0	0	0.3
Copepoda	6	7	0	2	3.8	3	1	5	3	3.0
Echinodermata	0	2	0	1	0.8	2	0	0	0	0.5
Gastropoda	0	2	7	2	2.8	0	0	0	4	1.0
Nematoda	12	0	11	10	8.3	1	8	7	10	6.5
Ostracoda	8	6	1	4	4.8	1	3	6	1	2.8
Polychaeta	35	28	42	20	31.3	18	14	14	8	13.5
Total live taxa	6	6	5	6	-	5	7	5	5	-
[1]Total live inds. (sample^{-1})	62	47	62	40	52.8	25	28	32	26	27.8
[2]Total live inds. (10 cm^{-2})	24	18	24	16	20.7	10	11	13	10	10.9

Table 4.13 140-m site. Abundances of macrofaunal (>300 µm) Metazoa in the 0-1 cm sediment layer. Data are presented for 4 replicates in each season sampled. Total metazoans are given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2. *Mean = Average of 4 replicates.

	spring intermonsoon					SW monsoon				
	55901					56		56101		
	#5	#7	#11	#13	*Mean	033#1	036#4	#7	#27	*Mean
Amphipoda	0	0	1	0	0.3	0	1	0	0	0.3
Bivalvia	1	2	0	1	1.0	0	1	0	0	0.3
Copepoda	6	6	0	2	3.5	3	1	2	2	2.0
Echinodermata	0	2	0	1	0.8	2	0	0	0	0.5
Gastropoda	0	2	7	2	2.8	0	0	0	4	1.0
Nematoda	10	0	6	2	4.5	0	6	2	7	3.8
Ostracoda	8	6	1	0	3.8	1	1	2	1	1.3
Polychaeta	31	15	13	8	16.8	13	10	8	5	9.0
Total live taxa	5	6	5	6	-	5	5	3	4	-
[1]Total live inds. (sample^{-1})	56	33	28	16	33.3	19	20	14	19	18.0
[2]Total live inds. (10 cm^{-2})	22	13	11	6	13.0	7	8	5	7	7.1

Figure 4.18 140-m site. Mean percentage abundance of major macrofaunal (> 300 µm) metazoan taxa in the 0-5 cm and 0-1 cm sediment layers during spring intermonsoon (a,c), SW monsoon (b,d). Data are mean percentage abundances based on 4 replicate multicore (25.5 cm^2) samples per season. Percentage values are shown for the top 5 ranked taxa in each season and vertical fraction.



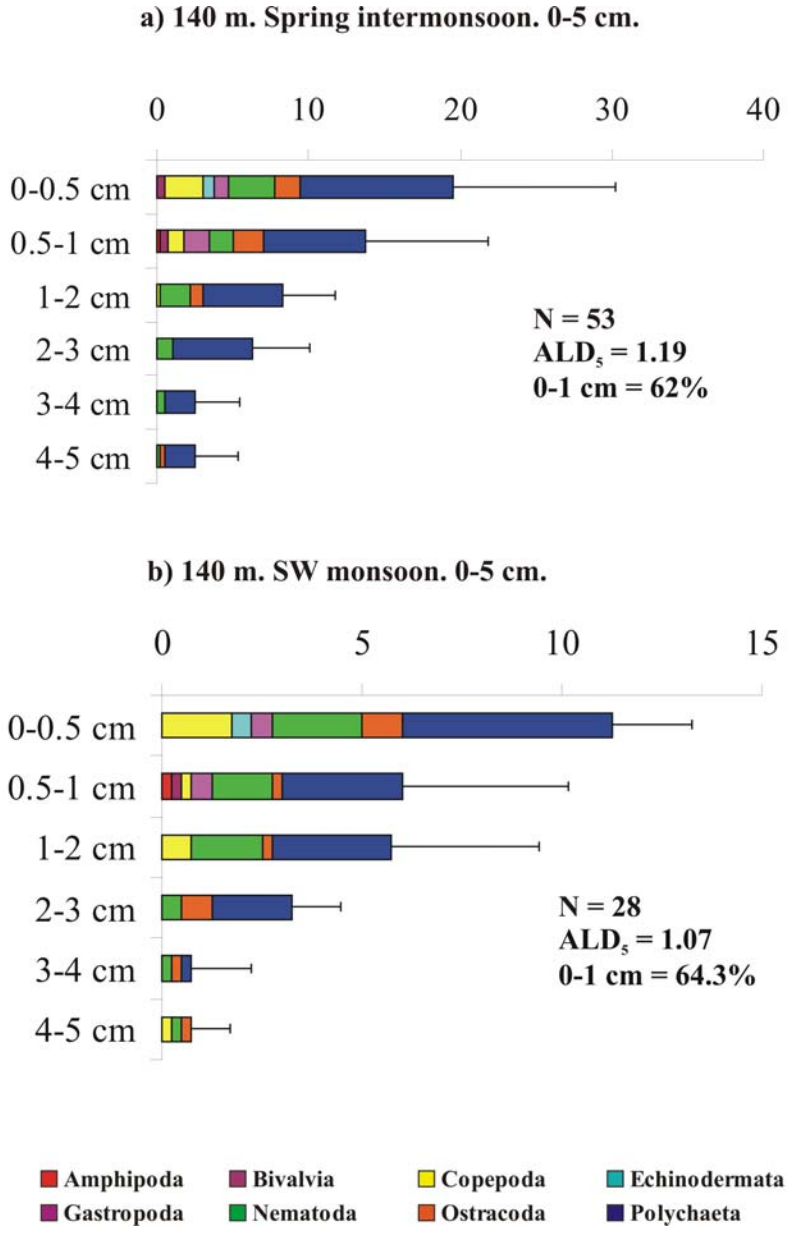
4.5.1.2 Taxonomic composition

Eight major metazoan taxa were found at 140 m during both seasons. The top 5 most abundant taxa in rank order were polychaetes, nematodes, ostracods, gastropods and harpacticoid copepods (Figure 4.18). Each taxon displayed a specific seasonal trend in relative abundance. The most abundant group, the polychaetes, declined in percentage abundance in the total live assemblage (0-5 cm) from 59.2% during the spring intermonsoon to 48.6% following the SW monsoon. Gastropods displayed a similar trend, declining from 5.2% to 3.6% following the SW monsoon. However, nematodes, ostracods and harpacticoid copepods (all of them meiofaunal taxa) displayed the opposite trend, increasing in percentage abundance following the SW monsoon. This was most apparent for the nematodes, which increased from 15.6% (mean standing crop 8.3) to 23.4% (mean standing crop 6.5) of the total metazoan assemblage from spring intermonsoon to SW monsoon.

4.5.1.3 Vertical distribution patterns

During the spring intermonsoon, 63% of all macrofauna were found in the upper 0-1 cm sediment layer (Figure 4.19). Following the SW monsoon, this percentage increased slightly to 64.3% as reflected in a shallowing of the Average Living Depth from $ALD_5 = 1.19$ to $ALD_5 = 1.07$. At major taxon level, the vertical distribution profiles before and after the SW monsoon displayed little change from spring intermonsoon to SW monsoon, with the same 7 metazoan taxa colonizing the upper 0-1 cm sediment layer during both seasons sampled. However, abundances decreased following the SW monsoon. The vertical distribution of some taxa is based on a few individuals or a single individual, so no clear conclusions can be drawn.

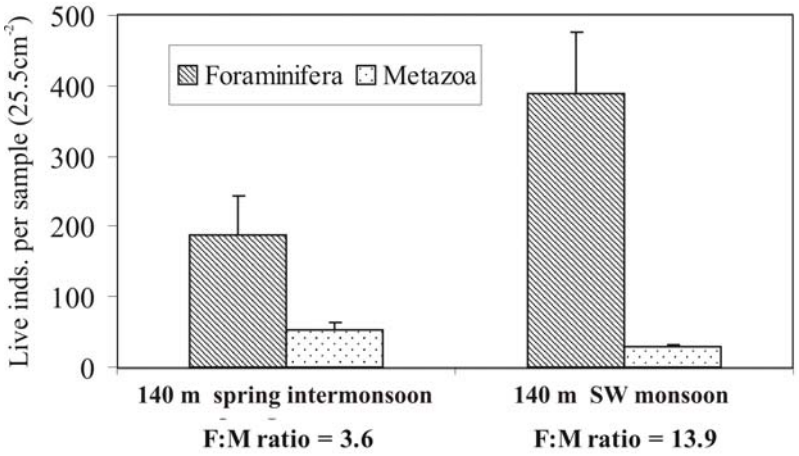
Figure 4.19 140-m site. Vertical distribution of live macrofaunal (>300 µm) metazoan major taxa in the 0-5 cm sediment layer during a) spring intermonsoon, b) SW monsoon. Data are mean values of total live individuals from 4 replicates (25.5 cm^2) per season. y-axis = depth in sediment (cm), x-axis = abundances (no. per core). Error bars are 95% Confidence Intervals. N = Mean total live individuals. ALD_5 = Average Living Depth in 0-5 cm. Mean percentage abundance of total live in the upper 0-1 cm sediment layer is also shown.



4.5.1.4 Foraminifera: Metazoa ratio

Foraminifera greatly outnumbered metazoan macrofauna at 140m, and displayed an increase in dominance following the SW monsoon (Figure 4.20). The ratio between Foraminifera and Metazoa (F:M ratio) varied widely between replicate samples within each season, but was consistently > 3. The mean F:M ratio increased substantially from the spring intermonsoon to after the SW monsoon (from 3.6 to 13.9 respectively) as the mean abundance of macrofaunal metazoans decreased and the mean abundance of macrofaunal Foraminifera increased substantially.

Figure 4.20 140-m site. Mean abundance of live macrofaunal (> 300 µm) Foraminifera and Metazoa in the 0-5 cm sediment layer during spring intermonson and SW monsoon seasons, with the ratio between Foraminifera and Metazoa (F:M ratio) shown for each season sampled (based on mean abundance of 4 replicates per season). 95% Confidence Intervals are shown.



4.5.2 300-m

4.5.2.1 Abundance

Abundances of metazoan macrofauna (> 300 µm) at the 300-m site in the total sample (0-5cm) and the upper 0-1 cm sediment layer are shown in Tables 4.14 and 4.15. (see Appendix C for full abundance data, all vertical sediment layers).

Table 4.14 300-m site. Abundances of living macrofaunal (>300 µm) Metazoa in the 0-5 cm sediment layer. Data are presented for 4 replicates in each season (intermonsoon and monsoon). Total live Foraminifera is given as [1]Total live individuals per sample (25.5 cm^2) and [2]Total live individuals per 10 cm^2. *Mean = Average of 4 replicates.

	spring intermonsoon					SW monsoon				
	55803	55902				56037	561			
	#5	#5	#12	#26	*Mean	#1	05#7	07#6	15#2	*Mean
Amphipoda	0	0	0	0	0.0	0	0	0	0	0.0
Bivalvia	0	0	0	0	0.0	0	0	0	0	0.0
Copepoda	0	0	0	0	0.0	0	0	0	0	0.0
Echinodermata	0	0	0	0	0.0	0	0	0	0	0.0
Gastropoda	0	0	0	0	0.0	0	0	0	0	0.0
Nematoda	11	5	8	24	12.0	21	19	30	21	22.8
Ostracoda	0	0	0	0	0.0	0	0	0	0	0.0
Polychaeta	3	3	5	1	3.0	2	3	0	2	1.8
Total live taxa	1	2	1	2	-	2	2	1	2	-
[1]Total live inds. (sample^{-1})	14	8	13	25	15.0	23	22	30	23	24.5
[2]Total live inds. (10 cm^{-2})	5	3	5	10	5.9	9	9	12	9	9.6

Table 4.15 300-m site. Abundances of macrofaunal (>300 µm) Metazoa in the 0-1 cm sediment layer. Data are presented for 4 replicates in each season (intermonsoon and monsoon). Total metazoans is given as [1]Total individuals per sample (25.5 cm^2) and [2]Total individuals per 10 cm^2. *Mean = Average of 4 replicates.

	spring intermonsoon					SW monsoon				
	55803	55902				56037	561			
	#5	#5	#12	#26	*Mean	#1	05#7	07#6	15#2	*Mean
Amphipoda	0	0	0	0	0.0	0	0	0	0	0.0
Bivalvia	0	0	0	0	0.0	0	0	0	0	0.0
Copepoda	0	0	0	0	0.0	0	0	0	0	0.0
Echinodermata	0	0	0	0	0.0	0	0	0	0	0.0
Gastropoda	0	0	0	0	0.0	0	0	0	0	0.0
Nematoda	11	5	2	21	9.8	20	24	27	21	23.0
Ostracoda	0	0	0	0	0.0	0	0	0	0	0.0
Polychaeta	3	3	6	1	3.5	2	2	0	2	1.5
Total live taxa	2	2	2	2		2	2	2	2	
[1]Total live inds. (sample^{-1})	14	8	8	22	13.0	20	26	27	21	23.5
[2]Total live inds. (10 cm^{-2})	5	3	3	9	5.1	8	10	11	8	9.2

There was a high level of variability between the abundances of metazoan macrofauna in replicate samples, but in general values were low. Total abundances increased from the spring intermonsoon to the SW monsoon. In the 0-5 cm sediment layer, the mean for the total macrofauna was 15 individuals per 25.5 cm^2 (6 per 10 cm^2), increasing to 25 individuals per 25.5 cm^2 (10 per 10 cm^2) following the SW summer monsoon. The total abundances in the 0-1 cm sediment layer followed a similar trend, with the mean total abundances decreasing from 13 individuals per 25.5 cm^2 (5 per 10 cm^2), to 24 individuals per 25.5 cm^2 (9 per 10 cm^2) following the SW summer monsoon.

4.5.2.2 Taxonomic composition

Only two metazoan taxa, Polychaeta and Nematoda, were found at the 300-m site during each season sampled (Figure 4.21). Nematodes were dominant, rising in percentage abundance in the 0-5 cm sediment layer from spring intermonsoon to SW monsoon (80% to 92.9%; 12 to 23 standing crop respectively). This trend was even more apparent in the upper 0-1 cm sediment layer where nematodes increased from 73% to 98% (10 to 23 standing crop respectively).

4.5.2.3 Vertical distribution patterns

The percentage abundance of live Metazoa in the upper 0-1 cm sediment layer increased substantially from 65% to 96% from the spring intermonsoon to the SW (Figure 4.22). Polychaetes constituted 20% of the 0-5 cm assemblage during the spring intermonsoon and monsoon. This was reflected in a shallowing of the Average Living Depth following the SW monsoon from ALD_5 = 0.65 to ALD_5 = 0.44. Polychaetes were restricted to the upper 0-1 cm sediment layer in both seasons sampled and reduced in percentage abundance to 7.1% following the SW monsoon (26.4% to 6.1% in the upper 0-1 cm). Nematodes penetrated the deepest in the sediment, and displayed a decrease in penetration depth from 0-4 cm during the spring intermonsoon to 0-3 cm following the SW monsoon.

Figure 4.21 300-m site. Mean percentage abundance of major macrofaunal (> 300 µm) metazoan taxa in the 0-5 cm and 0-1 cm sediment layer during spring intermonsoon (a,c) and SW monsoon (b,d) seasons. Data are mean percentage abundance based on 4 replicate multicore (25.5 cm^2) samples per season.

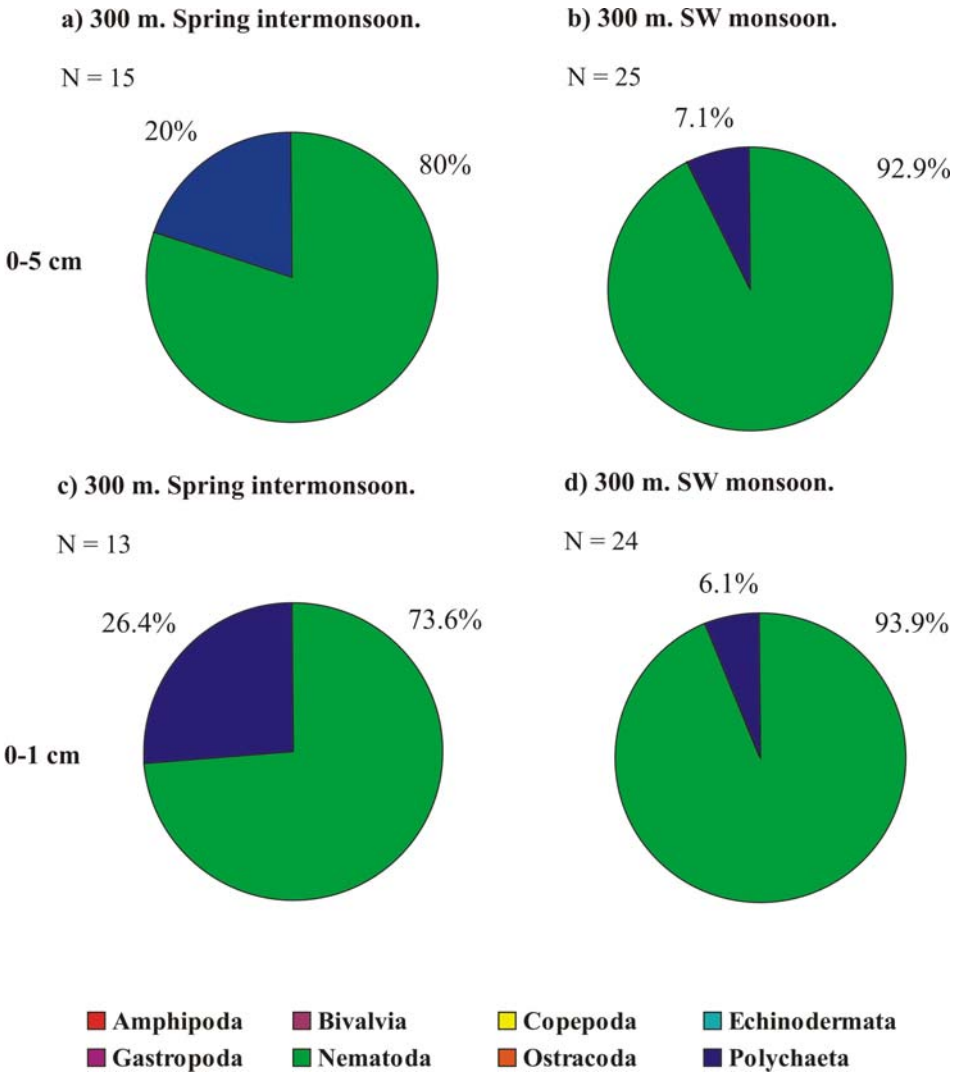
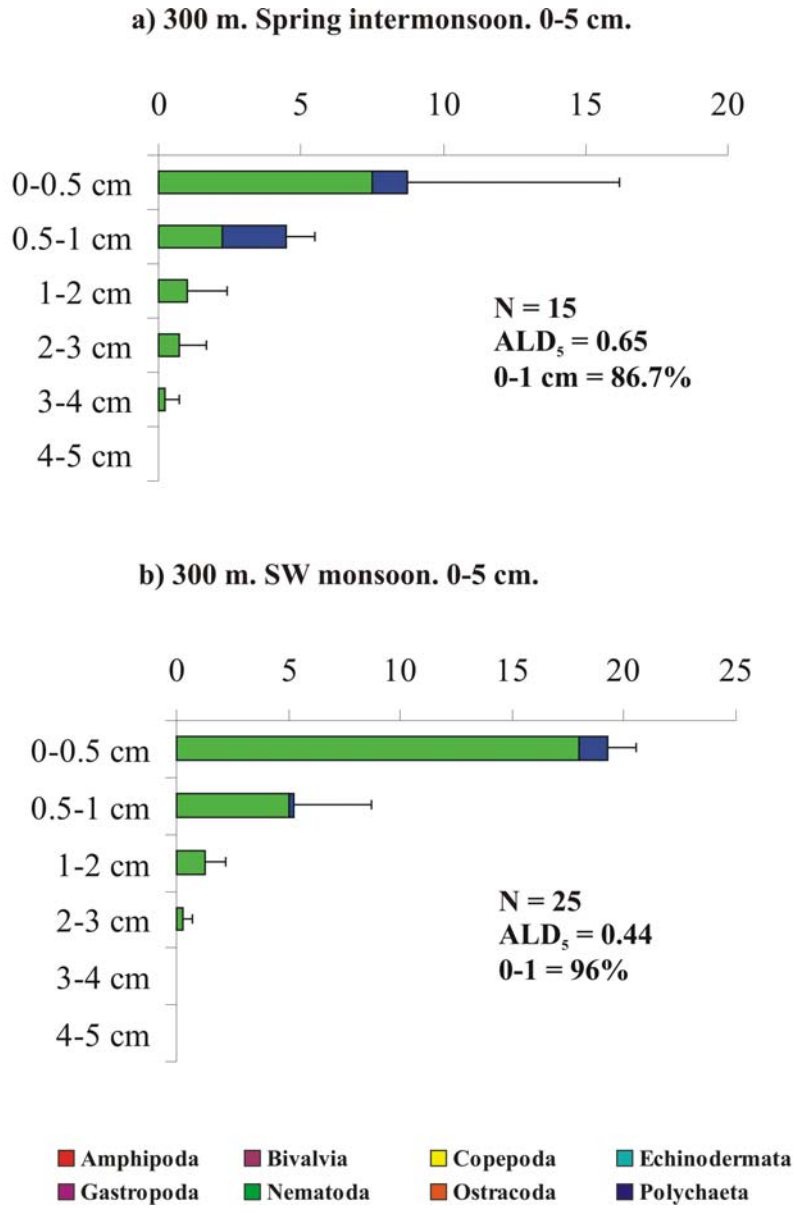


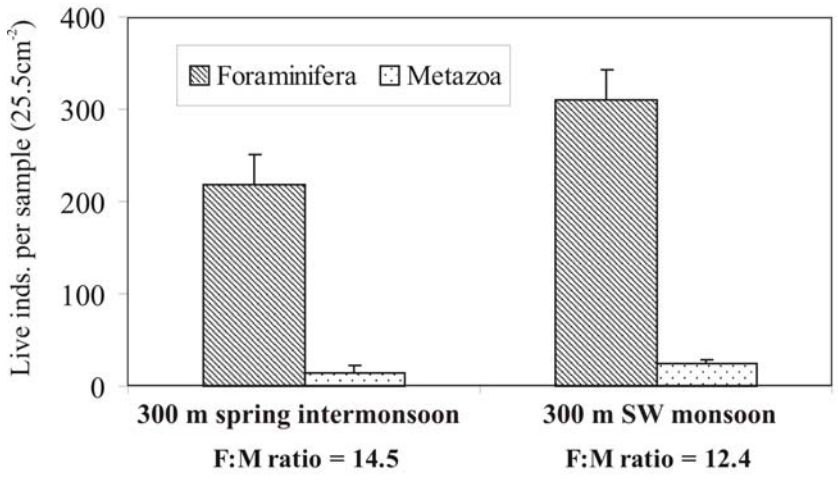
Figure 4.22 300-m site. Vertical distribution of live macrofaunal (>300 µm) metazoan major taxa in the 0-5 cm sediment layer during each season sampled a) spring intermonsoon b) SW monsoon. Data are mean values of total live individuals from 4 replicates (25.5 cm^2) per season. y-axis = depth in sediment (cm), x-axis = abundances (no. per core). Error bars are 95% Confidence Intervals. N = Total live individuals. ALD_5 = Average Living Depth in 0-5 cm. Mean percentage abundance of total live in the upper 0-1 cm sediment layer is also shown.



4.5.2.4 Foraminifera: Metazoa ratio

The F:M ratio was high (F:M = 12.4-14.5) owing to the very low abundances of metazoan macrofauna during both seasons (Figure 4.23). A slight decrease in the F:M ratio following the SW monsoon may reflect the increase in nematode abundance, counterbalancing the increase in abundance of Foraminifera.

Figure 4.23 300-m site. Mean abundance of live macrofaunal (> 300 μm) Foraminifera and Metazoa in the 0-5 cm sediment layer from the spring intermonson and the SW monsoon, with the ratio between Foraminifera and Metazoa (F:M ratio) shown for each season sampled.



4.6 General Discussion

4.6.1 Abundance

A seasonal increase in the total foraminiferal standing stock occurred at both the 140-m site (74 to 153 individuals per 10 cm^2) and 300-m site (86 to 122 individuals per 10 cm^2) from the spring intermonsoon to the SW monsoon respectively. This was driven by the increase in abundance of a few calcareous species, especially *Uvigerina* ex. gr. *semiornata* which displayed an almost 2–fold increase (54 to 118 individuals per 10 cm^2) at the 140-m site and a more modest increase (41 to 69

individuals per 10 cm^2) at the 300-m site over the same time interval. Other dominant species that exhibited an increase in standing stock include the calcareous species *Cancris auriculus* (5 to 16 individuals, 140-m site) and *Bolivina* aff. *dilatata* (1 to 9.8 individuals, 140-m site), and the agglutinated species *Reophax dentaliniformis* (16 to 20.8 individuals, 300-m site). Previous field studies of the dynamics of benthic foraminiferal communities in relation to organic matter have also observed higher numbers of living benthic Foraminifera associated with an increased organic matter input (Gooday 1988; Gooday and Lambshead 1989; Gooday and Turley 1990; Berger and Herguera 1992; Gooday 1993; Pfannkuche 1993; Kitazato and Ohga 1995; Ohga and Kitazato 1997; Smart and Gooday 1997; Gooday and Rathburn 1999). Diz et al. (2006) reported that an increased availability of labile organic carbon on the seafloor in the Ria de Vigo (NW Spain) following an upwelling event and associated flux of phytodetritus to the benthic environment caused an increase in the abundance of the dominant foraminiferal species. Altenbach (1987) reported a significant increase in benthic foraminiferal biomass four weeks after the sedimentation of the spring phytoplankton bloom. In laboratory experiments, Heinz et al. (2001; 2002) showed an increase of foraminiferal abundance twenty one days after the addition of an algal food source in feeding experiments on deep-sea sediments (919 m water depth) from the western Mediterranean. This was interpreted as reflecting reproduction triggered by the higher organic matter levels. The metabolic response of Foraminifera is even faster, occurring within a few days of sedimentation of organic material on the sea-floor (Graf 1989; Heeger 1990; Altenbach 1992; Linke 1992).

There are two possible interpretations of the statistically significant increase in standing stock in some opportunistic species of benthic Foraminifera on the Pakistan margin following the SW monsoon. Firstly, it is likely that some species reproduced in response to the presumed organic matter flux associated with the SW monsoon, or as a result of oxygen stress. Previous studies support the idea that organic enrichment or environmental stress (e.g. oxygen depletion) may induce reproduction. Moodley et

al. (1997) reported a higher mean density of Foraminifera belonging to five dominant genera in the 38-63 μm fraction of sediments from the northern Adraitic Sea exposed to anoxia for a period of eleven days in a microcosm experiment. In another experiment addressing the population response of shallow-water Foraminifera (c. 32 m water depth) from the Adriatic Sea to a simulated phytodetrital flux event, Duijnstee et al. (2005) found an increase in the numbers of small (38-63 μm) benthic Foraminifera following the addition of food, probably a result of rapid reproduction. These studies suggest that juveniles resulting from a reproductive event associated with the SW monsoon on the Pakistan margin will have been concentrated in the < 300 μm fraction which was not examined because of time limitations. It is therefore not possible to demonstrate conclusively that rapid reproduction occurred, based on the present data.

A second interpretation for the significant seasonal increase in live individuals in the > 300 μm size fraction is the rapid growth of smaller individuals already present in the 63-300 μm fraction as a result of feeding on high quality organic matter following the presumed phytodetrital flux event. Some individuals < 300 μm in length during the spring intermonsoon may have ingested enough organic matter of high nutritional value to promote rapid growth and an increase in test length between the two seasons sampled, so that they were retained in the > 300 μm fraction after the SW monsoon. This seems to be the most likely explanation for the increase in abundance. Nevertheless, lack of data for the 63-300 μm fraction means that it is not clear if the dominant foraminiferal species were r-strategists, displaying a quick population growth in reaction to the organic matter flux event, or if they were k-strategists, displaying slower growth combined with reproduction.

4.6.2 Taxonomic composition

4.6.2.1 Calcareous species

Previous observations suggest that calcareous species tend to dominate in low-oxygen/organic enriched areas (e.g. Bernhard and Sen Gupta 1999; Gooday et al. 2000a) and the results of this study support this idea. The foraminiferal assemblage was dominated (>60%) by calcareous Foraminifera at both the 140-m and 300-m sites on the Pakistan margin. The calcareous species *Uvigerina* ex. gr. *semiornata* dominated communities and increased from 54 to 118 live individuals per 10 cm^2 at 140 m and from 41 to 69 individuals per 10 cm^2 at 300 m from the spring intermonsoon to the SW monsoon. Species of the genus *Uvigerina* often occur among low-diversity assemblages in hypoxic environments (Loubere et al. 1995) where they are able to exploit elevated carbon concentrations (Van der Zwaan et al. 1999). Although previous studies have confirmed the frequent association of the genus *Uvigerina* with low bottom-water oxygen values (Lohmann 1978; Streeter and Shackleton 1979; Bernhard 1992; Sen Gupta and Machain-Castillo 1993; Rohling et al. 1997), it is the flux rate of particulate organic carbon and the food supply which seems to be the critical factor in constraining the abundances of species in this genus (Lutze 1986; Altenbach and Sarnthein 1989; Altenbach 1992; Altenbach et al. 1999; Gooday 2003; Licari and Mackensen 2005; Schönfeld and Altenbach 2005). Indeed, the genus *Uvigerina* does not occur exclusively in hypoxic environments and is associated with organic enrichment irrespective of bottom water oxygen concentrations (Corliss et al. 1986; Schönfeld and Altenbach 2005). According to Altenbach et al. (1999), the well-known species *U. peregrina* is most common where flux rates to the seafloor are in the range 2-3 $gC.m^2.yr^{-1}$. *Uvigerina mediterranea*, which is closely similar to *U.* ex. gr. *semiornata*, prefers somewhat higher flux rates (~10 $gC.m^2.yr^{-1}$) while an undescribed species (*Uvigerina* sp. 221) is associated with even more eutrophic conditions (flux rates of 20-30 $gC.m^2.yr^{-1}$).

The common occurrence of many uvigerinids in carbon-rich, and sometimes oxygen-poor conditions makes them useful as 'indicator' species for such areas (Sen Gupta and Machain-Castillo 1993; Kaiho 1994; Thomas and Gooday 1996; Schmiedl and Mackensen 1997; Loubere and Fariduddin 1999; Van der Zwaan et al. 1999; De Rijk et al. 2000; Fontanier et al. 2003; Hess and Kuhnt 1996; Kawagata et al. 2006). Species of *Uvigerina* have been reported fairly often from modern OMZ regions, although this genus is not always present (Bernhard and Sen Gupta 1999, Table 12.2) and is rarely as overwhelmingly dominant as it is on the Pakistan margin. Maas (2000) reported a very similar, probably conspecific species, illustrated as *U. semiornata*, from 200 m on the Pakistan margin. *Uvigerina* ex. gr. *semiornata* was also the dominant foraminiferal species in the > 300 μm size fraction at a 100-m site on the Oman margin, eastern Arabian Sea where it constituted > 46.8 % of the total live assemblage (Aranda da Silva 2005).

Other important calcareous genera found at 140 m and 300 m on the Pakistan Margin include *Bolivina* (*B.* aff. *dilatata*), *Cancris* (*C. auriculus*) and *Globobulimina* (*G.* cf. *G. pyrula*). These genera (represented by *B. seminuda*, *B. inflata*, *C. auriculus*, *G.* aff. *turgida* and *G. turgida*) were also dominant components of the live foraminiferal assemblage at corresponding sites (400 m and 412 m water depth) on the Oman Margin (Gooday et al. 2000a; Aranda da Silva 2005). The genus *Globobulimina* has been linked to high productivity regions (Loubere 1984; Fariduddin and Loubere 1997; Gooday et al. 2001a). However, *in situ* feeding experiments conducted by Nomaki et al. (2005a) suggest that whilst *Globobulimina* spp. ingests fresh labile organic matter (phytodetritus) it shows a slower response to labile organic matter (phytodetritus) compared to other calcareous species. Fontanier et al. (2003) suggest that *Globobulimina* is not able to compete for labile food particles with very opportunistic species living in surficial sediments. Competition with other species, particularly *U.* ex. gr. *semiornata*, may explain the decrease in percentage abundance of *G.* cf. *G. pyrula* at both the 140-m site (3% to 0.9%; standing crop 5.8 to 3.5) and

the 300-m site (7.3% to 5%; standing crop 16 to 18.5) from the spring intermonsoon to the SW monsoon respectively.

Miliolids were rare at both the 140-m and 300-m sites (1 individual at the 140-m site during the SW monsoon season only), an observation consistent with the suggestion by Bernhard and Sen Gupta (1999) that miliolids are generally absent from low-oxygen settings. Miliolids were also rare from the OMZ core on the Oman margin (Gooday et al. 2000a; Aranda da Silva 2005).

4.6.2.2 Agglutinated species

In general, agglutinated Foraminifera are less common in low-oxygen regimes than calcareous species (Bernhard and Sen Gupta 1999). It is therefore surprising that agglutinated species were more common at the persistently hypoxic 300-m site compared to the seasonally hypoxic 140-m site. However, there are examples of agglutinated Foraminifera in low oxygen environments. For example, Bernhard et al. (1997) reports *Trochammina* sp. from the Santa Barbara Basin and Hess and Kuhnt (1996) reported a significant dominance of the agglutinated genus *Reophax* (*R. scorpiurus*, *R. bilocularis* and *R. dentaliniformis*), from oxygen-depleted ashfall layer (2 to 6 cm thick) at three deep-water stations along the western margin of the Philippines resulting from the 1991 Mt. Pinatubo eruption.

In this study, agglutinated species at the both sites were dominated by the genus *Reophax*. Two species of *Reophax* (*R. bilocularis* and *R.* sp. 1) were observed at the 140-m site; *R. bilocularis* was present in the top-10-ranked species during both seasons. At the 300-m site, three species of *Reophax* (*R. bilocularis*, *R.* sp. 2 and *R. dentaliniformis*) were present. *Reophax dentaliniformis* was the most abundant multilocular agglutinated species and the second-ranked species in the foraminiferal assemblage during both seasons, increasing in abundance from 16 to 21 live individuals (per 10 cm^2) from the spring intermonsoon to the SW monsoon and retaining a relatively shallow Average Living Depth (ALD_5 = 0.47-0.49) from the

spring intermonsoon to the SW monsoon. *Reophax dentaliniformis* is commonly regarded as a fairly deep-infaunal species. Its shallower Average Living Depth in the core of the OMZ, may reflect either the influence of low bottom-water oxygen concentrations, or a response to the high organic matter availability at the sediment surface (see below). Although the genus *Reophax* is not commonly associated with low oxygen/high organic enrichment areas, the presence of Re*ophax* spp. in persistently hypoxic sediments at the boundary and in the core of the Pakistan margin OMZ, together with the observation by Bernhard et al. (1997) of *Reophax* spp. in the hypoxic Santa Barbara Basin, suggests that this genus can tolerate low-oxygen concentrations and may even be able to exploit the high availability organic matter in such areas. However, it appears that *Reophax* is not always present in oxygen–deficient environments. For example, *Reophax* aff. *advenus* was the second most abundant foraminiferal species at a 100-m site (O_2 = 0.46 mll^{-1}) on the Oman margin, northeastern Arabian Sea, but live individuals of *Reophax* were absent at a site within the core of the Oman margin OMZ (400 m, O_2 = 0.13 mll^{-1}) (Aranda da Silva 2005).

Most agglutinated foraminiferal species did not display any clear response to the presumed flux of organic matter to the seafloor during the SW monsoon. Indeed, many species decreased in abundance at both 140 m and 300 m on the Paksitan margin following the SW monsoon. However, the increase in abundance of *Reophax dentaliniformis* suggests that this species responded in some way to an input of labile organic matter. This contradicts previous studies that found that agglutinated species do not respond positively to inputs of labile organic matter or feed preferentially on phytodetrital food sources (Gooday et al. 2002c). Instead, the increase in the abundance of *R. dentaliniformis* may reflect an indirect response to the organic matter flux, which presumably leads to an increase in bacterial biomass, a potential food source for this species, following the SW monsoon.

4.6.2.3 Monothalamous species

Monothalamous Foraminifera, including allogromiids, saccamminids and other unilocular agglutinated species, constituted a minor component of the live assemblages; 2 - 6% at the 140-m site and 9% at the 300-m site. Such taxa are generally rare in hypoxic settings as they are considered to be more sensitive to hypoxia/anoxia than hyaline calcareous or agglutinated species (Bernhard 1999). Allogromiids and saccamminids have been reported occasionally from other severely hypoxic settings including the Black Sea (Gooday et al. 2006) and the Santa Barbara Basin (Bernhard et al. 2003) and their presence at the permanently hypoxic 300-m Pakistan margin site suggests that some species can tolerate low-oxygen conditions. Allogromiids were also found at a site within the core of the Oman margin OMZ (400 m, O_2 = 0.13 ml^{-1}) and represented a surprisingly large percentage (10.4%) of the total live assemblage (> 300 μm) (Aranda da Silva 2005). However, Gooday et al. (2000a) reported that soft-shelled allogromiids and saccamminids were only a minor faunal element in the >63 μm size fraction at the same site. Monothalamous Foraminifera also show an overall decline in their total abundance and diversity between the spring intermonsoon and the SW monsoon at both sites sampled in this study, possibly linked to the increased competition for food from the much more abundant calcareous species.

Other monothalamous species found on the Pakistan margin include two small, undescribed, bathysiphonids (*Bathysiphon* spp.) which occur in the core of the OMZ (300 m) and in one case (*Bathysiphon* sp. nov. 1), at the 140-m site at the upper boundary of the OMZ. These species were rare (< 4 individuals of each species at each site/season sampled). However, they are important since small *Bathysiphon* species were also reported in two separate studies at a site within the OMZ core (400-412 m water depth, O_2 ~ 0.13 ml^{-1}) on the Oman margin (Gooday et al. 2000a; Aranda da Silva 2005) and are known from other organic-rich environments, such as the Gullmar Fjord, Sweden (Höglund 1947).

4.6.3 Diversity

Wet sorting revealed low-diversity assemblages with thirty six species identified at the two sites sampled. Diversity was not greatly affected by water depth or season. An average of 16 species was observed at the 140-m site during the spring intermonsoon. The number of species found in each replicate was highly variable, probably owing to the small-scale patchiness of the benthic environment. Following the SW monsoon and the associated shift to a hypoxic environment at the 140-m site, the number of species recorded was reduced to 12, presumably as a response to the oxygen-deficient bottom water encompassing the whole site. Only a few opportunistic species (most of them calcareous) did well under these conditions, leading to an increase in dominance, particularly by *Uvigerina* ex. gr. *semiornata*. At the 300-m site, the low diversity assemblage reflected persistent hypoxia. The slight decrease in diversity indices (but not species richness) and the corresponding increase in dominance during the SW monsoonal period, was due to the increased abundance of *U.* ex. gr. *semiornata*. These results support the general observation that macrofauna (> 300 μm) in disturbed and/or organically enriched areas often exhibit depressed diversity (e.g. Levin and Gage 1998; Levin et al. 2000; Glover et al. 2001)

4.6.4 Vertical distribution in the sediment

4.6.4.1 Population-level patterns

A comparison of the vertical distribution of Foraminifera at the seasonally hypoxic 140-m site and the permanently hypoxic 300-m site along the Pakistan continental margin provided some insight into the effect of food and bottom-water oxygen concentration on the vertical distribution of the live Foraminifera within the sediment. Table 4.16 summarises the Average Living Depth (ALD_5) and the percentage of live Foraminifera in the upper 1 cm sediment layer for the 140-m and 300-m sites during the spring intermonsoon and the SW monsoon. An upward vertical migration of Foraminifera was observed in sediments at both sites following

the SW monsoon. This was reflected in both a shallowing of the Average Living Depth of the foraminiferal assemblage, and an increase in the percentage abundance in the upper 1 cm of the sediment following the SW monsoon (Table 4.16).

Table 4.16 Mean vertical distribution of Foraminifera at 140 m and 300 m during spring intermonsoon (April 2003) and SW monsoon (October 2003). Data shown are Average Living Depth in the total sample (0-5 cm). Percentage of live Foraminifera in the upper 1 cm is shown in brackets.

	140-m site	300-m site
ALD_5 spring intermonsoon	0.57 (89.0 %)	0.41 (93.5 %)
ALD_5 SW monsoon	0.39 (98.5 %)	0.33 (97.6 %)

In general, these results support the findings of the TROX model of Jorissen et al. (1995). This proposes that the depth to which foraminiferal species occur in the sediment is dependent on a balance between food and oxygen availability (see Chapter 2). The general concentration of Foraminifera in the surface layers of samples from 140 m and 300 m is consistent with this model. In particular, the restriction of most live individuals to the upper 1 cm of sediment at the persistently hypoxic 300-m site, is not unexpected. Presumably, they are forced to the surface by lack of oxygen. However, at the seasonally hypoxic 140-m site, live Foraminifera were still generally restricted to the upper 1 cm of the sediment, even during the spring when oxygen levels were 2.05 ml^{-1}. The slightly deeper Average Living Depth of Foraminifera at the 140 m site during the spring intermonsoon may be explained by the relatively high oxygen levels combined with a higher abundance of metazoa and consequent higher degree of bioturbation at this site. This may have facilitated a deeper oxygen penetration and downward biotransport of food (Levin et al. 1997) enabling Foraminifera to colonise deeper vertical layers within the sediment. The subsequent shallowing of the Average Living Depth at 140 m during the SW monsoon season could be interpreted as a response by the Foraminifera to the sharp decrease in bottom-water oxygen concentration at this time of year. At 300

m, there is a less pronounced seasonal shallowing of the Average Living Depth. Assuming that this change is real, it is probably a response to an increased food supply following the SW monsoon, since bottom water oxygen concentrations are relatively stable over the monsoonal cycle in the OMZ core. Thus, is seems likely that the vertical distribution of the Foraminifera at these sites is influenced by the increase in labile organic matter on the seafloor surface following the presumed phytodetrital flux associated with the SW monsoon and by oxygen profiles within the sediment.

The idea that food and oxygen exert a strong influence on sediment penetration by benthic Foraminifera is consistent with other studies. There is considerable evidence that food (carbon content) is the main factor driving the population dynamics of benthic Foraminifera (Jones and Ross 1979; Altenbach 1992; Gooday 1994; Rathburn and Corliss 1994; Basson and Murray 1995; Mackensen et al. 1995; Murray and Alve 2000; Altenbach et al. 2003). It has also been suggested that seasonal deposition of phytodetritus may cause some species to migrate towards the surface in order to exploit and utilize labile organic matter (Gooday 1988; Gooday and Lambshead 1989; Gooday and Turley 1990; Gooday 1993; Kitazato and Ohga 1995; Kitazato et al. 2000). On the other hand, seasonal vertical migration of Foraminifera at a bathyal site (1450 m) in Sagami Bay, Japan, is believed to reflect a change in thickness of the oxygenated sediment layer as a result of phytodetritus deposition, rather than, or in addition to, a direct response to the phytodetritus itself (Kitazato and Ohga 1995; Ohga and Kitazato 1997).

Further evidence of how food availability can influence the vertical distribution of Foraminifera has emerged from experimental studies. For example, Nomaki et al. (2005a) observed an upwards migration of Foraminifera following a simulated pulse of phytodetritus to the seafloor during *in situ* experiments using sediments from Sagami Bay. However, Heinz et al. (2001, 2002) observed no migration of deep-sea Foraminifera to the upper sediment layers following the addition of three different

algal food sources (*D. tertiolecta*, *Amphiphora* sp. and *Pyramimonas* sp.) in laboratory feeding experiments on sediments collected from the western Mediterranean Sea (919 m water depth).

4.6.4.2 Species-level patterns

In oxygenated settings, benthic Foraminifera colonise deeper sediment layers with individual species tending to live in particular vertical microhabitats (Corliss 1985; Gooday 1986; Jorissen 1999), although the levels that they occupy are not consistent from place to place. It has been suggested that different microhabitats reflect feeding preferences as well as tolerances to oxygen (Nomaki et al. 2005a). In the Pakistan Margin OMZ, individual species were generally restricted to the upper 1 cm sediment layer and even typically deep-infaunal species such as *Globobulimina* cf. *G. pyrula* displayed relatively shallow Average Living Depths ($ALD_5 < 1.21$).

A seasonal comparison of the Average Living Depth of individual species was relatively inconclusive. However, a few species displayed a consistent pattern of seasonal vertical migration. The Average Living Depth of *Uvigerina* ex. gr. *semiornata* and *Cancris auriculus* became shallower from the spring intermonsoon to the SW monsoon season (*U*. ex. gr. *semiornata* at 140 m and 300 m; *C. auriculus* at 140 m only). Although a lack of oxygen is probably one factor driving these species towards the sediment surface (especially at the seasonally hypoxic 140-m site), the shallowing of the Average Living Depth following the SW monsoon may also be a response to the presumed deposition of labile organic matter (phytodetritus) on the sediment surface during this season. Changes in the vertical distributions of other species were more puzzling. *Globobulimina* cf. *G. pyrula* underwent a shallowing of its Average Living Depth at the 300-m site following the SW monsoon, compared to a deepening of its Average Living Depth at the 140-m site. The direction of movement at 300 m suggests a response to the increased food availability on the sediment surface (similar to *U*. ex. gr. *semiornata* and *C. auriculus*). However, the deepening of the Average Living Depth of this species at

140 m is unexpected, since the 140-m site was seasonally hypoxic during the SW monsoon.

4.6.5 Response of the metazoan macrofauna

A 'community-level' response and a strong coherence between foraminiferal and metazoan abundance across strong environmental gradients of organic enrichment or bottom-water oxygen has been observed in previous studies, e.g. on the Peru margin OMZ (Levin et al. 2001) and the north Carolina margin (Gooday et al. 2001a). However, the present study reveals contrasting responses of Foraminifera and Metazoa to oxygen and food availability. At 140 m, the total foraminiferal assemblage increased in abundance, whilst the total metazoan assemblage declined (21 to 11 individuals per 10 cm^{-2}) from the spring intermonsoon to the SW monsoon. The Foraminifera:Metazoa ratio (F:M ratio) increased from 3.6 (spring intermonsoon) to 13.9 (SW monsoon) at the 140-m site. At the 300-m site, the Foraminifera and Metazoa both increased in abundance; the F:M ratio was > 12 during both seasons, and declined only slightly from 14.5 to 12.4 from the spring intermonsoon to the SW monsoon. These different temporal responses presumably reflect the greater tolerance of Foraminifera (as a group) to hypoxia compared to Metazoa. This is consistent with previous evidence from both field and experimental studies (Josefson and Widbom 1988; Moodley et al. 1998).

The different responses by the metazoan assemblages at the 140-m and 300-m sites reflects differences in their taxonomic composition. At the 140-m site, between 5 and 8 different taxa were present, including polychaetes, amphipods, bivalves, echinoderms, gastropods, ostracods, copepods and nematodes. The apparent lack of change in the metazoan macrofauna at the higher taxon level between seasons, however, may have masked a response at the species level. At 300 m, a sparse, macrofaunal metazoan community consisting only of nematodes with occasional polychaetes was associated with the persistently hypoxic conditions and exhibited

few obvious differences before and after the SW monsoon. The abundance of metazoan macrofaunal groups may be primarily influenced by oxygen concentration (Levin et al. 2000). This explains the lower higher-taxon diversity and abundance of the metazoan macrofauna at the persistently hypoxic 300-m site compared to the seasonally hypoxic 140-m site. Levin et al. (1997) found high abundances of metazoan macrofauna (123 individuals per 10 cm^2) at a site in the core (400 m) of the Oman margin OMZ. Here, macrofaunal Metazoa were more abundant than Foraminifera (72 individuals per 10 cm^2). However, this may be explained by the slightly higher bottom water oxygen concentrations (~ 0.13 mll^{-1}) in the Oman margin OMZ core (Gooday et al. 2000a) compared to the Pakistan OMZ.

Metazoan meiofaunal taxa tend to be more tolerant than macrofaunal taxa to hypoxia (Josefson and Widbom 1988) and previous studies have shown that low oxygen does not affect nematode abundance (Levin et al. 1991; Lambshead et al. 1994; Cook et al. 2000). On the Pakistan margin, average nematode abundance was constant at the 140-m site within the upper boundary of the OMZ (7 individuals per 10 cm^2 during both seasons sampled) and was higher at the 300-m site within the OMZ, increasing in abundance from 5 to 9 individuals per 10 cm^2 from the spring intermonson to the SW monsoon. Cook et al. (2000) reported similar results on the Oman margin. They found a significantly higher abundance of nematodes at 700 m within the OMZ than at oxygenated sites below the OMZ (1250 m and 3400 m). At the 300-m site on the Pakistan margin, and at a corresponding site on the Oman margin (Gooday et al. 2000a), nematodes were the only meiofaunal metazoan group present. Here, Cook et al. (2000) found a close coupling between nematode abundance and food input. These results suggest that nematodes (as a group) are not affected by the low oxygen concentrations and, like Foraminifera, can take advantage of the high organic matter availability within OMZs (see also Neira et al. 2001). Similarly, the increase in nematode abundance from the spring intermonsoon to the SW monsoon at the 300-m site is likely be a response to the phytodetrital flux associated with the SW monsoon. In previous studies nematode abundances have been found to increase following a

phytodetrital flux to the seafloor (Poremba 1994). However, there is no evidence that nematodes directly exploit phytodetritus and the increase of abundance in nematodes may therefore reflect an indirect response to a flux event involving the consumption of bacteria (which increase in biomass following a phytodetrital flux event) in surficial sediments rather than the direct exploitation of phytodetritus.

4.6.6 Limitations of this study

Data from size fractions < 300μm (63-300μm fraction) would considerably enhance understanding of the benthic foraminiferal population dynamics since many smaller species and juvenile specimens of larger species are present in these finer fractions. Such data would provide much valuable information about growth rates and reproduction patterns. Time constraints have also limited this study to two sites on the OMZ transect. Examination of additional sites would provide a full picture of community changes across the OMZ.

4.7 Conclusions

This study focuses mainly on 'live' benthic Foraminifera in the macrofaunal size range (> 300 μm). The oxygen-deficient benthic environment within the Pakistan Margin OMZ promotes a low diversity assemblage dominated (> 60 %) by calcareous species at 140 m and 300 m. Thirty six species were recorded at the two sites and diversity was not greatly affected by water depth or season. Agglutinated and monothalamous (including soft-shelled) taxa were present, but relatively rare, except for the genus *Reophax* which was relatively abundant, particularly in the core of the OMZ. At both sites, Foraminifera were generally (>86 %) restricted to the upper 0-1 cm layer of sediment and a shallowing of the Average Living Depth was observed from the spring intermonsoon to the SW monsoon. Metazoans were fairly common (means of 11 - 21 individuals per 10 cm^2) at 140 m site, and Foraminifera were 3.6 to 13.9 times more abundant than Metazoa during the spring intermonsoon and the SW monsoon respectively. Metazoans were rare at the 300 m (means of 6 -

10 individuals per 10 cm^2) and Foraminifera were 12.4 to 14.5 times more abundant than Metazoa. A few opportunistic foraminiferal species increased in abundance following the SW monsoon. One of these species, the buliminid *Uvigerina* ex. gr. *semiornata*, dominated communities at 140 m and 300 m and increased significantly in standing stock at both sites following the SW monsoon (140 m, 54 to 118 individuals per 10 cm^2; 300 m, 41 to 69 individuals per 10 cm^2). The Nematoda was the only metazoan group to also increase in abundance at the 300-m site following the SW monsoon. These results indicate that low oxygen concentrations (down to 0.1 $ml l^{-1}$) does not affect the abundance of deep-sea Foraminifera and nematodes and that these groups are strongly correlated with food availability. Calcareous species, in particular *U.* ex. gr. *semiornata*, appear to play a central role in the upper OMZ of the Pakistan Margin OMZ. More generally, these results suggest that Foraminifera may become key players in benthic OM cycling across increasing areas of the sea-floor, as areas of hypoxia continue to expand in the world's oceans.

5 Selective feeding by benthic Foraminifera in the upper part of the Pakistan margin oxygen minimum zone

5.1 Introduction

Benthic Foraminifera are among the most abundant eukaryotic organisms living on the seafloor. These protists are especially abundant in hypoxic settings, where they often dominate the biomass along with bacteria. Under these conditions, Foraminifera play a key role in carbon consumption and cycling on the seafloor. It is therefore important that the trophic ecology of Foraminifera is investigated so that their role in benthic carbon cycling can be better understood.

In this study, fatty acid biomarkers were used to conduct the first comprehensive analysis of foraminiferal feeding behaviour within an Oxygen Minimum Zone (OMZ) ($O_2 \leq 0.5$ $ml l^{-1}$). The feeding behaviour of six abundant species of Foraminifera was assessed in cores recovered from the Pakistan continental margin at a water depth of 300 m, a permanently hypoxic site in the core of the OMZ, where the bottom-water oxygen concentration was ≤ 0.11 $ml l^{-1}$. Samples were taken during the spring intermonsoon and following the summer SW monsoon in order to assess the effect on the foraminiferal diets of a phytodetrital flux event to the seafloor that is presumed to have occurred during the SW monsoon. In addition, the feeding behaviour of the most abundant foraminiferan in the upper OMZ, *Uvigerina* ex. gr. *semiornata*, was compared at two contrasting sites, the above-mentioned 300-m site and a seasonally hypoxic ($O_2 \leq 0.5$ $ml l^{-1}$) site on the continental slope (140 m water depth). The fate of a seasonal flux of organic matter (OM), including fresh phytoplankton-derived material following the summer SW monsoon, is discussed in terms of the role of individual species of Foraminifera in organic matter degradation and cycling in an oxygen-depleted benthic environment.

5.2 Materials and Methods

5.2.1 Sampling procedure and laboratory processing

Sediment cores for the analysis of foraminiferal feeding behaviour were obtained using a megacorer. Replicate cores (78.6 cm^2 surface area) were collected from the 140-m and 300-m sites during two seasons, the spring intermonsoon (March-May 2003, and the SW monsoon (August-October 2003) (See chapter 3 for a description of locality). None of the cores recovered had visible phytodetritus layers which prevented any analysis of the phytodetritus itself. The evidence that a flux event did occur is summarised in chapter 3.

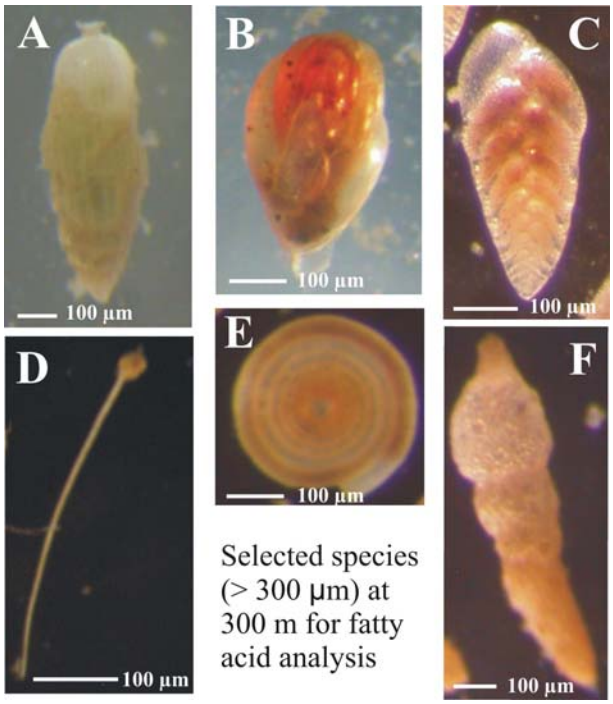
Each core was sliced into 1 cm thick layers to a depth of 5 cm. For foraminiferal fatty acid analysis, only individuals from the top 0-1 cm of the sediment were used. The top 1 cm sediment layer was sieved wet on a 300-µm screen. The sieved residue was then kept chilled (< 5 °C) in a refrigerator or over ice to prevent decomposition of the foraminiferal fatty acids and macrofaunal Foraminifera were sorted as quickly as possible from the sieved residue under a low-power binocular microscope. Samples were kept in a small glass petri dish containing chilled, filtered seawater which was placed in a larger dish filled with ice. An organic stain such as rose Bengal could not be used to assess if the Foraminifera were "live" as this could potentially alter their fatty acid composition. Instead, specimens were judged to be live (and therefore feeding) at the time of sampling based on the presence of obvious test contents in most or all constituent chambers. Unstained cytoplasmic colouration varied from species to species, and included greens and reds. Foraminifera were sorted into individual species and cleaned in filtered (2 µm screen) seawater to remove any attached organic particles. Thirty individuals of a particular species were then placed into 1.1 ml glass vials and frozen at –20 °C prior to extraction of fatty acids.

5.2.2 Foraminiferal species analysed for fatty acid content

The persistently hypoxic ($O_2 \leq 0.11$ ml^{-1}) 300-m site was chosen to compare the feeding behaviour of different species of Foraminifera because most live individuals were restricted to the upper 1 cm of the sediment (93.5 % during spring intermonsoon rising to 97.6 % during the SW monsoon; Chapter 4) therefore limiting the vertical distribution of different species in the sediment and associated differences in food availability and quality. This enabled any trophic differences between species to be more clearly interpreted as species-specific responses to the organic matter available instead of reflecting microhabitat preferences. Six of the top-10 ranked species, in terms of abundance**,** in the live foraminiferal assemblage at 300 m were sorted from the > 300-µm fraction in order to obtain sufficient biomass for fatty acid analyses. These included three calcareous species, *Uvigerina* ex. gr. *semiornata*, *Bolivina* aff. *dilatata*, *Globobulimina* cf. *G. pyrula* and three agglutinated species, *Ammodiscus* aff. *cretaceus*, *Bathysiphon* sp. nov. 1 and *Reophax dentaliniformis* (See Appendix A for taxonomic notes and figures of each species) (Figure 5.1). This diverse group of species was chosen in order to explore whether individual species living in the same environment reflected different feeding patterns. The astrorhizid *Bathysiphon* sp. nov. 1 was the only monothalamous species analysed for fatty acid content since other monothalamous species, namely allogromids and saccamminids, were not present in high enough numbers.

Uvigerina ex. gr. *semiornata*, the dominant foraminiferan in the upper OMZ was further analysed for its fatty acid content at both the seasonally hypoxic 140-m site and the permanently hypoxic 300-m site during the spring intermonsoon and the SW monsoon. This was in order to assess how foraminiferal feeding behaviour is affected by changes in the quality and quantity of organic matter as a result of different biogeochemical conditions and oxygen regimes during these two seasons.

Figure 5.1 Six foraminiferal species (> 300 µm) at the 300-m site selected for fatty acid analysis. A. *Uvigerina* ex. gr. *semiornata*. B. *Globobulimina* cf. *G. pyrula*. C. *Bolivina* aff. *dilatata*. D. *Bathysiphon* sp. nov. 1. E. *Ammodiscus* aff. *cretaceus*. F. *Reophax dentaliniformis*. A-C are calcareous species. D-F are agglutinated species. Shipboard photographs of unfixed specimens.



5.2.3 Fatty acid analysis

The foraminiferal fatty acids were prepared as PFB (Pentafluorobenzyl) Esters, following a method adapted from Sonesson et al. (1987) and Guezennec et al. (1996), and analysed on a gas chromatograph coupled to an electron capture detector (GC-ECD). This approach, which is not often used by marine ecologists, was adopted because of the limited numbers of foraminiferal specimens available and the high sensitivity of the PFB ester derivative method. The method generates data expressed as Mol % and not weight percent as with conventional FID-GC. It was used successfully in previous studies of foraminiferal fatty acid analysis (Suhr et al. 2003; 2006; Ward et al. 2002; 2003; Topping et al. 2006).

5.2.3.1 Glassware

To prevent the contamination of samples, a series of sterilisation stages was carried out throughout the laboratory procedure. All glassware used in any stage of the fatty acid analysis was first thoroughly soaked and washed with industrial detergent (Decon), rinsed in hot tap water and soaked for a minimum of 12 hours in distilled water. The glassware was then further sterilised by heating in a muffle furnace at 550 °C for 12 hours. As an added precaution, each vial, syringe and glass pipette used in the laboratory procedure was rinsed with solvent (Chloroform : Methanol 2:1 v:v) prior to the addition of any reagent or sample. Open-top caps with removable Teflon-coated septa were used for each sample and discarded after a single use.

5.2.3.2 Total lipid extraction

Each sample for fatty acid analysis contained 30 live Foraminifera stored in a 1.1 ml borosilicate glass vial with Teflon-lined screw-caps. Lipids were first extracted by adding 500 µl Chloroform : Methanol (2:1 v:v) solution (Folch et al. 1957) and the sample stored at –20 °C for at least 24 h to ensure full extraction of lipids. Five µl of either 21:0 or 23:0 (fatty acids that were rare or absent from the natural environment) were then added to each sample as an internal standard to enable quantification of fatty acids in the Foraminifera. Following this, 125 µl of 0.88 % Potassium Chloride (wt/v) was added. Each sample was thoroughly mixed using a vortex mixer and the upper aqueous layer discarded. Solvent was removed from the remaining organic layer containing the fatty acids by being 'blown down under nitrogen' using a nitrogen evaporator.

5.2.3.3 Saponification

Free fatty acids were then produced from the organic layer by saponification (alkaline hydrolysis) of the sample at 78 °C for 1 hour after adding 100 µl Potassium Hydroxide (1 M in 95% Ethanol). This was followed by a brief period of cooling,

and then 250 µl H_2O was added to each vial and ca. 1-2 drops of 0.8 M Hydrochloric acid were used to acidify the sample. The low pH of the sample was checked using pH paper and then the free fatty acids were extracted from the sample through a series of solvent washes. First, 250 µl Diethyl Ether was added to the sample and the sample was thoroughly mixed using a vortex mixer. The upper organic layer was then extracted and transferred to a second clean vial. This was then repeated and a further 250 µl Diethyl Ether was added to the original vial, mixed thoroughly and the upper organic layer extracted. This second wash was to ensure the complete extraction of fatty acids. Samples were then 'blown down under nitrogen' using a nitrogen evaporator to remove any excess solvent.

5.2.3.4 Derivatization

The free fatty acids were derivatized to Pentafluorobenzyl (PFB) Esters to enable detection of the fatty acids on a gas chromatograph coupled to an electron capture detector (GC-ECD). Derivatization was achieved by adding 30 µl Acetonitrile, 100 µl 3.5% PFB in Acetonitrile and 100 µl Triethylamine to each of the samples, agitating the sample between the addition of each reagent. Samples were left for 15 minutes at room temperature and agitated occasionally to aid the reaction. In order to extract the fatty acid PFB Esters, 500 µl Isooctane was added to each sample, and the vial was thoroughly mixed using a vortex mixer and centrifuged. The upper layer containing the fatty acids was transferred into a new vial. This procedure was then repeated and the new vial containing the fatty acid PFB Esters was 'blown down under nitrogen' using a nitrogen evaporator to remove solvents.

5.2.3.5 Purification

High Performance Thin-Layer Chromatography (HPTLC) was used to purify the fatty acid PFB Esters. HPTLC plates were first prepared by placing them in a mixture of Hexane : Diethyl Ether : Acetic Acid (18 : 2 : 0.2 ml). The plates were removed from this solvent mix before the solvents reached the top of the plate, and

left to dry briefly. 200 µl Isooctane was added to each sample and samples were individually transferred to form a concentrated dot at the base of the HPTLC plate (4 samples per HPTLC plate). A PFB Ester standard was also added to the base of the plate to allow identification of the bands containing the PFB Esters. The samples were left to dry briefly and then the HPTLC plate was placed in a fresh mixture of Hexane : Diethyl Ether : Acetic Acid (18 : 2 : 0.2 ml) and the samples were left to run together. Plates were dried briefly, sprayed with 2'-7'- Dichlorofluorescein (DFC) dissolved in Methanol. Plates were subsequently dried under vacuum prior to placing under UV light to identify the location of the PFB Ester groups on the HPTLC plate. The area containing the purified PFB Esters for each sample was scraped off and transferred into a vial containing 2 ml Isooctane. 1 ml $NaHCO_3$ was then added and shaken thoroughly. The samples were then frozen at – 20 °C for a minimum of 1 hour to allow the aqueous layer to freeze. The liquid organic layer containing the fatty acids PFB Ester was then removed into a new vial and the organic layer was then 'blown down under nitrogen' to evaporate any remaining solvent. Before the sample was completely dry, it was transferred to a 1.1ml vial and 'blown down' further. 100 µl Isooctane was then added and the sample frozen at – 20 °C prior to analysis on a GC-ECD.

5.2.3.6 Gas Chromatograph Electron-Capture Detector

Fatty acid PFB-Esters were analysed on a Gas Chromatograph (Carlo-Erba Trace 2000 series) coupled to an Electron Capture Detector (ECD) fitted with a ZBWAX fused silica capillary column (30 m length and 0.32 mm internal diameter). Each sample was injected in a volume of 1 µl. Hydrogen was used as a carrier gas (2 ml min^{-1}) and Nitrogen as the make-up gas (at a flow rate of 35 ml min^{-1}). A three-stage temperature programme was run; initial temperature 80 °C, increasing to 190 °C at a rate of 40 °C min^{-1} and then to 230 °C at 4 °C min^{-1}, after which the temperature remained constant at 230 °C for 47 minutes.

5.2.3.7 Identification of individual fatty acids and biomarker groups

The fatty acid standard Marinol (derivatised as a PFB Ester) was used to identify each individual fatty acid from the chromatogram produced. Only those fatty acids readily identified by the gas chromatograph, and with a known organic matter source from previous studies, were further analysed. Table 1 in Appendix B gives a list of the fatty acids analysed in this study and their suggested sources and potential for use as biomarkers with corresponding references from previous studies. Fatty acids of known phytodetrital/algal origin include long-chain polyunsaturated fatty acids including Eicosapentaenoic acid (EPA) 20:5(*n*-3), 20:4(*n*-3), 18:3(*n*-3), 18:4(*n*-3), and 16:4(*n*-1). However, care must be taken when interpreting sources of fatty acids. For example, 20:5(*n*-3) has also been found in high concentrations in deep-sea bacteria (Delong and Yayanos 1986). Characteristic bacterial biomarkers include high amounts of branched chain fatty acids, 15:1, 17:0, 17:1 and 18:1(*n*-7). The ratio between two 18:1 fatty acids, 18:1(*n*-9) and 18:1(*n*-7) is also commonly used as an indicator of feeding behaviour and levels of bacterial ingestion (Yano et al. 1997). 18:1(*n*-9) is found in many algal classes but can also be synthesised *de novo* from 18:0 by most metazoan organisms. It is also speculated to be a storage reserve in many deep-sea organisms (Lewis 1967; Morris 1971a; Morris 1971b; Albers et al. 1996; Parrish and Wangersky 1990; Kattner and Hagen 1998; Pond et al. 2000a). However, whilst there is evidence that 18:1(*n*-7) can be produced by metazoan organisms via carbon chain elongation of 16:1(*n*-7) (Sargent and Henderson 1986), it is also present in large amounts in bacteria. High concentrations of 18:1(*n*-7), and thus a low ratio of 18:1(*n*-9) to 18:1(*n*-7), therefore reflect a diet rich in bacteria. Fatty acid data in this study are presented as Mol percentage composition (%) to give an indication of the relative proportions of fatty acids in each sample (30 Foraminifera), and as weight (ng) per sample (30 Foraminifera) quantified from the internal fatty acid standard. Care must be taken therefore in interpreting the results since, for example, a decrease in percentage composition of a particular fatty acid from the spring intermonsoon to SW monsoon season may reflect an increase in another fatty acid.

5.2.4 Statistical analysis

The software PRIMER (version 5.1) (Clarke and Warwick 1994, Carr, 2001) was used to perform multivariate statistical analysis (multidimensional scaling and ANOSIM, one-way analysis of similarity) on square-root transformed data (total fatty acids; Mol %; four replicates per species for each season). Multidimensional scaling (MDS) constructs a "map" or configuration of samples from a (dis)similarity matrix, by ranking the similarities of each sample. It therefore enables an interpretation of the relative values of similarity of samples to each other, since samples with the highest similarity to each other will be positioned closest on the MDS plot. The ANOSIM statistical test was conducted to assess the similarities and compare the total fatty acid profile (percentage composition, Mol %) of different species and of any seasonal changes in fatty acids for an individual species. Results of the ANOSIM test for similarity are presented in the text using a P value for the level of significance, followed by the statistical test used. For the ANOSIM test, a value of $P < 3$ represents a significant difference between samples and a value of $P < 1$ represents a strong significant difference between samples. A 2 sample t-test assuming unequal variance was also conducted to test the significance in differences between average total quantity (ng) of fatty acid in the six species of Foraminifera between the spring intermonsoon and SW monsoon seasons. This was chosen as the data were single values (average total quantity) rather than being multivariate and so did not meet the prerequisites of the ANOSIM test or other multivariate statistical tests. For the t-test, P values of < 0.05 indicate a significant difference. Percentage composition (Mol %) and quantity (ng) fatty acid data are presented in Appendix C. Appendix D lists the results for statistical analyses conducted in all chapters. In this chapter, 95% confidence intervals are also presented for averaged data.

5. 3 Results and Discussion

The results and discussion are presented in two main sections. First, a seasonal comparison of the fatty acid compositions of six abundant species of Foraminifera at the permanently hypoxic ($O_2 \leq 0.5$ ml^{-1}) 300-m site for the spring intermonson (March-May, 2003) and the SW monsoon (August-October, 2003) (Section 5.3.1). Second, a more detailed treatment of the fatty acid composition and inferred feeding behaviour of *Uvigerina* ex. gr. *semiornata*, the dominant foraminiferan within the upper OMZ (0-300 m), at the 300-m site and the seasonally hypoxic 140-m site during the spring intermonsoon (March-May, 2003) and the SW monsoon (August-October 2003) (section 5.3.2). A general discussion of foraminiferal feeding patterns in the upper OMZ (0-300 m water depth) is given in Section 5.4.

5.3.1 Feeding behaviour of six species of Foraminifera at the 300-m site: a seasonal comparison

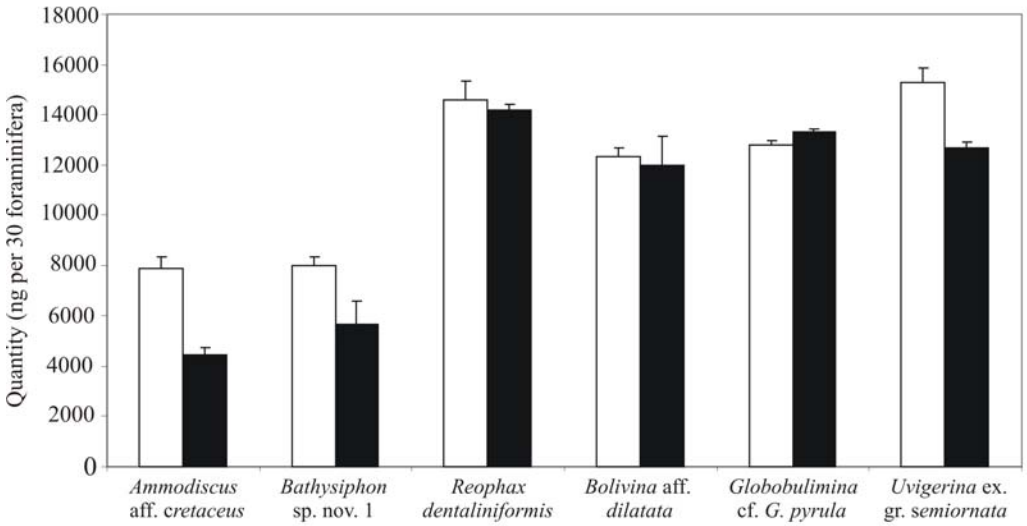
5.3.1.1 Total quantity (ng) of fatty acids

The average quantities (ng) of total fatty acids in six species of Foraminifera at the 300-m site sampled during the spring intermonsoon and SW monsoon are presented in Appendix C. Three species, *Uvigerina* ex. gr. *semiornata*, *Ammodiscus* aff. *cretaceus* and *Bathysiphon* sp. nov. 1, exhibited a significant ($P < 0.05$, 2-sample t-test) decrease in average quantity (ng) from spring intermonsoon to SW monsoon. *Bolivina* aff. *dilatata* and *Reophax dentaliniformis* also displayed a decrease in average quantity (ng), although this was not significant. However, when the seasonal abundances of these species are considered, different responses are revealed. A faunal analysis of the "live" macrofaunal (> 300 μm) foraminiferal assemblage at 300 m (see Chapter 4), showed that the agglutinated species *Ammodiscus* aff. *cretaceus* and *Bathysiphon* sp. nov. 1 declined in standing stock following the SW monsoon (mean values per 10 cm^{-2}: 6 to 3 and 4 to 2 individuals).

Table 5.1 300-m site. Average quantity [*](ng per 30 Foraminifera) of fatty acid in six species of Foraminifera during spring intermonsoon (April 2003) and following the SW monsoon (October 2003). Data are mean average quantities (to the nearest whole number) of four replicates per season. 95% Confidence Intervals are displayed. Species showing a significant change in average quantity ($P < 0.05$, 2 sample t-test) are marked as [1]significant decrease in quantity, [2]significant increase in quantity. Results of statistical tests are shown in Appendix D of this thesis. Figure 5.8 (below) is a graphical representation of these data.

	Average quantity (ng*)		95% Confidence Interval	
	intermonsoon	monsoon	intermonsoon	monsoon
Ammodiscus aff. *cretaceus*[1]	7862	4476	498	250
Bathysiphon sp. 1[1]	7981	5650	375	962
Reophax dentaliniformis	14593	14167	773	266
Bolivina aff. *dilatata*	12351	11952	310	1192
Globobulimina cf. *G. pyrula*[2]	12801	13332	166	86
Uvigerina ex. gr. *semiornata*[1]	15274	12672	600	216

Figure 5.2 300-m site. Average quantity (ng per 30 Foraminifera) of fatty acid in six species of Foraminifera during spring intermonsoon (April 2003) (white bars) and following the SW monsoon (October 2003) (black bars). Data are mean average quantities (to the nearest whole number) of four replicates per season. 95% Confidence Intervals are displayed.



In contrast, *Uvigerina* ex. gr. *semiornata*, the dominant calcareous species at the 300-m site in both seasons sampled, increased significantly ($P < 0.05$, 2-sample t-test) in standing stock from the spring intermonsoon to the SW monsoon (mean values per 10 cm^{-2}: 41 to 69 individuals respectively). The calcareous species *Bolivina* aff. *dilatata* also displayed a significant ($P < 0.05$, 2-sample t-test) increase in standing stock from the spring intermonsoon to the SW monsoon (mean values per 10 cm^{-2}: 2 to 6 individuals respectively).

These faunal changes suggest that there was a difference in the population response of the agglutinated and calcareous taxa following the SW monsoon and the associated organic matter flux to the seafloor. The decline in standing stock and associated decrease in average fatty acid content (ng) of *Ammodiscus* aff. *cretaceus* and *Bathysiphon* sp. nov. 1 (Table 5.1, Figure 5.2) could reflect reduced food intake and utilisation of storage fatty acids by these species following the SW monsoon, perhaps linked to increased competition from other more opportunistic species such as *Uvigerina* ex. gr. *semiornata*. The increase in standing stock combined with a decrease in average fatty acids (ng) of specimens of *Bolivina* aff. *dilatata* and *U*. ex. gr. *semiornata* from the spring intermonsoon to the SW monsoon is more puzzling. The increase in mean abundance suggests that these species were able to exploit the increased availability of labile organic matter on the seafloor during the SW monsoon season (following the phytodetrital flux to the seafloor). Therefore, the reduced average fatty acid content (ng) of fatty acids in individuals of these species is unlikely to be a result of reduced food intake, but instead may reflect changes in their population dynamics following the SW monsoon. The observed increase in the > 300 μm standing stock may result from the rapid growth during the SW monsoon of smaller individuals that were previously < 300 μm in size. This is consistent with a decrease in average test length of *U*. ex. gr. *semiornata* in the > 300 μm size fraction from spring intermonsoon to SW monsoon (test length 870 μm to 620 μm, based on measurements of 50 individuals per season). The reduction in test length

and volume would result in a reduced average fatty acid content (quantity, ng) of fatty acids in the Foraminifera.

The calcareous species *Globobulimina* cf. *G. pyrula* exhibited a significant increase ($P < 0.05$, 2-sample t-test) in average fatty acid content (ng) following the SW monsoon, although the standing stock of 16 individuals remained stable during each season (Chapter 4). *Globobulimina* cf. *G. pyrula* is a deep-infaunal species and these results suggest that it displayed a delayed response to the input of organic matter compared to more opportunistic species such as *Uvigerina* ex. gr. *semiornata*. A slower rate of food uptake meant that smaller individuals had not grown sufficiently to enter the > 300 μm fraction, leading to an apparently stable standing stock of this species between the spring intermonsoon and the SW monsoon. The agglutinated species *Reophax dentaliniformis* also displayed an increase in standing stock from spring intermonsoon to SW monsoon (mean values per 10 cm^{-2}: 16 to 21 individuals respectively) but a decrease (although not significant) in average fatty acid content (weight, ng). These results suggest that *Reophax dentaliniformis* responded in a similar way to the calcareous species and was able to exploit a particular food source within the benthic environment following the SW monsoon.

5.3.1.2 Fatty acid composition

The total fatty acid profiles (percentage compostion, Mol %) of the six species of Foraminifera analysed during spring intermonsoon (March-May, 2003) and SW monsoon (August-October, 2003) are shown in Figures 5.3 and 5.4 (Mol % data are presented in Appendix C). During both seasons sampled, all Foraminifera contained substantial amounts of the saturated fatty acids 16:0 (spring intermonsoon 12.8% to 23.2 %, SW monsoon 13.9% to 28.5%) and 18:0 (spring intermonsoon 7.8% to 17.1%, SW monsoon 5.7% to 23.1%) (Figures 5.3 and 5.4). Both of these fatty acids occur in many classes of organisms and sediments (see Table 1, Appendix B). They are therefore not particularly useful as biomarkers since they have multiple origins, although 18:0 is considered as a bacterial/detrital biomarker.

During the spring intermonsoon, 18:1(*n*-9) was also a dominant fatty acid (6% to 15.5 % of total fatty acids). However, following the SW monsoon, the percentage of this fatty acid decreased in all six species analysed and constituted only 2.7% to 10.5% of total fatty acids. 18:1(*n*-9) could not be used directly to interpret the diets since it is present in high amounts in many algal classes (Ackman et al. 1968, Kattner and Hagen 1998) and may also be a storage substance (wax ester) in organisms such as copepods and euphausiids (e.g. Morris 1971a, Morris 1971b, Pond et al. 2000a). However, the high abundances of this potential storage (reserve) fatty acid may indicate that the Foraminifera were dependent on their energy reserves during the spring intermonsoon and were not consuming high quality organic matter at the time of sampling. 20:4(*n*-6) was present in moderate amounts in all species during the spring intermonsoon (5.7% to 9.2%) but decreased in percentage of total fatty acids following the SW monsoon (2.0% to 5.2%). This fatty acid is found in many algal classes (Ackman 1968, Sargent et al. 1987). Yano et al. (1997) suggest that its presence in deep-sea organisms serves to ensure membrane integrity.

Figure 5.3 300-m site. Percentage composition of fatty acids in three agglutinated species of Foraminifera during spring intermonsoon (April 2003) (white bars) and following the SW monsoon (October 2003) (black bars). Data are average percentage composition (Mol %) of four replicates per season. 95% Confidence Limits are given. Raw data for these graphs are presented in Appendix C.

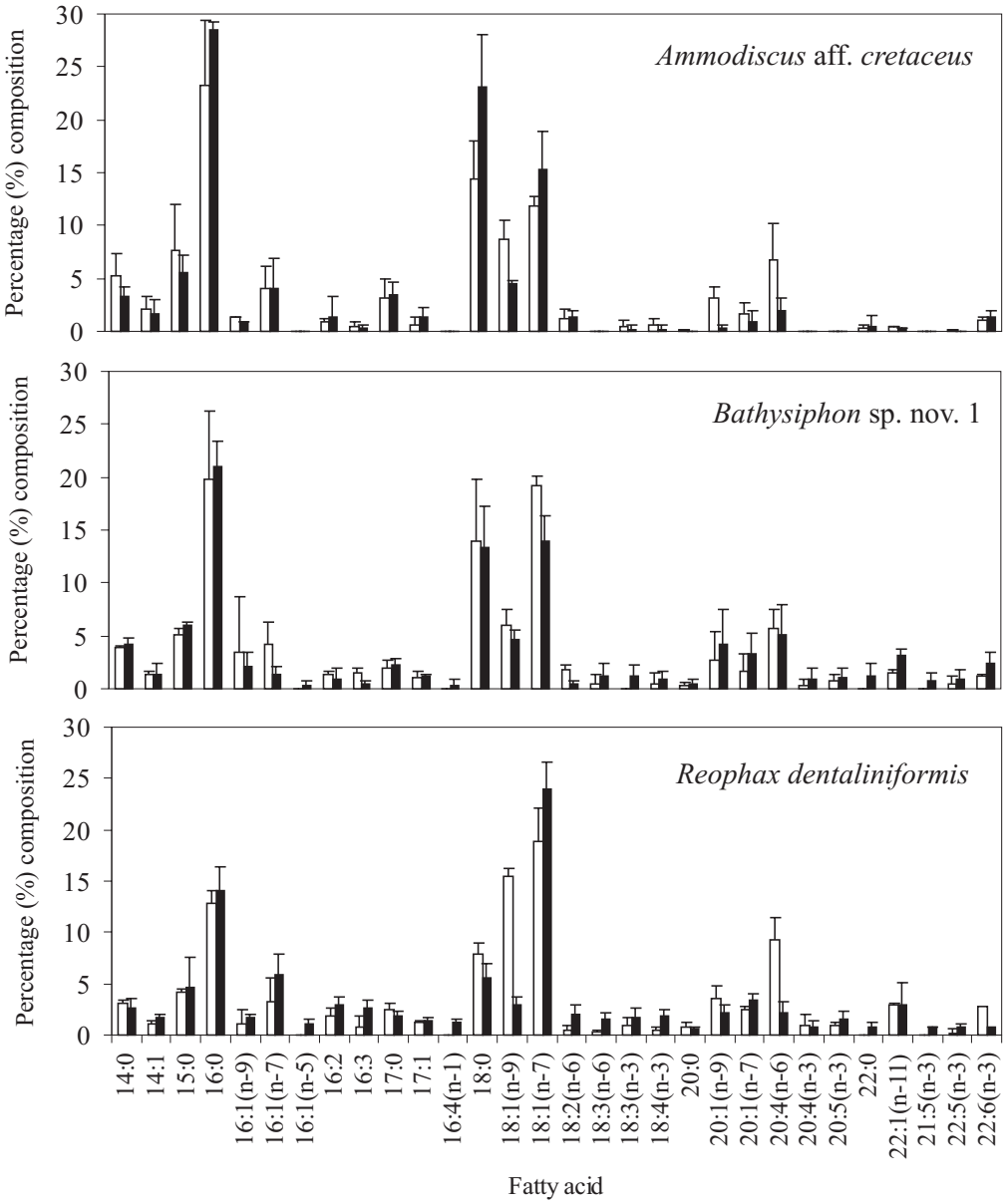
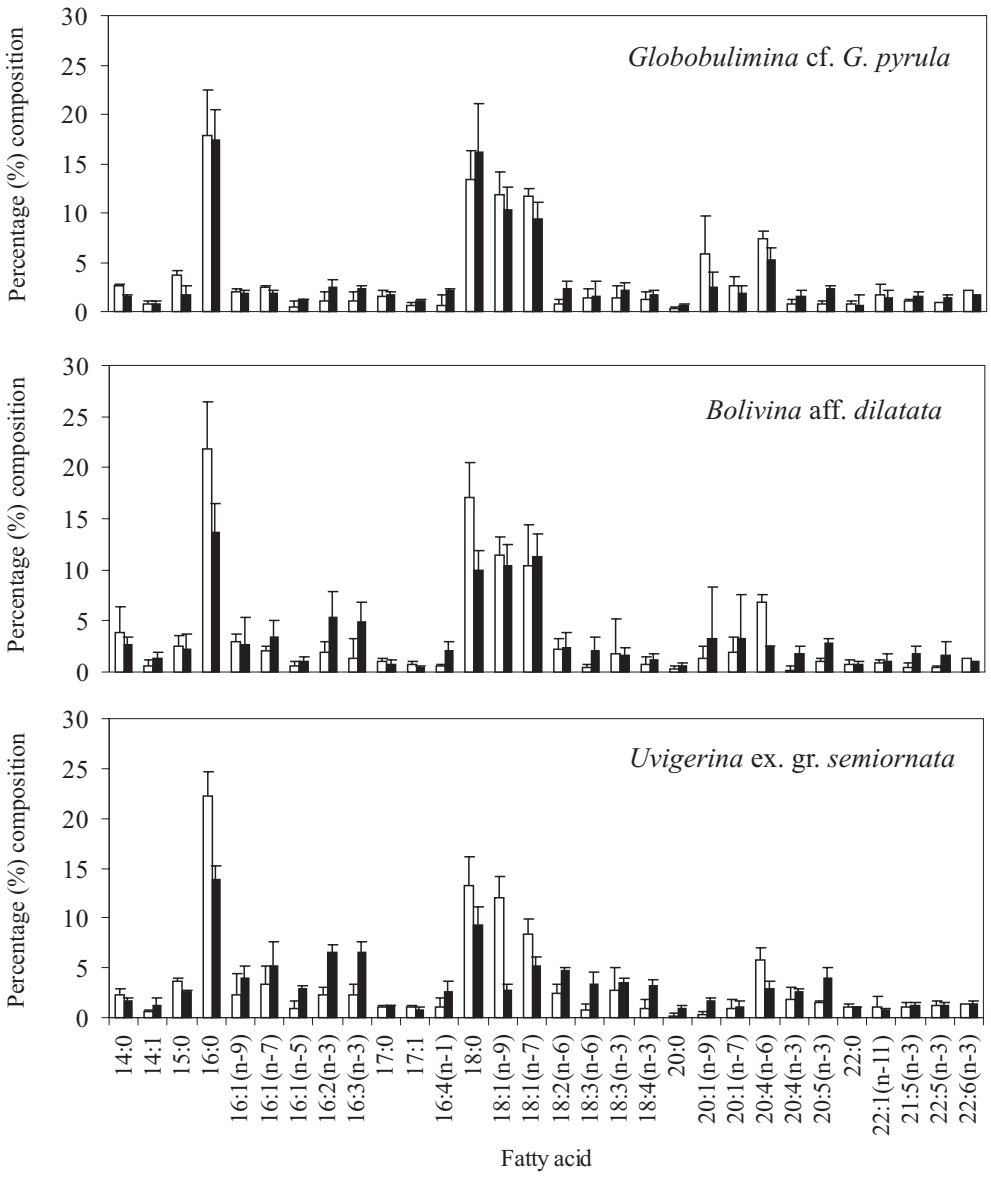


Figure 5.4 300-m site. Percentage composition of fatty acids in three calcareous species of Foraminifera during spring intermonsoon (April 2003) (white bars) and following the SW monsoon (October 2003) (black bars). Data are average percentage composition (Mol %) of four replicates per season. 95% Confidence Limits are given. Raw data for these graphs are presented in Appendix C.



5.3.1.3 Fatty acid biomarker groups

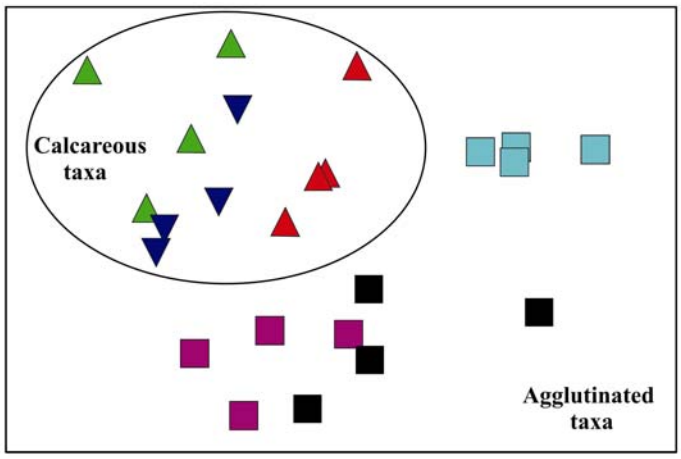
Despite similarities in the dominant fatty acids present in all six species of Foraminifera analysed, multivariate analysis revealed clear differences in the fatty acid profiles, both within each season sampled and between seasons. Multidimensional scaling of the complete fatty acid profiles of six dominant species at 300 m during the spring intermonsoon (Figure 5.5a) illustrated a clear grouping and a significant difference ($P < 3$, ANOSIM) between the fatty acid profiles of the three calcareous taxa, *Uvigerina* ex. gr. *semiornata*, *Bolivina* aff. *dilatata* and *Globobulimina* cf. *G. pyrula*, and the three agglutinated taxa, *Ammodiscus cretaceus*, *Bathysiphon* sp. nov. 1 and *Reophax dentaliniformis* (Figure 5.5a, samples of calcareous taxa are circled). Clear differences were also seen between individual species, and in some cases replicate samples of particular species formed clear groupings in the MDS plot (Figure 5.5a). The total fatty acid profiles (percentage composition, Mol %) of all species were significantly ($P < 3$, ANOSIM) different from each other except for the fatty acid profiles of the calcareous species *Uvigerina* ex. gr. *semiornata* and *Bolivina* aff. *dilatata*. Some overlap of replicate samples for these two species is apparent in the MDS plot (Figure 5.5a). In general, however, the results indicate that during the spring intermonsoon, each species was feeding on somewhat different components of the food available.

The separation of calcareous and agglutinated taxa, and the grouping of individual species, was even clearer following the SW monsoon (Figure 5.5b), with a significant difference ($P< 3$, ANOSIM) in the fatty acid profiles (average percentage composition) of all six species analysed and a clear grouping of replicate samples of each species (except one outlier of *Bolivina* aff. *dilatata*).

Figure 5.5 300-m site. Multidimensional scaling (MDS) of full fatty acid profiles (Mol %) of six dominant species at 300 m during a) spring intermonsoon (March-May 2003) and b) SW monsoon (August-October 2003). Four replicates are displayed for each species. Based on a Bray-Curtis Similarity Matrix of square-root transformed data (Stress = 0.14). In each plot, all samples of calcareous species are circled (except one outlier of *Bolivina* aff. *dilatata* following the SW monsoon in plot b).

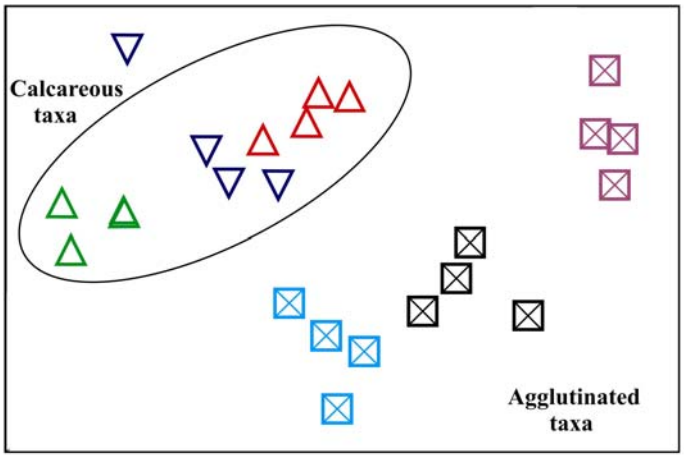
a) 300-m site. Spring intermonsoon.

▲= *Uvigerina* ex. gr. *semiornata* ▼= *Bolivina* aff. *dilatata* ▲= *Globobulimina* cf. *G. pyrula*. ■= *Ammodiscus* aff. *cretaceus*, ■= *Bathysiphon* sp. nov. 1, ■= *Reophax dentaliniformis*.



b) 300-m site. SW monsoon.

△ = *Uvigerina* ex. gr. *semiornata*, ▽= *Bolivina* aff. *dilatata*, △ = *Globobulimina* cf. *G. pyrula*, ⊠ = *Ammodiscus* aff. *cretaceus*, ⊠ = *Bathysiphon* sp. nov. 1, ⊠ = *Reophax dentaliniformis*.



The significant ($P < 3$, ANOSIM) differences in the fatty acid profiles of calcareous and agglutinated forms during both seasons analysed can be explained by two factors. First, the higher diversity of fatty acids found in the calcareous forms (Figures 5.3 and 5.4). Second, the contrasting amounts of fatty acid biomarker groups present in these two forms. The percentage compositions of the main fatty acid biomarker groups in all six species during the spring intermonsoon and the SW monsoon are displayed in Table 5.2 and Figure 5.6. Total algal biomarkers are shown, along with a component of this group, the polyunsaturated fatty acids (PUFAs). PUFAs are shown separately as they indicate the freshness of the phytodetritus (Wakeham et al. 1997b; Suhr and Pond 2006), with higher percentages of PUFAs reflecting a more recent deposition of phytodetritus. Total bacterial biomarkers and zooplankton biomarkers are also shown.

Phytodetrital biomarkers

During the spring intermonsoon, total algal biomarkers were high in the three calcareous species (29.1 % in *Bolivina* aff. *dilatata*, 29.4 % in *Globobulimina* cf. *G. pyrula* and 37.3 % in *Uvigerina* ex. gr. *semiornata*). There was no significant difference ($P < 11.4$, ANOSIM) in the percentage of total algal biomarkers between any of the calcareous species. PUFAs (a component of the total algal fatty acids) constituted 19.6 – 25.4 % of the total fatty acids in the three calcareous species, with the highest percentage found in *U*. ex. gr. *semiornata* (Table 5.2, Figure 5.6a). The relatively high percentages of total algal biomarkers and PUFAs suggests that all the calcareous species analysed were feeding on a relatively labile component of organic matter and had a similar phytodetrital/algal intake during the spring intermonsoon, and that *U.* ex. gr. *semiornata* ingested the highest percentage of labile organic matter of phytodetrital/algal origin.

Table 5.2 300-m site. Percentage composition of fatty acid biomarker groups during spring intermonsoon and SW monsoon seasons in six abundant Foraminifera: a) three agglutinated species, b) three calcareous species. Data are average values based on 4 replicates per season. Since the data are for selected fatty acid groups, the percentages do not total 100. C = 95% Confidence Intervals. SFAs = Saturated Fatty Acids, MUFAs = Monounsaturated Fatty Acids, PUFAs = Polyunsaturated Fatty Acids (a component of total algal biomarkers).

a) Agglutinated species

Fatty acid biomarker groups	***Ammodiscus* aff. *cretaceus***				***Bathysiphon* sp. nov. *1***				***Reophax dentaliniformis***			
	intermonsoon		monsoon		intermonsoon		monsoon		intermonsoon		monsoon	
	Mol%	C	Mol%	C	Mol%	C	Mol%	C	Mol%	C	Mol%	C
SFAs	54.2	2.4	64.2	1.7	44.7	8.8	43.9	3.8	31.0	1.0	30.8	1.2
MUFAs	34.1	0.8	29.1	2.9	41.1	8.4	41.7	1.5	49.9	0.6	49.0	3.0
PUFAs	11.7	2.1	6.7	1.3	14.1	2.5	14.4	3.6	19.1	1.0	20.2	3.8
Algae (all classes)	19.0	1.4	14.1	2.1	22.0	6.6	17.3	4.1	29.6	3.7	29.9	2.2
Bacteria (all classes)	41.3	2.1	51.2	1.8	46.0	0.4	46.0	1.6	36.8	1.2	42.5	2.0
Diatom	7.2	2.0	6.5	2.6	9.8	2.6	7.8	2.3	10.2	2.7	18.5	1.6
Flagellates	3.9	1.0	2.7	1.0	3.3	1.6	7.1	1.3	6.7	0.4	8.0	0.9
Cyanobacteria	13.7	0.1	16.8	3.2	21.6	1.3	23.4	1.6	19.9	2.5	28.4	1.2
Zooplankton	3.5	0.9	0.6	0.4	4.2	2.2	6.7	2.7	6.4	0.9	5.1	1.2
18:1(*n*-9):18:1(*n*-7)	0.7	0.1	0.3	0.1	0.3	0.1	0.2	0.1	0.8	0.1	0.1	0.0

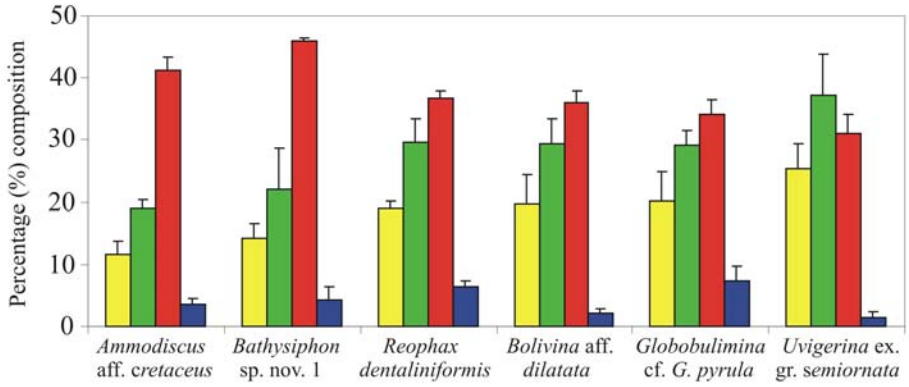
b) Calcareous species

Fatty acid biomarker groups	***Bolivina* aff. *dilatata***				***Globobulimina* cf. *G. pyrula***				***Uvigerina* ex. gr. *semiornata***			
	intermonsoon		monsoon		intermonsoon		monsoon		intermonsoon		monsoon	
	Mol%	C	Mol%	C	Mol%	C	Mol%	C	Mol%	C	Mol%	C
SFAs	47.3	4.8	30.5	4.9	40.0	4.8	39.6	4.4	43.8	5.2	30.6	3.1
MUFAs	33.1	1.0	40.3	6.2	39.9	2.2	34.1	2.9	30.8	2.2	28.2	4.1
PUFAs	19.6	4.7	29.2	3.3	20.1	4.8	26.2	2.0	25.4	3.9	41.2	3.6
Algae (all classes)	29.3	4.1	45.2	2.6	29.1	2.5	37.3	3.2	37.3	6.5	52.7	3.6
Bacteria (all classes)	36.0	1.8	29.9	2.6	34.2	2.2	33.8	2.3	31.2	2.9	27.1	1.8
Diatom	9.1	2.1	23.5	5.1	9.6	2.1	13.8	1.0	13.4	3.2	27.2	2.6
Flagellates	5.9	2.0	7.1	2.3	7.3	1.3	7.5	1.2	6.0	3.4	9.1	1.6
Cyanobacteria	13.4	3.0	14.9	3.0	13.5	0.5	13.4	1.1	11.7	0.9	13.1	0.7
Zooplankton	2.2	0.7	4.3	3.2	7.4	2.3	3.7	0.7	1.3	1.1	2.5	0.3
18:1(*n*-9):18:1(*n*-7)	1.1	0.4	0.9	0.1	1.0	0.2	1.1	0.1	1.4	0.2	0.5	0.1

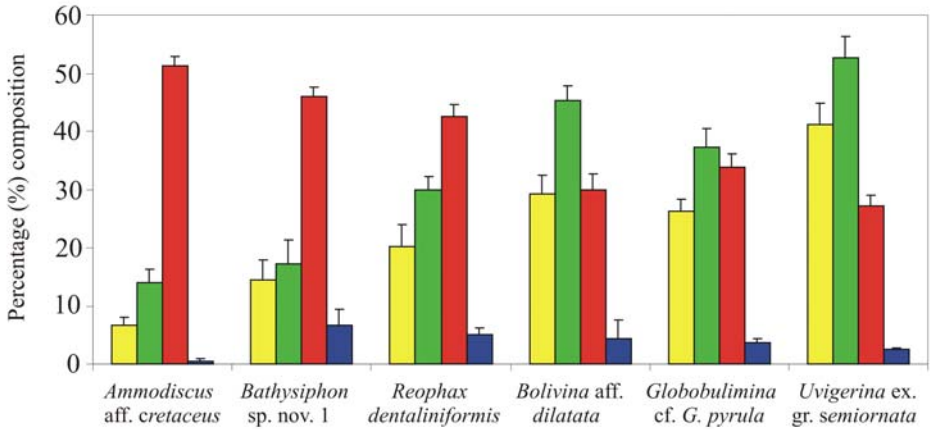
Figure 5.6 300-m site. Percentage composition (Mol %) of dominant biomarker fatty acid groups in six abundant species of Foraminifera during a) spring intermonsoon, b) SW monsoon. Data are average percentage composition (Mol %) of fatty acid biomarker groups (four replicates per season). Since the data are for selected fatty acid groups, the percentages do not total 100. 95% Confidence Intervals are given. Raw data for these figures (Mol % of fatty acid biomarker groups) are presented in Table 5.2. Note the increase in bacterial biomarkers in the three agglutinated species from spring intermonsoon to SW monsoon, and an increase in algal biomarkers (and a component of this group, the PUFAs) in the three calcareous species from spring intermonsoon to SW monsoon.

= Polyunsaturated Fatty Acids (PUFAs) = Algal biomarkers (all classes)
= Bacterial biomarkers (all classes) = Zooplankton biomarkers

a) 300-m site. Spring intermonsoon.



b) 300-m site. SW monsoon.



Total algal biomarkers were also relatively high in the three agglutinated taxa during the spring intermonoon (19.0 % in *Ammodiscus* aff. *cretaceus*, 22.0 % in *Bathysiphon* sp. nov. 1 and 29.6 % in *Reophax dentaliniformis*). However, in contrast to the calcareous specices, PUFAs constituted a lower proportion of the total fatty acids (11.7 % in *A.* aff. *cretaceus*, 14.1 % in *B.* sp. nov. 1 and 19.1 % in *R. dentaliniformis*). *Reophax dentaliniformis* displayed a significantly higher ($P < 3$, ANOSIM) amount of algal biomarkers compared to *A.* aff. *cretaceus*. When individual algal classes are considered in all six species (Table 5.2), diatom biomarkers comprised between 7.2 % (*A.* aff. *cretaceus*) and 13.4 % (*Uvigerina* ex. gr. *semiornata*) of the total fatty acids. Calcareous species and *R. dentaliniformis* contained the highest percentage of flagellate biomarkers (5.9 - 7.3 %) compared to *A.* aff. *cretaceus* and *B.* sp. nov. 1 (3.3 - 3.9 %).

Following the SW monsoon, the three calcareous species, *Uvigerina* ex. gr. *semiornata*, *Bolivina* aff. *dilatata* and *Globobulimina* cf. *G. pyrula*, yielded significantly ($P < 3$, ANOSIM) higher amounts of both total algal biomarkers (37.3 - 52.7 %) and PUFAs (26.2 - 41.2 %) (Table 5.2, Figure 5.6b). In contrast, the three agglutinated species *Ammodiscus* aff. *cretaceus*, *Bathysiphon* sp. nov. 1 and *Reophax dentaliniformis* all displayed much lower percentages of total algal biomarkers (14.1 - 29.9 %) and PUFAs (3.6 - 6.7 %). Calcareous species also contained higher proportions of fatty acid biomarkers for diatoms (13.2 - 27.2 %) and flagellates (7.1 to 9.1 %) than the agglutinated species (6.5 to 18.5 % and 2.7 to 8.0 % respectively).

The seasonal increase in the proportions of total algal biomarkers and PUFAs in the three calcareous species from the spring intermonsoon to the SW monsoon indicates that labile organic matter (phytodetritus) was more readily available in the benthic environment during the SW monsoon. This supports the evidence for a phytodetrital flux to the seafloor during this season (summarised in Chapter 3). The three agglutinated species analysed did not yield increased proportions of total algal

biomarkers or PUFAs, indicating that they were less able to exploit the increased availability of labile organic matter (phytodetritus) following the SW monsoon.

Bacterial biomarkers

During the spring intermonsoon, bacterial biomarkers predominated in all species except for *Uvigerina* ex. gr. *semiornata* which contained a higher percentage of algal biomarkers (Table 5.2, Figure 5.6a). Agglutinated taxa contained the highest amounts of total bacterial biomarkers (36.8 - 46 %) compared to the calcareous taxa which contained a significantly lower ($P<3$, ANOSIM) percentage (31.2 - 36 %). This suggests that during the spring intermonsoon, agglutinated forms ingested a higher proportion of bacteria compared to the calcareous taxa. The exception was the agglutinated species *Reophax dentaliniformis* in which the percentage of bacterial biomarkers was significantly ($P < 3$, ANOSIM) lower than in *Ammodiscus* aff. *cretaceus* and more similar to the calcareous species *Globobulimina* cf. *G. pyrula*. Following the SW monsoon, agglutinated species again yielded a significantly higher ($P < 3$, ANOSIM) percentage of total bacterial biomarkers (42.5 - 51.2 %) than the calcareous species (27.1 - 33.8 %) (Table 5.2, Figure 5.6b). The agglutinated species *A.* aff. *cretaceus* and *R. dentaliniformis* displayed a significant ($P < 3$, ANOSIM) percentage increase in total bacterial biomarkers from spring intermonsoon to the SW monsoon. The other agglutinated species *Bathysiphon* sp. nov. 1 did not exhibit a significant change. In contrast, the percentage of total bacterial biomarkers in all three calcareous species, *Uvigerina* ex. gr. *semiornata*, *Bolivina* aff. *dilatata* and *G.* cf. *G. pyrula* decreased significantly ($P < 3$, ANOSIM) from the spring intermonsoon to the SW monsoon.

During both seasons, the dominant bacterial biomarker in all species was 18:1(*n*-7) (Figures 5.3 and 5.4). This was highest in the agglutinated taxa (11.9 - 15.3 % in *Ammodiscus* aff. *cretaceus*, 18.9 - 24.4 % in *Reophax dentaliniformis*, 18.9 - 22.1 % in *Bathysiphon* sp. nov. 1.). It was present, in smaller amounts, in the three calcareous taxa, (10.4 - 11.4 % in *Bolivina* aff. *dilatata*, 9.3 - 11.6 % in *Globobulimina* cf. *G. pyrula*, 5.2 - 8.3 % in *Uvigerina* ex. gr. *semiornata*). The three

agglutinated species and the calcareous species *G*. cf. *G. pyrula* all contained a higher percentage of 18:1(*n*-7) following the SW monsoon, whilst the two other calcareous species analysed, *B*. aff. *dilatata* and *U*. ex. gr. *semiornata*, yielded a lower percentage of 18:1(*n*-7) following the SW monsoon. Agglutinated species also contained higher percentages of biomarkers for cyanobacteria than calcareous species during both seasons sampled: 13.7 - 21.6 % during the spring intermonsoon and 16.8 - 28.4 % during the SW monsoon (agglutinated) compared to 11.7 - 13.5 % during the spring intermonsoon and 13.1 - 14.9 % during the SW monsoon (calcareous).

A low 18:1 isomer ratio of the fatty acids 18:1(*n*-9): 18:1(*n*-7) has been suggested as a clear indicator of a high bacterial intake (Yano et al. 1997). During the spring intermonsoon, low values of this ratio were seen in the three agglutinated taxa (between 0.3 and 0.8) supporting the interpretation of a diet rich in bacteria for these species (Table 5.2). The higher value for the calcareous taxa (between 1.0 and 1.4) during the spring intermonsoon indicates a lower bacterial intake. Following the SW monsoon, this ratio decreased in all three agglutinated taxa (between 0.1 and 0.3) indicating an even higher consumption of bacteria in this season. The 18:1 isomer ratio also decreased in all calcareous species following the SW monsoon (between 0.5 and 1.1), indicating a higher bacterial intake. However this interpretation may be misleading as the lower ratios result from the decrease in the amount of 18:1(*n*-9), a potential storage fatty acid, and do not reflect an increase in the bacterial biomarker 18:1(*n*-7). The decrease in 18:1(*n*-9) in the calcareous taxa *Uvigerina* ex. gr. *semiornata* and *Bolivina* aff. *dilatata* following the SW monsoon appears to contradict the suggestion that this fatty acid is a storage substance (Lewis 1967, Morris 1971a, Morris 1971b, Albers et al. 1996, Parrish and Wangersky 1990, Kattner and Hagen 1998, Pond et al. 2000a). If this were the case, one would expect an increased storage of fatty acids following the presumed SW monsoon-associated deposition of organic matter and the consequent higher availability of labile food. Indeed, Suhr et al. (2003) found an almost four-fold increase in 18:1(*n*-9) in the

calcareous species *Globocassidulina subglobosa* and *Quinqueloculina seminula* following a phytodetrital deposition event at a 500-m site off the Antarctic peninsula. It is suggested that the lower percentage of 18:1(*n*-9) in calcareous species following the SW monsoon may reflect a lower dependence on storage (reserve) fatty acids by the Foraminifera as a result of the increased availability and consumption of labile organic matter following the SW monsoon. Rapid ingestion by Foraminifera of high quality organic matter would enable faster rates of growth and reproduction, not dependent on high amounts of 18:1(*n*-9).

Zooplankton biomarkers

During the spring intermonsoon, zooplankton biomarkers (long-chain 20:1(*n*-9) and 22:1(*n*-11) monounsaturated fatty acids only) comprised a small percentage of the total fatty acid content of the Foraminiferal cells (1.3 - 7.4 % of the total fatty acid content in all species) (Table 5.2, Figure 5.6a). During the SW monsoon, zooplankton biomarkers comprised a larger component of the fatty acid profile of all species analysed, but there was a high variability between each species, with the highest percentage in *Bathysiphon* sp. nov. 1 (6.7 %) and the lowest percentage in *Uvigerina* ex. gr. *semiornata* (2.5 %) (Table 5.2, Figure 5.6b).

5.3.2 Feeding behaviour of *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites: a seasonal comparison

A faunal survey at 140 m and 300 m water depth on the Pakistan continental margin revealed that the calcareous foraminiferan *Uvigerina* ex. gr. *semiornata* was the most abundant species at both sites during each season sampled (72.4 to 77.2 % of the live foraminiferal assemblage at the 140-m site and 47.8 to 56.9 % at the 300-m site) (See Chapter 4 for more details). Because of the potentially important role of this species in benthic carbon cycling in the upper part of the OMZ (0-300 m water depth), and the common association of the genus Uvigerina with high organic matter input (Corliss et al. 1986; Altenbach et al. 1999; Schönfeld and Altenbach 2005), its

feeding behaviour was analysed in more detail during the spring intermonsoon and the following summer monsoon at these two sites.

5.3.2.1 Total quantity (ng) of fatty acids

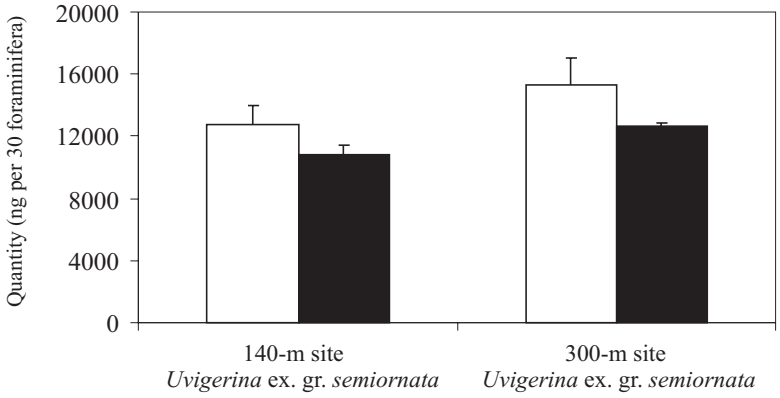
Analysis of the fatty acid content (average total fatty acids, ng per 30 Foraminifera) in *Uvigerina* ex. gr. *semiornata* revealed a significantly ($P < 0.05$, paired t-test) lower average quantity in foraminiferal samples from the 140-m site compared to the 300-m site during both seasons sampled (Table 5.3, Figure 5.7). This may reflect a different availability or quality of organic matter in the surface sediments of these two sites, which in turn, may be influenced by the contrasting oxygen regimes at each site (R. Jeffreys, pers. comm.). For example, the seasonally hypoxic 140-m site was fully oxygenated ($O_2 = 2.05$ mll^{-1}) during the spring intermonsoon but became hypoxic ($O_2 = 0.11$ mll^{-1}) following the SW monsoon. The seasonal oxygenation of this site resulted in the survival of higher numbers of metazoa, which may have increased competition for food in the surface sediments. In addition, metazoans such as polychaetes may have subducted labile organic matter from the surface layers into burrows, thereby reducing the amount of labile organic matter in the upper 1 cm of the sediment where the majority of Foraminifera live. Levin et al. (1997) observed maldanid polychaetes peforming this activity on the north Carolina slope and suggested that the downward transport of organic matter by polychaetes may have important implications for the food availability in the surface sediments. In contrast the 300-m site was permanently hypoxic and metazoans were very scarce, resulting in potentially more food being available to the Foraminifera. A second interpretation for the lower average quantity (ng) of total fatty acids in Foraminifera at the 140-m site compared to the 300-m site is that it results from a more intense degradation of organic matter because of the higher concentrations of oxygen, especially during the spring intermonsoon. This is supported by the fact that surficial sediments contained a higher percentage of organic carbon at 300 m (~ 2-3 %) than at 140 m (~ 1-1.5 %) (S. Vandewiele unpub. data). In addition, quantities of organic compounds such as phospholipids, pigments and total hydrolysable amino acids were higher and these

compounds were also of higher quality (preservation) in sediments at the 300-m site compared to the 140-m site.

Table 5.3 Average quantity *(ng per 30 Foraminifera) of total fatty acids in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites during the spring intermonsoon (April 2003) and the SW monsoon (October 2003). Data are mean averages (to the nearest whole number) of four replicates per season. 95% Confidence Intervals are displayed. [1]At both sites, there is a significant decrease in average quantity ($P < 0.05$, 2 sample t-test). Results of statistical analyses are presented in Appendix D. Figure 5.7 (below) presents these data in graphical form.

	Average quantity (ng*)		95% Confidence Interval	
	intermonsoon	monsoon	intermonsoon	monsoon
140-m site[1]	12718	10841	1307	1750
300-m site[1]	15274	12672	600	216

Figure 5.7 Seasonal comparison of average quantity (ng per 30 Foraminifera) of total fatty acids in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites during spring intermonsoon (April 2003) (white bars) and following the SW monsoon (October 2003) (black bars). Data are averages of four replicates per site and season. 95% Confidence Intervals are given.



Finally, the maximum pigment concentrations (indicating the highest quantity and quality of phytodetritus) were found at 300 m where bioturbation was lowest (C. Woulds, unpub. data). These lines of evidence point to the conclusion that organic matter quality was highest where Metazoa were absent and that carbon preservation was highest at the 300-m site within the persistent OMZ compared to the seasonally hypoxic 140-m site.

At both sites, the quantity of total fatty acids in *Uvigerina* ex. gr. *semiornata* declined significantly ($P < 0.05$) from the spring intermonsoon to the SW monsoon. This appears to contradict the overall trend for an increase in labile organic matter at both sites following the SW monsoon, as reflected by an increase in the average quantity of surface sediment lipids (R. Jeffreys unpub. data). However, as previously discussed, the observed decline in quantity of total fatty acids in foraminiferal samples may be misleading. The increased percentage composition of total algal biomarker fatty acids and in particular a component of this group, the PUFAs, in *U.* ex. gr. *semiornata* following the SW monsoon indicates an increased consumption of the higher quality, readily available organic matter by this species. Therefore, the decline in the quantity of fatty acids is probably not a result of reduced feeding by this species or of increased stress and utilization of storage reserves. Instead, it may be attributed to the rapid growth of smaller individuals and the resulting increase of the standing stock in the > 300 μm fraction following the SW monsoon. This would lead to a decrease in average test length and therefore a reduction in the quantity of total fatty acids in each foraminiferal cell.

5.3.2.2 Fatty acid composition

Fatty acid spectra at the 140-m and 300-m sites (average percentage composition data) are summarised in Figure 5.8 (Mol % data are in Appendix C). All samples of *Uvigerina* ex. gr. *semiornata* contained a high diversity of fatty acids, a total of thirty in each sample analysed. Multivariate analysis (average percentage composition data) revealed a clear grouping of replicate samples from the same site and season

(Figure 5.9), reflecting significant (P < 3 %) differences in the percentage composition of the total fatty acids between each site and each season sampled. These important differences were principally a result of different percentages in the dominant biomarker groups, bacterial, algal and zooplankton, especially between the two seasons sampled.

Figure 5.8 140-m and 300-m sites. Fatty acid percentage composition of *Uvigerina* ex. gr. *semiornata* during spring intermonsoon (April 2003) (white bars) and following the SW monsoon (October 2003) (black bars). Data are average percentage composition (Mol %) of 4 replicates per season. 95% Confidence Intervals are displayed. Data for these graphs are presented in Appendix C.

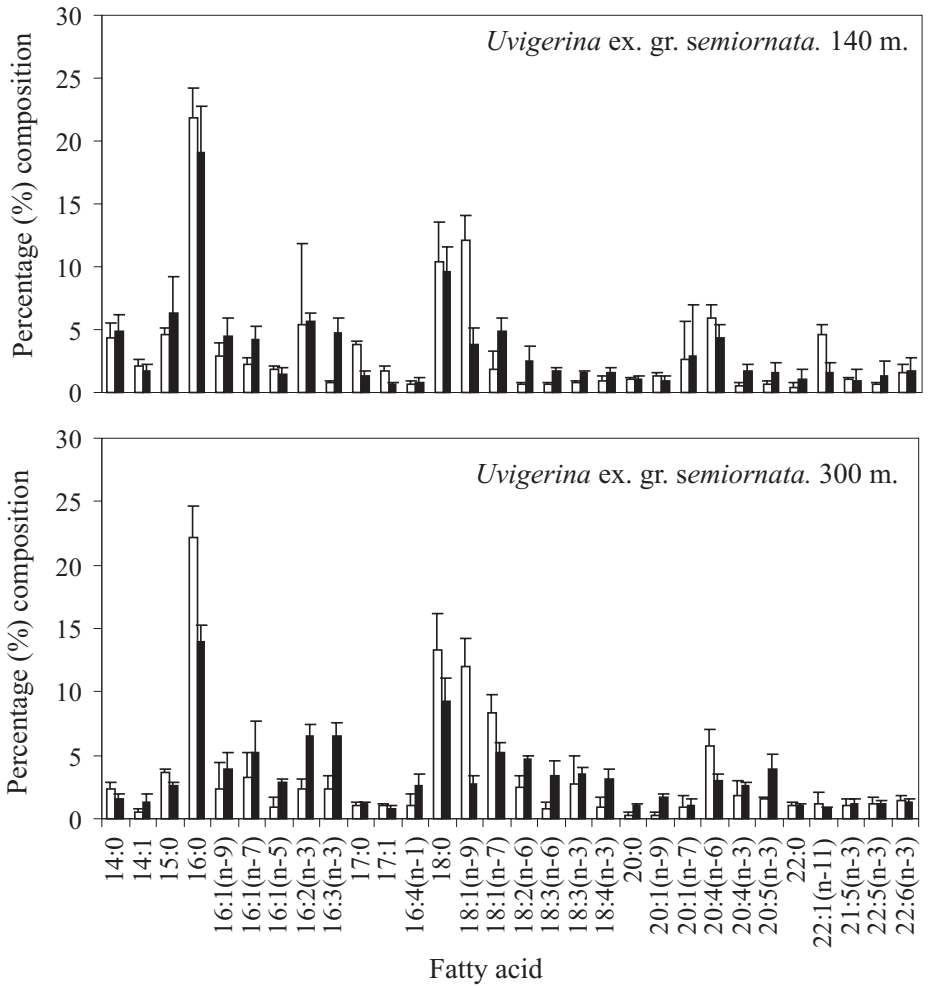
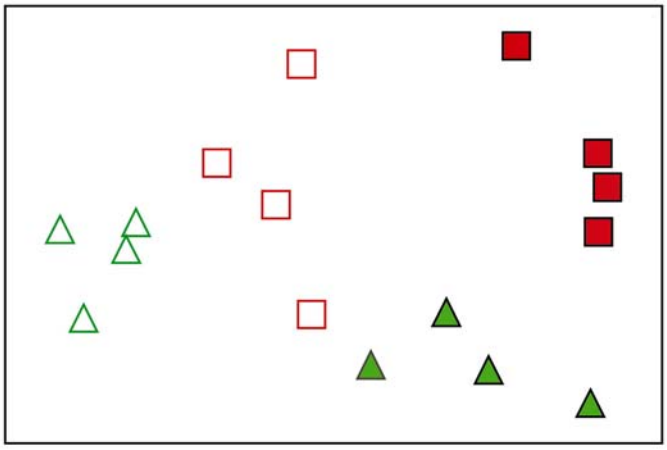


Figure 5.9 Comparison of total fatty acid profiles in *Uvigerina* ex. gr. *semiornata* during spring intermonsoon (April 2003) and SW monsoon (October 2003) at the 140-m and 300-m sites. MDS plot of full fatty acid profiles (Mol %). 4 replicates are displayed for each site and season Plot based on a Bray-Curtis Similarity Matrix of square-root transformed data (Stress = 0.07).

■ = 140-m site, spring intermonsoon, □ = 140-m site, SW monsoon
▲ = 300-m site, spring intermonsoon, △= 300-m site, SW monsoon



Dominant fatty acids

During the spring intermonsoon and the SW monsoon seasons, the fatty acid profiles of *Uvigerina* ex. gr. *semiornata* at both sites were dominated by the saturated fatty acids 16:0 (bacteria, algae), 19.1 - 21.9 % at the 140-m site, and 13.9 - 22.2 % at the 300-m site, and 18:0 (bacteria, detritus), 9.2% - 10.3 % at the 140-m site and 13.3 - 13.9 % at the 300-m site (Figures 5.3 and 5.4). 20:4(*n*-6), a major cell membrane constituent in deep-sea organisms (Yano et al. 1997), was present in moderate amounts at both sites and constituted a slightly higher percentage following the SW monsoon; 2.9 % - 5.9 % at the 140-m site and 4.4 - 5.8 % at the 300-m site. The potential storage fatty acid 18:1(*n*-9) was dominant in all Foraminifera sampled during the spring intermonsoon (12.2 % at the 140-m site, 12.0 % at the 300-m site) which suggests that the Foraminifera at both sites were not consuming much labile organic matter during the spring intermonsoon season and instead were reliant on their storage reserves during this season. However, following the SW monsoon,

18:1(*n*-9) constituted a much lower percentage of the total fatty acids (3.9 % at the 140-m site and 2.7 % at the 300-m site). The low percentage contribution of 18:1(*n*-9) at both sites following the SW monsoon suggests *Uvigerina* ex. gr. *semiornata* was consuming large amounts of labile organic matter during this season and was therefore not relying on its storage reserves.

5.3.2.3 Fatty acid biomarker groups

Phytodetrital biomarkers

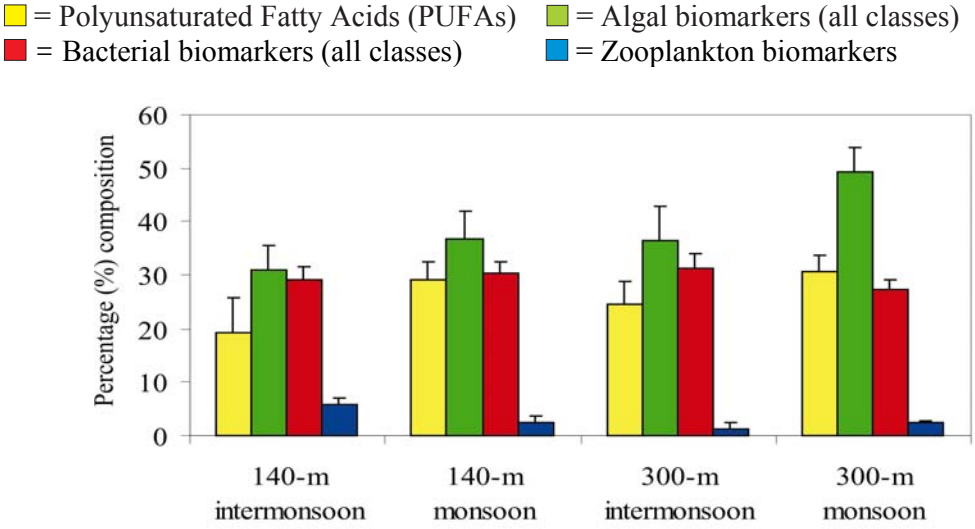
During the spring intermonsoon, total algal biomarkers contributed a large percentage of total fatty acids (31 % at the 140-m site and 36.5 % at the 300-m site) (Table 5.4, Figure 5.10). PUFAs (a component of the total algal biomarkers and an indicator of freshly deposited phytodetritus) comprised 19.2 % of total fatty acids at the 140-m site and 24.4 % at the 300-m site. The percentage contribution of diatom and flagellate biomarkers was relatively consistent in individuals of *U*. ex. gr. *semiornata* from both sites (13.3 - 13.4 % diatom biomarkers and 6.0 % flagellate biomarkers).

Following the SW monsoon, the proportion of total algal biomarkers in *U*. ex. gr. *semiornata* increased at both sites (36.6 % at the 140-m site and 49.3 % at the 300-m site) (Table 5.4, Figure 5.10). This increase was also reflected in the proportions of PUFAs (29.2 % at the 140-m site and 30.6 % at the 300-m site). The higher percentages of both PUFAs and algal biomarkers at the 300-m site during both seasons may reflect the lower degradation rate and therefore higher preservation of organic matter at the permanently hypoxic 300-m site (see also section 5.3.2.1 in this chapter and chapter 3). Biomarkers for diatoms were abundant and constituted 21.8 % of total fatty acids in *U*. ex. gr. *semiornata* at the 140-m site and 27.2 % at the 300-m site. Flagellates were less abundant, constituting 7.7 % at the 140-m site and 9.1 % at the 300-m site.

Table 5.4 Percentage composition (Mol %) of dominant fatty acid biomarker groups in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites. SFAs = Saturated Fatty Acids, MUFAs = Monounsaturated Fatty Acids, PUFAs = Polyunsaturated Fatty Acids. Since the data are for selected fatty acid groups, the percentages do not total 100. Data are average Mol % (four replicates per species) (to 1 d.p.). C = 95% Confidence Interval. Figure 5.10 (below) displays some of these data in graphical form.

	Uvigerina* ex. gr. *semiornata							
	140-m site				300-m site			
Fatty acid	intermonsoon		monsoon		intermonsoon		monsoon	
biomarker groups	Mol%	C	Mol%	C	Mol%	C	Mol%	C
SFAs	46.4	4.9	43.3	2.2	43.8	5.2	42.7	3.4
MUFAs	28.8	1.8	25.0	3.2	29.7	1.3	24.8	3.4
PUFAs	19.2	6.7	29.2	3.3	24.4	4.3	30.6	3.1
Algae (all)	31.0	4.4	36.6	5.2	36.5	6.3	49.3	4.5
Bacteria (all)	29.1	2.6	30.3	2.0	31.2	2.9	27.1	1.8
Diatom	13.3	6.5	21.8	3.8	13.4	3.2	27.2	2.6
Flagellates	6.0	3.4	7.7	3.9	6.0	3.4	9.1	1.6
Cyanobacteria	3.5	1.8	9.0	2.1	11.7	0.9	13.1	0.7
Zooplankton	5.9	1.0	2.5	1.3	1.3	1.1	2.5	0.3
18:1(n-9):18:1(n-7)	6.7	4.8	0.8	0.1	1.4	0.2	0.5	0.1

Figure 5.10 Percentage composition (Mol %) of dominant fatty acid biomarker groups in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites. Data are average Mol % (four replicates per species). Since the data are for selected fatty acid groups, the percentages do not total 100. 95% Confidence Intervals are given.



Bacterial biomarkers

During the spring intermonsoon, there was no significant difference between the total bacterial biomarkers in *Uvigerina* ex. gr. *semiornata* at the 140-m site (29.1 %) and the 300-m site (31.2 %) (Table 5.4, Figure 5.10). Biomarkers for cyanobacteria contributed 3.5 % (140-m site) and 11.7 % (300-m site) of the total fatty acids. The bacterial biomarker 18:1(*n*-7) was moderately abundant, but formed a higher percentage of total foraminiferal fatty acids at the 300-m site (8.3 %) compared to the 140-m site (1.8 %). In addition, the 18:1 isomer ratio of 18:1(*n*-9):18:1(*n*-7) used to assess bacterial ingestion, was lower at the 300-m site (1.3) compared to at the 140-m site (6.7), indicating a higher degree of bacterial ingestion at the deeper locality. Other less abundant bacterial biomarkers included 15:0 (3.7 - 4.6 %), 17:0 (1.0 - 3.8 %) and 17:1 (1.1 - 1.7 %). Following the SW monsoon, there was no significant difference in the total bacterial biomarkers at each site; these constituted 30.3 % of the total fatty acids at the 140-m site and 27.1 % at the 300-m site (Table 5.4, Figure 5.10). Biomarkers for cyanobacteria were fairly abundant and higher at the 300-m site (13.1 %) compared to the 140-m site (9 %). 18:1(*n*-7) was less abundant and only slightly higher at the 300-m site (5.2 %) than at the 140-m site (4.9 %). The 18:1 isomer ratio of 18:1(*n*-9):18:1(*n*-7) was lower at the 300-m site (0.5) compared to the 140-m site (0.8), supporting the other fatty acid biomarker evidence for a higher degree of bacterial ingestionin the OMZ core. Other less abundant bacterial biomarkers included 15:0 (between 2.7 and 6.3 %), 17:0 (between 1.2 and 1.4 %) and 17:1 (between 0.7 and 0.8 %).

Zooplankton biomarkers

During the spring intermonsoon, biomarkers for zooplankton (the two long-chain monounsaturated fatty acids 20:1(*n*-9) and 22:1(*n*-11) found as storage substances in, e.g., calanoid copepods (Mayor 2005) were significantly ($P < 3$ %) higher at the 140-m site (5.9 %) compared to the 300-m site (1.3 %) (Table 5.4, Figure 5.10). The percentage contribution of biomarkers for zooplankton was the same (2.5 %) at both sites during the SW monsoon (Table 5.4, Figure 5.10).

5.3.2.4 Food sources and feeding patterns in Uvigerina

During the spring intermonsoon, the phytodetrital biomarkers were very similar at the 140-m and 300-m sites. The relatively high percentage of phytodetrital biomarker fatty acids found in *Uvigerina* ex. gr. *semiornata* (> 30% of total fatty acids at both sites; Table 5.4, Figure 5.10) suggests that phytodetritus-derived organic matter formed a large part of its diet during the spring intermonsoon, despite the fact that during this season, the average sediment surface lipid concentration was low and the organic matter was relatively refractory (degraded) (R. Jeffreys, unpub. data). Thus, even in the absence of a fresh influx of labile organic matter from the euphotic zone, *U*. ex. gr. *semiornata* was apparently feeding selectively on organic matter of phytodetrital origin in the sediment. Following the SW monsoon, the positive response of *U*. ex. gr. *semiornata* to the presumed flux labile organic matter (phytodetritus) from the euphotic zone was reflected in a higher percentage of biomarkers for phytodetritus in the total fatty acid profile of this species at both the 140-m site (36.6 %) and the 300-m site (49.3 %), indicating a higher ingestion of phytodetrital-derived organic matter compared to the spring intermonsoon season that preceded this organic matter flux.

Individuals of *U*. ex. gr. *semiornata* contained higher percentages of both phytodetrital and bacterial biomarkers at the permanently hypoxic 300-m site than at the seasonally hypoxic 140-m site. One possible explanation is the higher preservation potential of organic matter within low-oxygen environments, resulting from lower rates of microbial activity (Wakeham et al. 1997b, Schönfeld and Altenbach 2005). This interpretation is consistent with the higher percentage of organic carbon found in sediments from the 300-m site (ca. 2-3 %) compared to the 140-m site (ca. 1-1.5 %) (C. Woulds, unpub. data). The higher percentage of total bacterial biomarkers in *U*. ex. gr. *semiornata* at 300 m during both seasons is likewise consistent with the fact that bacterial biomass (derived from bacterial phospholipid analysis) formed a higher proportion of organic carbon in the surface 0-

0.5 cm layer at the 300-m site (~ 2.5 mgC/g dry sediment) compared to the 140-m site (~ 0.5 mgC/g dry sediment) (C. Woulds, unpub. data).

The higher percentage contribution of biomarkers of zooplankton in *Uvigerina* ex. gr. *semiornata* at the 140-m site during the spring intermonsoon may reflect an increased abundance of zooplankon in the surface waters above the 140-m site on the continental shelf compared to the surface waters above the 300-m site on the continental slope. This would result in a higher flux of zooplankton carcasses reaching the seafloor. Organic matter reaching the seafloor from the upper water column is also likely to be less degraded and therefore contain higher percentages of fatty acids as a result of the shorter water column on the shelf. Another possible reason may be increased foraminiferal feeding on the degrading remains of benthic metazoans such as harpacticoid copepods at the 140-m site. These organisms presumably contain similarly high amounts of the fatty acids 20:1(*n*-9) and 22:1(*n*-11). They were abundant at the 140-m site (10.5 % of total live metazoa in the 0-1 cm sediment layer, spring intermonsoon) but were absent in samples from 300 m. (See Chapter 4 for more details on metazoan abundance).

5.4 General Discussion

5.4.1 Links between the phytoplankton community and the diets of benthic Foraminifera on the Pakistan margin

The northern Arabian Sea exhibits a strong seasonality in total primary production (Brock et al. 1993; Barlow et al. 1999; Tarran et al. 1999)**.** It has some of the highest productivity values in the open ocean with an annual primary productivity of between 200 and 400 $gC.m^{-2}.yr^{-1}$ (Qasim 1982; Codispoti 1991; Antoine et al. 1996) and two maxima during the SW and NE monsoon (Qasim 1982; Caron and Dennett 1999; Rixen et al. 2000). As benthic organisms are primarily dependent for food on the flux of organic matter to the seafloor, the composition and abundance of the

phytoplankton community, and the timings of flux events of phytodetritus to the seafloor from the euphotic zone, are crucial for the nutrition of benthic organisms. The high abundance of fatty acid biomarkers for cyanobacteria in foraminiferal samples at the 140-m and 300-m sites during both the spring intermonsoon (between 13.4 and 21.6 %) and the SW monsoon (between 13.1 to 28.4 %) indicate the importance of these phototrophic prokaryotes as a trophic resource on the continental shelf and upper slope off Pakistan. This is supported by previous studies of the phytoplankton community of the Arabian Sea that recorded the dominance of prokaryote taxa, especially the cyanobacteria *Synechococcus* spp., in the total phytoplankton biomass. For example, in September-October 1986, Burkill et al. (1993a) found that cyanobacteria were a major component of the microbial foodweb in oligotrophic regions of the northern Indian Ocean (Gulf of Oman and the monsoonal upwelling region off the South East Arabian coast) with *Synechococcus* spp. accounting for up to 40% of the Particulate Organic Carbon (POC). Jochem (1995) reported that *Synechococcus* spp. dominated the phytoplankton community in the upper mixed layer, whilst prochlorophytes dominated communities near the bottom of the euphotic zone and below the deep chlorophyll maximum. Tarran et al. (1999) also found that *Synechococcus* spp. was abundant and reported counts of $> 10^8$ cells l^{-1} during both the SW monsoon and intermonsoon seasons in the northwestern Arabian Sea (Gulf of Oman).

Diatoms constituted the most important of micro-phytoplankton food sources in the diets of the foraminiferal species studied. Biomarkers for this group comprise 7.2 - 13.4 % of the average fatty acid composition during the spring intermonsoon and 6.5 - 27.2 % during the SW monsoon. This is supported by the finding that diatoms contributed significantly to phytoplankton standing stocks, especially in near-shore upwelling waters where a mixed community of diatoms and the cyanobacterium *Synechococcus* dominated during the SW monsoon (Tarran et al. 1999). The higher percentage of biomarkers for diatoms in the foraminiferal samples following the SW

monsoon is consistent with the reported highest abundance and diversity of diatoms during the SW monsoon (Tarran et al. 1999).

5.4.2 Do calcareous and agglutinated Foraminifera have different diets?

From the fatty acid analyses of six foraminiferal species (three agglutinated and three calcareous) collected from 300 m in the upper OMZ on the Pakistan Continental Margin during the spring intermonsoon (April 2003) and the SW monsoon (October 2003), two types of dietary preferences can be inferred; these correspond to calcareous and agglutinated taxa.

1) Unselective detrital feeders with a diet dominated by bacteria and detritus resulting from the ingestion of sediment and associated bacteria and degraded organic matter. This type of diet was observed in the three agglutinated taxa *Ammodiscus* aff. *cretaceus*, *Bathysiphon* nov. sp. 1 and *Reophax dentaliniformis*.
2) Species that selectively ingest labile, algal-derived material in response to the availability of phytodetritus on the seafloor, resulting in a diet high in algal biomarkers and particularly polyunsaturated fatty acids (PUFAs). This feeding pattern was observed in the three calcareous taxa, *Bolivina* aff. *dilatata*, *Globobulimina* cf. *G. pyrula* and *Uvigerina* ex. gr. *semiornata*, which all displayed some degree of selective feeding on algal derived organic matter.

5.4.2.1 Trophic ecology of agglutinated taxa

In this study, *Bathysiphon* sp. nov. 1 and *Ammodiscus* aff. *cretaceus* both exhibited an unselective detrital feeding strategy. This is consistent with the findings of Gooday et al. (2002c) that *Bathysiphon capillare* de Folin, a large species collected from 950 m on the Wyville-Thompson ridge, northern Rockall Trough, is a deposit feeder, randomly consuming sediment, detritus and associated bacteria. These species appeared indifferent to the increased quantity and quality of phytodetritus on

the seafloor following the SW monsoon, as indicated by the lack of a significant increase in biomarkers of phytodetritus in their fatty acid composition. However, another agglutinated species, *Reophax dentaliniformis*, seems to have a slightly different trophic strategy. During the spring intermonsoon, this species appeared to be an unselective detritus feeder, like *B*. sp. nov. 1 and *A*. aff. *cretaceus*. However, following the SW monsoon, the percentage of biomarkers for bacteria in the fatty acid profile of *R. dentaliniformis* increased. The fact that this apparent change in diet was coupled with an increase in the standing stock of this species suggests that *R. dentaliniformis* may have been preferentially feeding on bacteria, exploiting the increased bacterial biomass associated with the flux of labile organic matter to the seafloor. If this is the case, then *Reophax dentaliniformis* was responding indirectly to the phytodetrital flux and exploiting a food source that other Foraminifera did not. A similar response has been reported in nematodes that increased in abundance following a flux of labile organic matter to the seafloor, apparently because they were feeding on microbes associated with labile organic matter (Poremba 1994). There is little evidence that Foraminifera selectively ingest bacteria. Nomaki et al. (2006) did not observe selective uptake of bacteria by eight multichambered foraminiferal species, including both calcareous and agglutinated forms, in a feeding expeiment conducted on individuals from Sagami Bay, Japan. However, the possibility that some foraminiferal species feed selectively on bacteria cannot be dismissed. There is some circumstantial evidence that some deep-sea allogromiids are predominantly bacteria feeders (Gooday 2002b).

5.4.2.2 Trophic ecology of calcareous taxa

Fatty acid analyses suggest that the calcareous Foraminifera *Bolivina* aff. *dilatata*, *Globobulimina* cf. *G. pyrula* and *Uvigerina* ex. gr. *semiornata* all preferentially ingest phytodetritus. This is indicated by an increased percentage of biomarkers for algae in specimens collected after the SW monsoon, compared with the agglutinated taxa analysed from the same site and season. Selective exploitation of phytodetritus has been recorded by many authors from both the natural environment (Gooday

1988; Thiel et al. 1988; Gooday and Lambshead 1989; Lambshead and Gooday 1990; Gooday and Turley 1990; Heeger 1990; Gooday et al. 1992; Kitazato et al. 2003) and from experimental work (Nomaki et al. 2005a, Nomaki et al. 2005b, Nomaki et al. 2006). However, the diverse fatty acid profiles of the three calcareous species analysed in this study suggests that algal-derived organic matter was not their only source of nutrition, either during the spring intermonsoon or following the presumed phytodetrital flux to the seafloor associated with the SW monsoon. Previous studies suggest that some or all of these taxa may infact be omnivorous feeding unselectively when high quality phytodetritus is absent or in low concentrations. For example, Goldstein and Corliss (1994) used Transmission Electron Microscopy (TEM) to examine the cell contents of *Uvigerina peregrina* (shallow infaunal) and *Globobulimina pacifica* (deep infaunal) and discovered that the cytoplasm contained a variety of food items, indicating unselective feeding. Heeger (1990) also reported a variety of biogenic particles in the food vacuole of calcareous species from the deep Greenland-Norwegian Sea, ranging from pennate diatoms and dinoflagellates to bacteria and siliceous aggregates. Again, these observations suggested a generally unselective feeding behaviour. Therefore, whilst Foraminifera may often be selective in littoral settings where much more food is available (as recorded by e.g. Lee et al. 1966, Lee and Muller 1973, Lee, 1980, Ward et al. 2003), deep-sea species cannot rely on herbivory if they are to survive in oligotrophic conditions of the generally food-limited deep-sea floor. When high quality phytodetritus is available, following episodic fluxes of phytodetritus from the euphotic zone, opportunistic species, which are usually calcareous, will feed on it avidly (Gooday 1988; Nomaki et al. 2005a). When fresh phytodetritus is not available, some of these species will utilise more degraded food resources. However, it is clear that some species associated with the Palkistan Margin OMZ, notably *Uvigerina* ex. gr. *semiornata*, are capable of selective exploitation of phytodetritus.

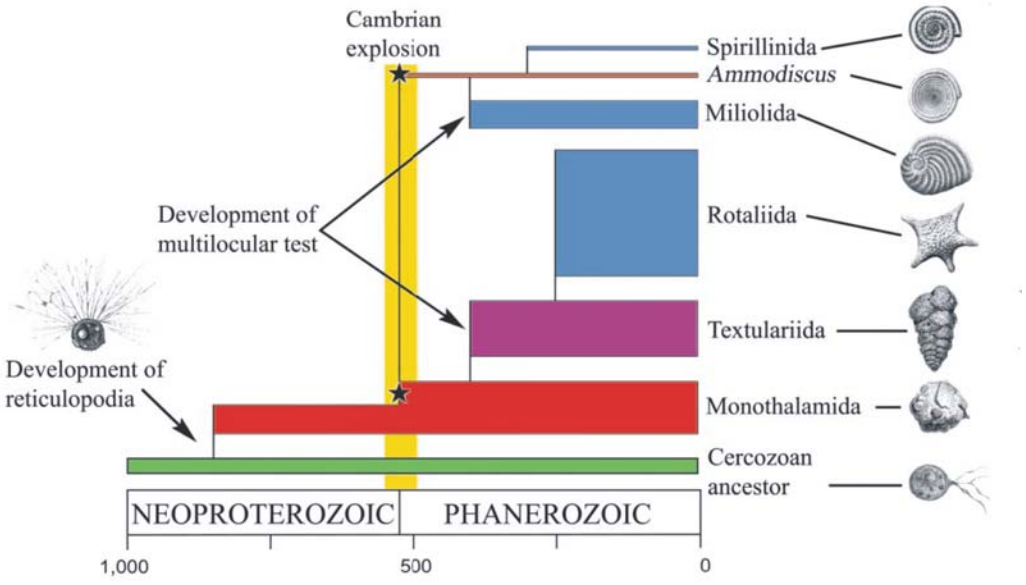
5.4.3 Links between feeding behaviour and foraminiferal phylogeny

The clear differences in feeding behaviour between the agglutinated and calcareous taxa analysed prompts the question of whether the feeding behaviour can be linked to phylogeny. In this study the most "primitive" Foraminifera analysed were the monothalamous astrorhizid *Bathysiphon* sp. nov. 1 and the ammodiscacean *Ammodiscus* aff. *cretaceus* (Figure 5.11), both unselective detritus feeders. There may be some connection between the lack of feeding on algal food sources by these species and the fact that monothalamous and primitive polythalamous agglutinated species evolved during the Neoproterozoic and Palaeozoic (Tappan and Loeblich 1988, Pawlowski et al. 2003b), before the evolution of the phytoplanktonic groups such as diatoms and coccolithophorids that dominate modern phytoplankton communities (Barron 1993; Siesser 1993). The ancient Palaeozoic ocean lacked calcareous plankton and was therefore a "siliceous ocean". Organic material reaching the seafloor during this time would have been quite different from modern phytodetritus, with chitinous and siliceous planktonic taxa such as radiolarians, dinoflagellates and "acritarchs" abundant. The dominant food sources available to early benthic foraminiferal forms colonizing the Palaeozoic seafloor are therefore more likely to have been bacteria and degraded organic matter in the sediment than in the modern algal dominated ocean (H. Kitazato, unpub. manuscript). It is conceivable that the diets of the more primitive forms analysed in this study reflect this evolutionary perspective in their relatively low diversity and percentage of algal biomarkers, and high percentage of bacterial/detrital biomarkers.

The polythalamous Foraminifera appeared in the fossil record during the Palaeozoic, ca. 350 Ma, after the monothalamous Foraminifera from which they are presumed to have evolved. The later evolution of polythalamous forms is supported by phylogenetic reconstruction based on molecular genetics (Pawlowski et al. 2003a) and evidence from the geological record (Tappan and Loeblich 1988). The polythalamous agglutinated Foraminifera *Reophax dentaliniformis* analysed in this study is a modern representative of some of the initial experiments in polythalamous

organisation. The feeding pattern of *Reophax dentaliniformis* in this study was predominantly unselective/detrital with a high percentage of bacterial/detrital biomarkers. However, a higher diversity and percentage composition of algal biomarkers was found compared with the more primitive monothalamous forms, suggesting that *Reophax dentaliniformis* also consumes algal groups, including diatoms and coccolithophorids.

Figure 5.11 Time scale of early foraminiferal evolution based on combined molecular and fossil data, highlighting the development of reticulopodia at the origin of the group, and the independent development of a multilocular test in the lineages leading to Textulariida, Rotaliida and Spirillinida, Miliolida. Only the taxonomic groups for which molecular data exist are illustrated. The height of each rectangle is proportional to the number of recognized families in the clade or to the number of different genetic lineages in the case of Monothalamida. Stars indicate the fossil appearance of some unilocular lineages. Note the early but separate origins of Monothalamida and *Ammodiscus*. From Pawlowski et al. (2003b).



The suborder Rotaliida is one of the most recently evolved major groups of Foraminifera. It first appeared in the Triassic and radiated during the Mesozoic (Jurassic and Cretaceous) (Tappan and Loeblich 1988; Holbourn et al. 2001; Pawlowski et al. 2003b). This radiation occurred at the same time as the explosive development of modern phytoplankton groups, that made their first appearance in the fossil record in the late Triassic (calcareous nannoplankton including coccolithophorids; Siesser 1993) and early Jurassic (diatoms; Barron 1993). The evolution of a calcitic scale by phytoplankton may have increased their photosynthetic capabilities, enabling them to colonise oligotrophic open ocean areas for the first time (Siesser 1993). This diversification of algal groups must have profoundly influenced and modified marine ecosystems, as it would have not only increased the diversity of potential food sources available in the oceans, but would also have increased organic carbon fluxes to the deep-sea environment allowing benthic organisms to flourish. The evolution and invasion of rotaliids into the deep sea may therefore have been closely related to their ability to exploit the increased supply, during the Mesozoic, of algal phytodetritus to the sea floor from the euphotic zone (H. Kitazato, unpub. manuscript). The rotaliids analysed in this study, *Uvigerina* ex. gr. *semiornata, Bolivina* aff. *dilatata* and *Globobulimina* cf. *G. pyrula*, all exhibited some ability to ingest algal-derived organic material and their fatty acid profiles contained a high diversity of algal biomarkers including biomarkers for diatoms and coccolithophorids. Therefore, it is proposed that whilst the most recently evolved groups utilise modern phytoplankton groups as a food source, more primitive taxa, including all monothalamous forms and many agglutinated taxa, remained unselective deposit feeders, randomly ingesting sediment, degraded organic matter and associated bacteria, including some refractory algal detritus.

5.4.4 Future directions for this study

The discussion and interpretation of potential food sources and foraminiferal feeding patterns would be enhanced with additional knowledge of the corresponding pelagic ecosystem, including the phytoplankton communities at the time of sampling and of

the precise timings of the downward flux of organic matter to the benthic environment. This could be achieved using a long time-series of sediment traps to assess the downward flux of organic matter to the sea-floor and flow cytometry to assess the phytoplankton communities.

5.5 Conclusions

Results of this study support the hypotheses that Foraminifera are omnivorous with algae, detritus and bacteria amongst the most common food sources. However, the results, together with previous studies of the trophic biology of Foraminifera, indicate that there is an important difference in the trophic biology of the more primitive foraminiferal forms, for example monothalamous forms (soft-shelled and agglutinated), and more "advanced" polythalamous forms (hard-shelled, agglutinated and calcareous), leading to species-specific trophic responses and potential resource-partitioning within the same site. Some monothalamous and agglutinated forms (for example *Ammodiscus* aff. *cretaceus*, *Bathysiphon* sp. nov. 1) are suggested to be unselective omnivores, ingesting the sediment and associated organic matter irrespective of its quality, and showing little response to a phytodetrital depositional event and higher availability of labile organic matter on the seafloor. The polythalamous agglutinated species *Reophax dentaliniformis* is suggested to have a more complex feeding behaviour compared to *Ammodiscus* aff. *cretaceus* and *Bathysiphon* sp. nov. 1. *Reophax dentaliniformis* contained a broad spectrum of food sources in its diet indicating an unselective feeding behaviour. However, the increased percentages of bacterial biomarkers and the lack of an increase in algal biomarkers in *R. dentaliniformis* following the SW monsoon suggests that this species may have been selectively feeding on bacteria. In contrast, polythalamous calcareous Foraminifera (for example *Bolivina* aff. *dilatata*, *Globobulimina* cf. *G. pyrula* and *Uvigerina* ex. gr. *semiornata*) appear to preferentially select labile phytodetritus, especially when it was abundant, although they were not exclusively herbivorous in either season sampled and appear to have relied on other organic matter (OM) sources, including bacteria, for some of their nutrition. *Uvigerina* ex. gr.

semiornata, the dominant foraminiferal species in the upper OMZ of the Pakistan Margin, is omnivorous, consuming many food sources from bacteria and sediment to phytodetritus. However, it appears to prefer a herbivorous diet and exhibits an ability to selectively ingest phytodetritus when it is available and is a highly successful opportunistic species that feeds mainly on the seasonal food supply of phytodetrital fluxes to the seafloor. This trophic flexibility at times when food availability is low, and the observed ability of *U*. ex. gr. *semiornata* to respond opportunistically to a natural flux event by preferentially ingesting algal-derived organic matter, may be vital characteristics for the success and dominance of *U*. ex. gr. *semiornata* in the upper OMZ of the Pakistan Continental Margin.

6 Uptake of algal carbon by *Uvigerina* ex. gr. *semiornata* within the Pakistan margin OMZ: laboratory and *in situ* ^{13}C enrichment experiments

6.1 Introduction

Benthic Foraminifera are known to exploit many nutritional food sources (Lee et al. 1966; Lee and Muller 1973; Lee 1974; DeLaca et al. 1981; Lipps 1983; Goldstein and Corliss 1994; Goldstein 1999). One of the highest quality food sources available on the seafloor is phytodetritus, derived from primary productivity in the euphotic zone. Many previous studies have reported that some foraminiferal species respond to deposits of phytodetritus on the seafloor following settlement of material originating from an algal bloom (Gooday and Turley 1990; Silva et al. 1996; Ohga and Kitazato 1997; Schmiedl and Mackensen 1997; Drazen et al. 1998; Gooday and Rathburn 1999; Kitazato et al. 2000; Fontanier et al. 2002; 2003). Other studies have used experimental techniques to analyse the response of the benthic fauna to a simulated flux event, using the stable isotope ^{13}C as a tracer to assess the uptake of labile algal matter by benthic organisms (Blair et al. 1996; Levin et al. 1999; Middelburg et al. 2000; Moodley et al. 2002; 2005; Witte et al. 2003a; 2003b; Nomaki et al. 2005a; 2006). Many of these studies reported a rapid uptake of phytodetrital food sources by Foraminifera. For example, Moodley et al. (2002) conducted *in situ* experiments at a deep-sea site (2170 m water depth) in the northeast Atlantic and found that macrofaunal Foraminifera (>300 μm) displayed the most rapid response to the simulated pulse of ^{13}C-labelled diatoms and ingested ca. 29 % of the added food source, whilst bacteria assimilated only ca. 21 %, despite the fact that they constituted ~ 95 % of the benthic biomass. Metazoan macrofauna displayed an even slower response, and ingested only 3.5 % of the ^{13}C-labelled diatoms. Nomaki et al. (2005a) also reported a rapid response by Foraminifera to an algal food source, recording a high assimilation rate of ^{13}C-labelled algae relative to

metazoan meiobenthos during a 6 day *in situ* incubation at 1449 m in Sagami Bay, Japan. Many of the observations of rapid, short-term processing by Foraminifera have shown that calcareous forms display the greatest ability to ingest algal-derived organic matter. At a species level, Nomaki et al. (2005a; 2006) recorded selective ingestion of algal-derived food sources, including the marine diatom *Chaetoceros sociale*, by calcareous species, particularly shallow-infaunal species including *Uvigerina akitaensis*, *Bolivina spissa* and *Bolivina pacifica*, during *in situ* feeding experiments in Sagami Bay. However, Levin et al. (1999) observed a rapid short-term (1 to 1.5 days) response by agglutinated Foraminifera in an *in situ* enrichment experiment using ^{13}C-labelled diatoms on the North Carolina continental slope (850 m water depth), indicating that other foraminiferal groups have the capability to exploit fresh phytodetritus.

Contradictory results were obtained at a much deeper, abyssal site (4800 m water depth) by Witte et al. (2003a, 2003b) who reported that metazoans exhibited a much faster response to a simulated organic matter pulse than Foraminifera. This suggests that at abyssal depths metazoans were more important in the short-term cycling of phytodetritus on the seafloor than protozoans. However, Foraminifera were not analysed at a species level in this study, which may have masked the rapid response by some species. Thus, even at abyssal depths, a few key species of benthic Foraminifera may be important in the rapid processing of organic matter.

Previous studies of foraminiferal responses to food pulses have been undertaken in oxic environments. The purpose of this study was to investigate carbon uptake in a seasonally hypoxic setting. Shipboard and *in situ* ^{13}C-labelled diatom feeding experiments were conducted on sediments from 140 m water depth on the Pakistan Margin, and fatty acid biomarkers were used to analyse the response of the foraminiferan *Uvigerina* ex. gr. *semiornata*, the dominant species at this site, to a simulated pulse of phytodetritus.

6.2 Methods

The aim of the ^{13}C-labelled diatom feeding experiments was to gain further insight into the trophic ecology of *Uvigerina* ex. gr. *semiornata* and to track the uptake of an algal food source by this species, using the stable isotope ^{13}C as a label. *Uvigerina* ex. gr. *semiornata* was chosen because of its importance in the foraminiferal assemblage on the Pakistan continental margin (discussed in more detail in chapters 4 and 5). To summarise briefly, *U*. ex. gr. *semiornata* was the dominant macrofaunal (> 300 μm) foraminiferal species at water depths of 140 m and 300 m on the Pakistan Margin. It displayed an opportunistic response to the natural phytodetrital flux to the seafloor following the SW monsoon and displayed a significant increase in both standing stock and percentage abundance in the total live foraminiferal assemblage (> 300 μm) (Chapter 4). In addition, this species exhibited evidence for selective feeding on phytodetritus (Chapter 5).

6.2.1 Experimental methods

Time-series of feeding experiments were carried out at the 140-m site following the SW monsoon (October 2003). This study involved two complementary experiments; one *in situ* and the other in a shipboard laboratory. In both cases, the bottom-water oxygen concentration and temperature were maintained at the ambient values at the time of sampling (October 2003) (O_2 = 0.11 mll^{-1}, temperature = 18.2 ºC) (See Table 3.1, Chapter 3 for environmental features of the 140-m site) and a monoculture of ^{13}C-labelled diatoms (*Thalassiosira weisflogii*) was added as a food source. The ^{13}C-label was used to track the consumption of the diatom food source.

6.2.1.1 Diatom monoculture

A monoculture of *Thalassiosira weisflogii* was used as a food source in both the shipboard and *in situ* feeding experiments. The diatoms were cultured in an autoclaved flask in ^{13}C-labelled seawater until the diatom cells were ~80% labelled with ^{13}C. Although the diatoms were grown axenically (as a monoculture), there

must have been unknown quantities of bacteria and flagellates growing in the culture (D. Pond, pers. comm.). The diatom detritus was then combined with kaolinite powder to act as a ballast to produce a slurry consisting of one part kaolinite and three parts algae (v/v). The slurry was freeze-dried and kept at -20°C until required in the incubation experiments. Before being added to the experiments, the slurry was defrosted and resuspended in Milli Q water. The dose of diatom slurry was adjusted for each experiment in order to maintain an average dose of 600-1000 mg C m^{-2}. The added carbon was equivalent to 0.8 ± 0.3 % of the average naturally present OM in the top 1 cm of sediment (Woulds et al. in prep) (see table 6.1. for a summary of the amount of ^{13}C algae used in all shipboard and *in situ* enrichment incubations at 140 m).

Table 6.1 Summary of the use of ^{13}C-labelled diatoms in all shipboard and *in situ* enrichment incubations at 140 m during the SW monsoon, cruise CD151 (October 2003). Abbreviations: SF13 = Shipboard experiments (2 replicate megacores of 78.5cm surface area for each time point). EF13 = Elinor Lander *in situ* incubations (sediment chamber, 30cm^2 surface area). Mass values are dry weight (dwt). Table adapted from Schwartz and Woulds (2003).

Incubation ID	Station number	Core number	Dates of incubation	Mass (mg dwt)	% Carbon	Carbon mass (mg dwt)
SF13-2day (A)	56101#4	6	20-22/09/2003	50.2	14	7.03
SF13-2day (B)	56101#10	6	20-22/09/2003	50.4	14	7.06
SF13-5day (A)	56101#2	3	20-25/09/2003	49.7	14	6.96
SF13-5day (B)	56101#2	2	20-25/09/2003	49.1	14	6.87
EF13-2.5day (A)	56101#29	N/A	25-27/09/2003	349.1	14	48.87

6.2.1.2 Shipboard feeding experiments

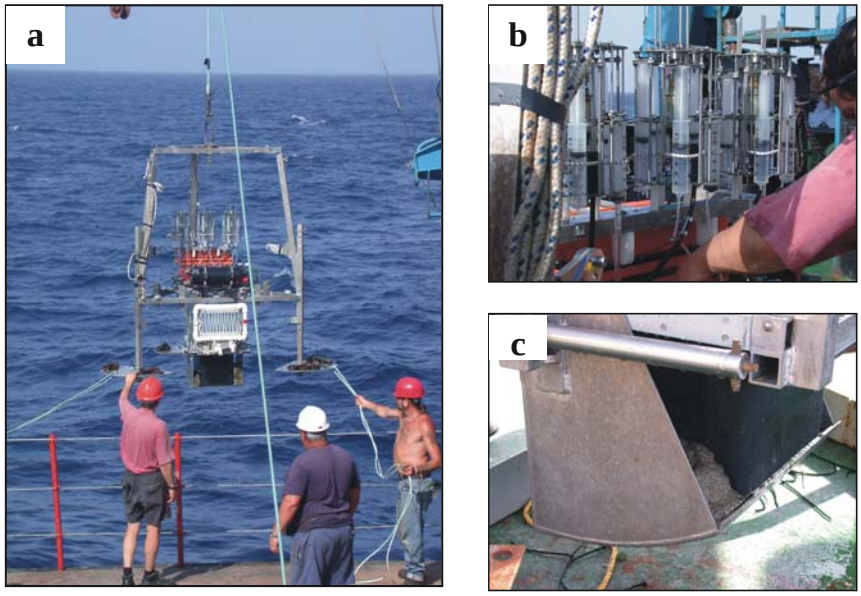
Shipboard laboratory feeding experiments were conducted using six replicate megacores collected at the 140-m site and incubated in a constant temperature laboratory (Figure 6.1). The oxygen concentration was maintained at ambient bottom-water levels using an oxystat system. Algal detritus (~ 50 mg, equivalent to a carbon delivery of 5-8 mg of C per megacore) (Table 6.1) of algal detritus was added to each of six megacores (78.5cm^2 surface area) at the start of the experiment. After a settling period of 30-60 minutes, a green layer of algal cells was visible on the surface of the cores. Following this, gentle water column stirring was initiated. Megacores were covered in black sheeting during the experiment in order to exclude light. Pairs of megacores were then incubated for two days or five days. Two megacores were used as time-zero controls, where the labelled algal slurry was added and then the megacores were immediately processed. The t=0 Foraminifera were used to allow comparison of the fatty acid composition of natural *Uvigerina* ex. gr. *semiornata* with that of Foraminifera exposed to the diatom food source for a period of two days or five days.

6.2.1.3 In situ feeding experiments

In situ feeding experiments were conducted at the 140-m site using a benthic lander (Black et al. 2001) (Figure 6.2). Once on the seafloor, the lid was closed on the benthic chamber (30cm^2 surface area) isolating an area of sediment from the natural environment. A known amount (~350 mg, equivalent to a carbon delivery of 25-35 mg of C) (Table 6.1) of ^{13}C-labelled algal slurry was added to the sediment chamber (900 cm^2 surface area) using an automated syringe. Gentle stirring of overlying water in the chamber was initiated after a period of 30-60 minutes to allow time for the algal detritus to settle. To maintain ambient dissolved oxygen concentration, chamber water was pumped through an oxystat gill in contact with bottom water for the duration of the experiment. After an incubation period of ~2.5 days, the benthic lander was recovered onboard RRS *Charles Darwin* and the sediment retained in the

Figure 6.1. Experimental set-up of shipboard laboratory ^{13}C-labelled diatom feeding experiments conducted in a constant temperature laboratory on board RRS *Charles Darwin*. From Schwartz and Woulds (2003).

Figure 6.2 Lander used for *in situ* ^{13}C-labelled diatom feeding experiments. a) Lander deployed from RRS *Charles Darwin*. b) Oxystat gill and sampling syringes to regulate and measure bottom-water oxygen concentration. c) Sediment chamber (900 cm^2). From Schwartz and Woulds (2003).



benthic chamber was sub-sampled for faunal analysis using two replicate megacores (78.5cm^2 surface area). No time-zero controls were possible in the case of the *in situ* experiments. Therefore, the fatty acid composition of natural Foraminifera was used to compare the fatty acid composition of *Uvigerina* ex. gr. *semiornata* before and after the 2.5 day exposure to the diatom food source.

6.2.1.4 Extraction of live Foraminifera

At the end of each timed feeding experiment (both shipboard and *in situ*), the megacore was sliced into 1 cm thick layers to a depth of 5 cm. Each layer was sieved wet on a 300-μm screen. For foraminiferal fatty acid analysis, only individuals from the upper 1 cm of the sediment were used. The sieved residue from this layer was kept chilled (< 5 °C) in a refrigerator or over ice to prevent decomposition of the fatty acids, and macrofaunal (> 300 μm) Foraminifera were sorted as quickly as possible under a low-power binocular microscope. Individuals sampled were all from a modal size group (~ 300-400 μm length) to ensure consistency throughout the experiment. Picked specimens were kept in a small glass petri dish containing chilled, filtered seawater which was placed in a larger dish filled with ice. An organic stain such as rose Bengal could not be used to distinguish 'live' Foraminifera as this could alter their fatty acid composition. Instead, specimens were judged to be 'live' (and therefore feeding) at the time of sampling based on the presence of obvious test contents in most or all constituent chambers. Foraminifera were sorted into individual species and cleaned in filtered (2 μm screen) seawater to remove any attached organic particles. Four replicate samples comprising thirty individuals of *Uvigerina* ex. gr. *semiornata* were sorted from each time point, placed into 1.1 ml glass vials, and frozen at –20 °C prior to fatty acid extraction.

6.2.2 Analytical methods

6.2.2.1 Lipid analysis

Detailed methods for the lipid analyses and fatty acid extractions are provided in chapter 5. In brief, lipids were extracted in Chloroform : Methanol (2:1 v/v) at – 20 ºC for a minimum of 24 hours to ensure full extraction. Internal standards (either the fatty acid 21:0 or 23:0, both present only in trace amounts in the natural environment) were added in known quantities to enable fatty acid quantification. Fatty acids were then prepared as PFB (Pentafluorobenzyl) Esters following a method adapted from Sonesson et al. (1987) and Guezennec et al. (1996) and analysed by gas chromatography (GC) coupled to an electron-capture detector (ECD). A list of dominant fatty acids, their sources and references is shown in Table 1 (Appendix B).

6.2.2.2 Gas Chromatography Mass Spectrometry

In addition to the quantitative analysis of fatty acids using gas chromatography, the level of ^{13}C-enrichment of thirteen individual fatty acids in *Uvigerina* ex. gr. *semiornata* was analysed by selective ion scan using a gas chromatograph (GC) equipped with a ZB Wax fused silica capillary column (30 m length and 0.32 mm internal diameter) coupled to a mass spectrometer (MS). The mass spectrometer ionises the PFB ester fatty acids as they elute from the GC column and then separates them according to their mass-to-charge (*m*/e) ratio. Chemical ionisation (CI) mass spectrometry was used as it is much less energetic than electron ionisation (EI) and reduces fragmentation of the fatty acid and gives 100% yield of intact fatty acid molecules. Each sample was injected in a volume of 1 µl, using helium as a carrier gas and the GC-MS was operated in negative CI mode. Fatty acids were analysed from Foraminifera sampled at each time point over the duration of both the shipboard and *in situ* feeding experiments. For each foraminiferal fatty acid, the relative proportions of 8 dominant mass ions (accounting for > 95 % of all mass ions present

in each fatty acid) were analysed, in order to overcome potential errors with non-uniform labelling of each fatty acid in the diatom food source resulting in different degrees of enrichment of the fatty acid chain. Two natural mass ions (100% ^{12}C and 1 ^{13}C) were analysed to account for any natural fatty acid that was in the foraminiferan before the experiment or any unlabelled fatty acid deriving from food other than the ^{13}C diatom food source that could have been ingested from the sediment during the experiment. In addition, six mass ions representing different degrees of ^{13}C-enrichment of the carbon chain in the fatty acid molecule (100% ^{13}C, -1 ^{13}C, -2 ^{13}C, -3 ^{13}C, -4 ^{13}C, -5 ^{13}C) were also analysed to account for fatty acids in the foraminiferan cell that originated from ingestion of the ^{13}C-labelled diatoms. The total percentage ^{13}C was then calculated by subtracting the total area of all ^{12}C mass ions from the total ion current (TIC) chromatogram (area of all 8 masses scanned) using the formula:

$$^{13}\text{C} = \text{TIC} - \text{total } ^{12}\text{C}$$

The percentage ^{13}C was then calculated for each individual fatty acid using the formula:

$$\%\ ^{13}\text{C} = \frac{\text{area of total } ^{13}\text{C}}{\text{area of TIC}} \times 100$$

The percentage of ^{13}C in each fatty acid was therefore used in combination with data for the change in quantity (ng) of the fatty acid (quantified from gas chromatography using internal fatty acid standards), to interpret the uptake of the diatom food source by the Foraminifera and to investigate assimilation pathways in the Foraminifera such as the potential synthesis of fatty acids in the foraminiferal cell.

6.2.3 Statistical analysis

Data were analysed using the programme PRIMER (Clarke and Gorley 2001). All statistical analysis was conducted on average quantity (ng per 30 Foraminifera) data. The main multivariate statistical test employed was analysis of similarity (ANOSIM,

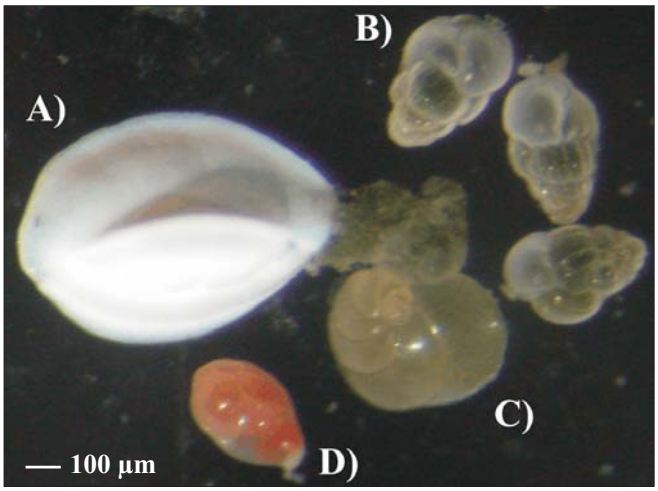
1-way crossed case (Clarke and Warwick 1994). This test was chosen since the data were multivariate (30 fatty acids identified for each sample) and the samples were separated by the single factor, namely time. For the ANOSIM test, a value of $P < 3$ represents a significant difference between samples and a value of $P < 1$ represents a strong significant difference between samples. Cluster analysis was also used to assess the similarities of the samples and create dendrograms. In each multivariate analysis, a Bray-Curtis similarity coefficient was used on square-root transformed data. 95% confidence intervals are shown for average data. A two sample t-test assuming unequal variance was also conducted to test for significance in differences between univariate data such as the average quantity (ng) of total fatty acid and individual fatty acids in *Uvigerina* ex. gr. *semiornata* at different time points over the duration of the feeding experiments. Percentage composition (Mol %) and quantity (ng) fatty acid data are presented in Appendix C. Results of statistical analysis are displayed in Appendix D.

6.3 Results and Discussion

6.3.1 Foraminiferal response to ^{13}C-labelled diatoms

In both the shipboard and *in situ* experiments, a positive uptake of the diatom monoculture was indicated by a bright green colouration of the cytoplasm of some Foraminifera, presumably reflecting the presence of chlorophyll. This visual evidence was observed in a number of shallow-infaunal calcareous species (Figure 6.3). Some species responded rapidly to the labile food source, notably *Uvigerina* ex. gr. *semiornata*, *Cassidulina laevigata* and *Cancris auriculus*, which all exhibited a bright green colouration of the cytoplasm after only two days (shipboard experiment).

Figure 6.3 Shipboard laboratory diatom feeding experiment (t = 2 day) at 140 m, following the SW monsoon (October 2003). Light photograph showing different foraminiferan species with coloured cytoplasm. The green colour in A-C is presumed to reflect the ingestion of diatoms. The red/orange colour of D is natural.
A) *Quinqueloculina* aff. *venusta* B) *Uvigerina* ex. gr. *semiornata* C) *Cancris auriculus* D) *Globobulimina* cf. *G. pyrula*

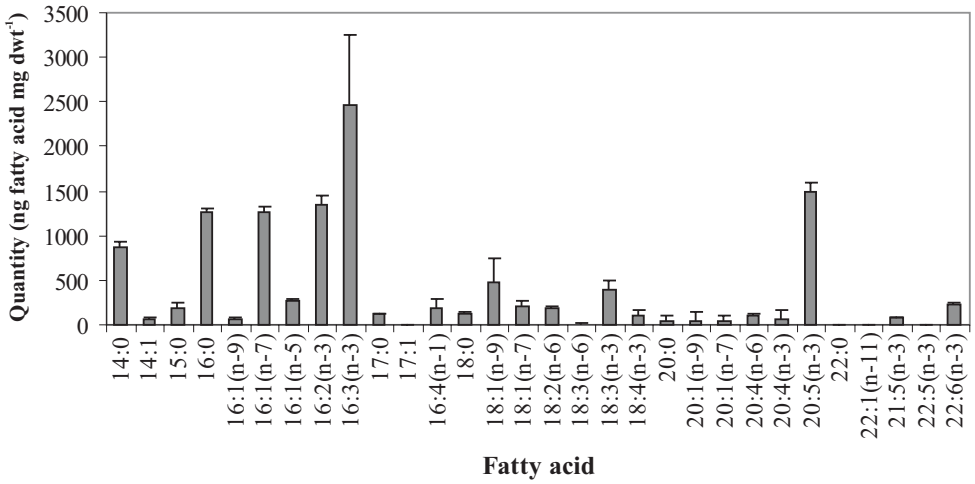


Other species, for example *Globobulimina* cf. *G. pyrula*, appeared to respond more slowly to the diatom food source, displaying a natural red/orange cytoplasmic colour during the two day laboratory experiment (Figure 6.3), but some green colouration after five days (laboratory feeding experiment t = 5). Some species, e.g. *Uvigerina* ex. gr. *semiornata*, *Cassidulina laevigata* and *Quinqueloculina* aff. *venusta*, gathered diatom material around their apertures. This suggests that they were actively feeding when sampled (see Lipps 1983 for review). However, Foraminifera have been observed to collect particles such as graphite around their aperture, suggesting that the collection of particles may be related to some other function such as camouflage (Murray 1973b) or the creation of agglutinated structures. Therefore fatty acid analysis of the cellular contents of Foraminifera was required to fully assess the ingestion of diatoms by the Foraminifera.

6.3.2 Diatom fatty acid composition

The fatty acid composition of the diatom monoculture, the food source used in the feeding experiment, is shown in Figure 6.4. (average quantity) (Tables of percentage composition, Mol %, and average quantity, ng, are shown in Appendix C). Dominant fatty acids in the diatom monoculture, based on both percentage contribution (Mol %) and average quantity (ng) of the total fatty acids, included the saturated fatty acid 16:0 (10.8%), the monounsaturated fatty acid (MUFA) 16:1(*n*-7) (11.0%) and the polyunsaturated fatty acids (PUFAs) 16:2(*n*-3) (11.8%), 16:3(*n*-3) (21.8%) and 20:5(*n*-3) (11.6%) (Figure 6.4).

Figure 6.4 ^{13}C-labelled diatom feeding experiments: average quantity (ng) of fatty acids in the diatom *Thalassiosira weisflogii* monoculture. Data are average total weight (ng) of fatty acids per mg dry weight (dwt) of two replicate samples.



16:0 is not particularly useful as a biomarker for diatoms, since it has been found in substantial amounts in many prokaryotic and eukaryotic organisms (Bell et al. 1986, Sargent et al. 1987). However, 16:1(*n*-7) is synthesized extensively by diatoms and therefore has been suggested as a biomarker for this algal group, especially if 16:0 is also dominant (Ackman et al. 1968, Sargent and Henderson 1986). The three

dominant PUFAs present in the *Thalassiosira* sp. monoculture (16:2(*n*-3), 16:3(*n*-3), 20:5(*n*-3)) are all established biomarker fatty acids for the Bacillariophyceae (diatom) as they are synthesized *de novo* by the diatom cell and often comprise a large part of the fatty acid profile of this algal group (Ackman et al. 1968, Sargent and Falk-Petersen 1988). The high amounts of these PUFAs in the diatom food source indicate the high quality and freshness of the organic matter. These fatty acids were therefore used as biomarkers to track the ingestion of *Thalassiosira* sp. throughout the course of the feeding experiment.

6.3.3 Tracking the uptake of ^{13}C-labelled diatoms by *Uvigerina*

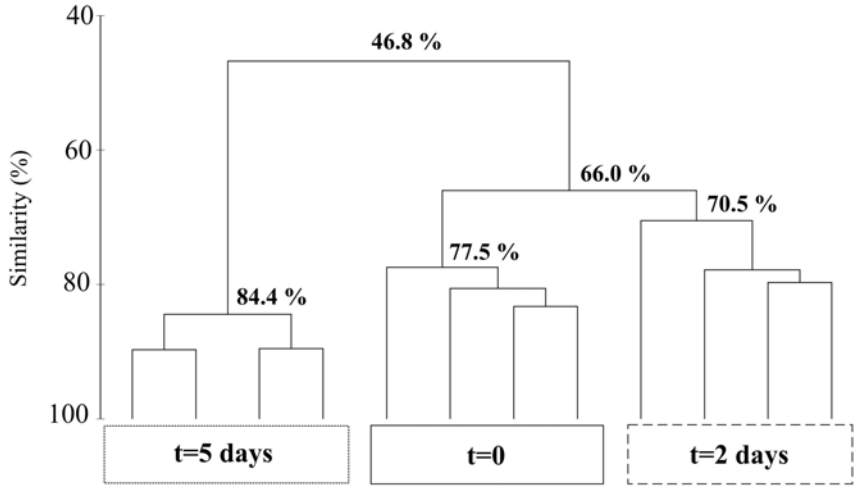
The following section presents the fatty acid composition (average quantity) for the total fatty acids (section 6.3.3.1), and individual fatty acids (6.3.3.2) over the duration of the shipboard and *in situ* ^{13}C-labelled diatom feeding experiments.

6.3.3.1 Total fatty acid composition

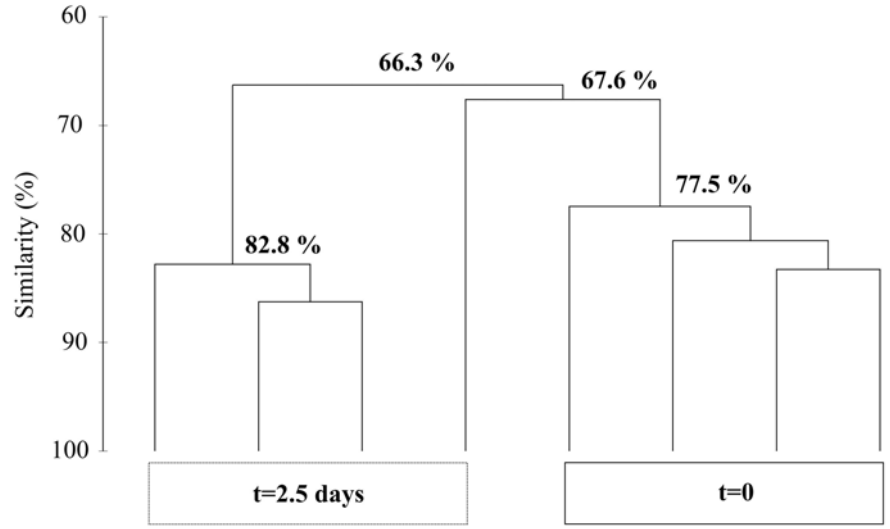
Foraminiferal fatty acid content (quantity, ng) after t=0, t=2 and t=5 days of exposure to the diatom food source in the shipboard experiment were 46.8 % similar (Bray-Curtis similarity test, Figure 6.5a), and samples from each time point were significantly ($P < 3$, ANOSIM) different from each other. However, replicate samples taken at each time point were all > 70% similar, reflecting a high degree of coherence in the foraminiferal fatty acid composition at each time point sampled during the experiment. Forminiferal fatty acid contents (average quantity data) at t=0 and t=2 days of exposure to the diatom food source were 66% similar, but the composition at t=5 days was only 46.8% similar to samples taken at the other time points. This indicates a greater divergence of foraminiferal fatty acid contents between the 2 day and 5 day time points compared to the natural and 2 day time point.

Figure 6.5 ^{13}C-labelled diatom feeding experiment at 140 m, SW monsoon (October 2003). Dendrogram of the average quantity (ng) of fatty acid in the foraminiferan *Uvigerina* ex. gr. *semiornata* in a) shipboard feeding experiments at t = 0, t = 2 days and t = 5 days. b) *in situ* feeding experiments sampled at t=0 (natural samples) and at t=2.5 days. Data are average quantity (ng) of four replicate samples per time point. Based on Bray-Curtis Similarity of square-root transformed data.

a) Shipboard laboratory ^{13}C-labelled diatom feeding experiments



b) *In situ* ^{13}C-labelled diatom feeding experiments



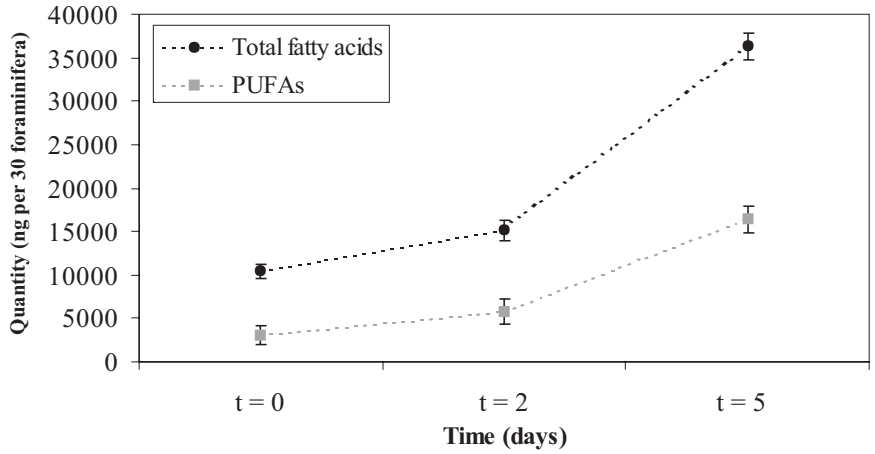
The average fatty acid content (quantity, ng) in *Uvigerina* ex. gr. *semiornata* sampled at natural and t=2.5 days (end of the in situ feeding experiment) were 66.3 % similar (Bray-Curtis similarity) (Figure 6.5b). Three replicate samples (30 individuals per sample) from the 2.5 days incubation were 82.8 % similar, but the fourth replicate grouped with the natural samples. Therefore, although there was a general divergence between the fatty acid composition of the natural and experimental (t=2.5 days) Foraminifera, the difference was not significant (P > 3, ANOSIM).

6.3.3.2. Total quantity (ng) of fatty acids

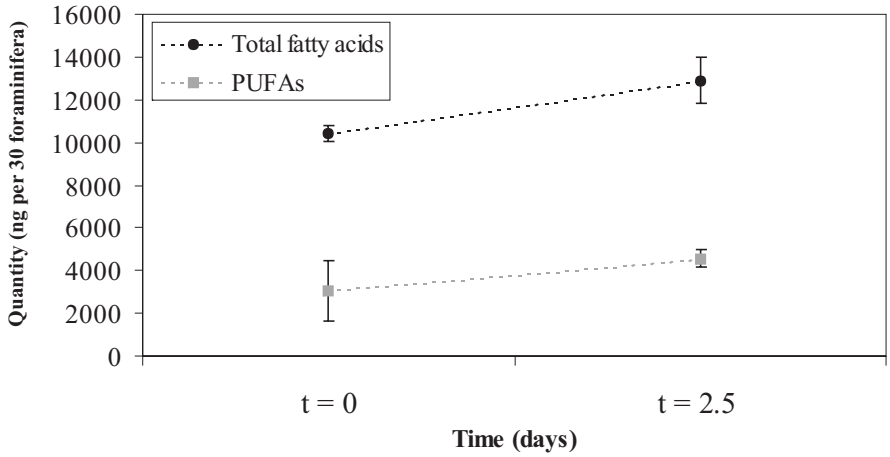
The average quantity (ng) of total fatty acids in *Uvigerina* ex. gr. *semiornata* increased significantly (P < 0.05, 2-sample t-test) over the duration of the 5 day shipboard experiment. Compared to the natural Foraminifera (t=0), there was a ~ 1.5 fold increase in the average total quantity of fatty acids after 2 days (t=2) and a ~ 3.5 fold increase after 5 days (t=5) of exposure to the diatom food source (Figure 6.6a and Appendix C). The average quantity (ng) of total fatty acids in this species also increased significantly (P < 0.05, 2-sample t-test) over the 2.5-day period of the *in situ* feeding experiment (Figure 6.6b). After 2.5 days, there was a ~ 1.2 fold increase in average total quantity compared to the natural Foraminifera.

Figure 6.6. ^{13}C-labelled diatom feeding experiments at 140 m, SW monsoon (October 2003): average quantity (ng per 30 Foraminifera) of total fatty acids and polyunsaturated fatty acids (PUFAs) in the foraminiferan *Uvigerina* ex. gr. *semiornata* from a) shipboard laboratory feeding experiments (sampled at t = 0, t = 2 days and t = 5 days), b) *in situ* feeding experiments sampled at t=0(natural samples) and t=2.5 days. Data are average total weight (ng) of four replicates per time-point. 95 % Confidence Intervals are shown. Note that dashed lines between samples are not based on actual data.

a) Shipboard laboratory ^{13}C-labelled diatom feeding experiment at 140 m



b) *In situ* ^{13}C-labelled diatom feeding experiment at 140 m



6.3.3.3 Quantity (ng) of polyunsaturated fatty acids

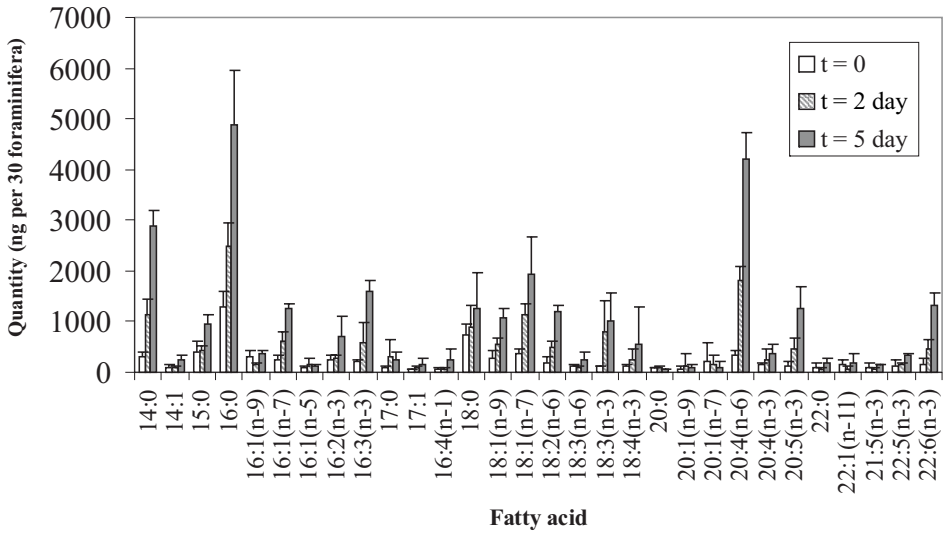
An important component of the total fatty acids, the polyunsaturated fatty acids (PUFAs), also increased significantly ($P < 0.05$, 2-sample t-test) from the start to the endpoint of both the shipboard (t=5 days) and *in situ* (t=2.5 days) experiments (Figure 6.6a,b). Polyunsaturated fatty acids were present in high quantities in the diatom food source, but were only present in small amounts in the natural Foraminifera. Therefore an increase in PUFAs in the experimental Foraminifera indicated ingestion of phytoplankton-derived organic matter, presumably originating from the introduced food source. Because each foraminiferan specimen was cleaned thoroughly before extracting the fatty acids, any diatom biomarker fatty acids certainly came from analysis of the cellular contents, indicating the ingestion of diatoms, and not from diatom-derived organic matter attached to the outer surface of the test.

6.3.3.4 Quantity (ng) of individual fatty acids

The change in average quantity (ng) of individual fatty acids in *Uvigerina* ex. gr. *semiornata* was analysed over the duration of both the shipboard and *in situ* feeding experiments. Thirty fatty acids were recognised in all *U*. ex. gr. *semiornata* samples. Figure 6.7a,b shows the entire spectrum of individual fatty acids (average quantity) over the duration of the shipboard and *in situ* experiments respectively. Figure 6.8a,b and Figure 6.9a,b show the changes in the quantity (ng) of sixteen dominant fatty acids over the course of the two experiments as individual plots.

Figure 6.7 ^{13}C-labelled diatom feeding experiments. Average quantity (ng per 30 Foraminifera) of the entire spectrum of fatty acids in the foraminiferan *Uvigerina* ex. gr. *semiornata* in a) shipboard ^{13}C-labelled diatom feeding experiment sampled at t = 0, t = 2 days and t = 5 days, b) *in situ* ^{13}C-labelled diatom feeding experiment sampled at t = 0 (natural samples), t = 2.5 days. Data are average quantity (ng per 30 Foraminifera) of total fatty acids of four replicates per time-point for each experiment. Data for these graphs are presented in Appendix C.

a) Shipboard laboratory diatom feeding experiment (t=0, t=2 days, t=5 days)



b) *In situ* diatom feeding experiment (t=0, t=2.5 days)

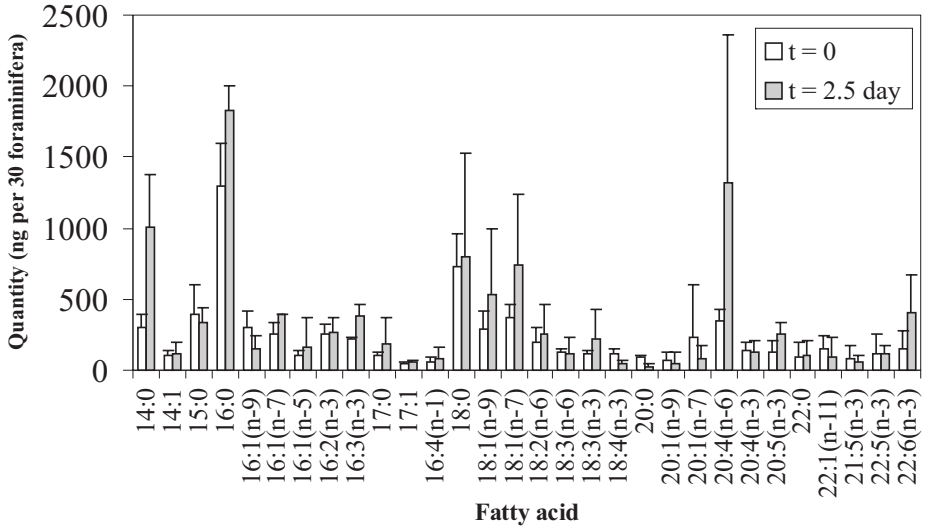


Figure 6.8a Quantities of selected individual fatty acids (FA) in the foraminiferan *Uvigerina* ex. gr. *semiornata* at time points t=0, t=2 days and t=5 days of a shipboard ^{13}C-labelled diatom feeding experiment at 140 m, SW monsoon. Data are average quantity (ng per 30 Foraminifera) (mean of 4 replicate samples). 95% Confidence Intervals are given.

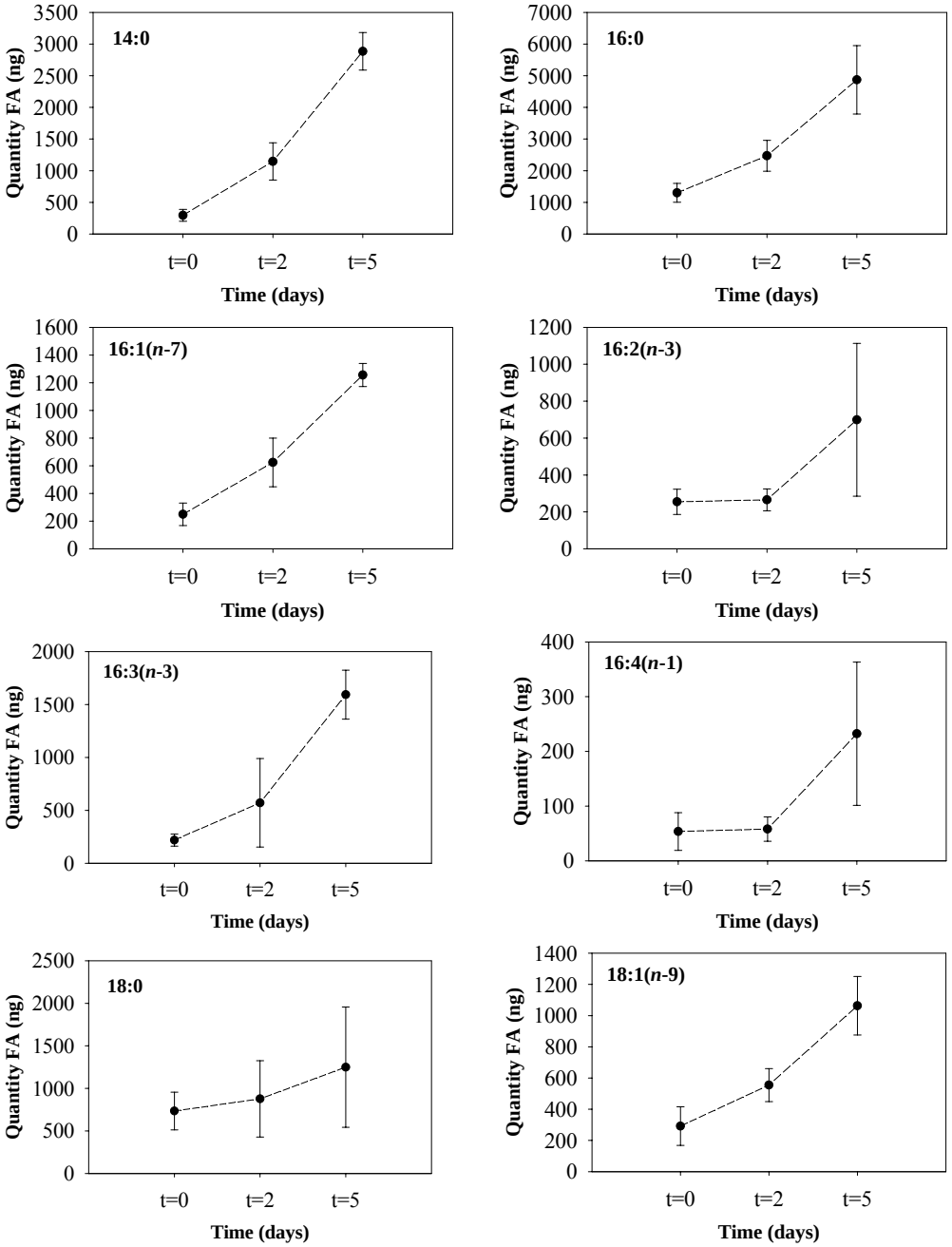


Figure 6.8b Quantities of selected individual fatty acids (FA) in the foraminiferan *Uvigerina* ex. gr. *semiornata* at time points t=0, t=2 days and t=5 days of a shipboard ^{13}C-labelled diatom feeding experiment at 140 m, SW monsoon. Data are average quantity (ng per 30 Foraminifera) (mean of 4 replicate samples). 95% Confidence Intervals are given.

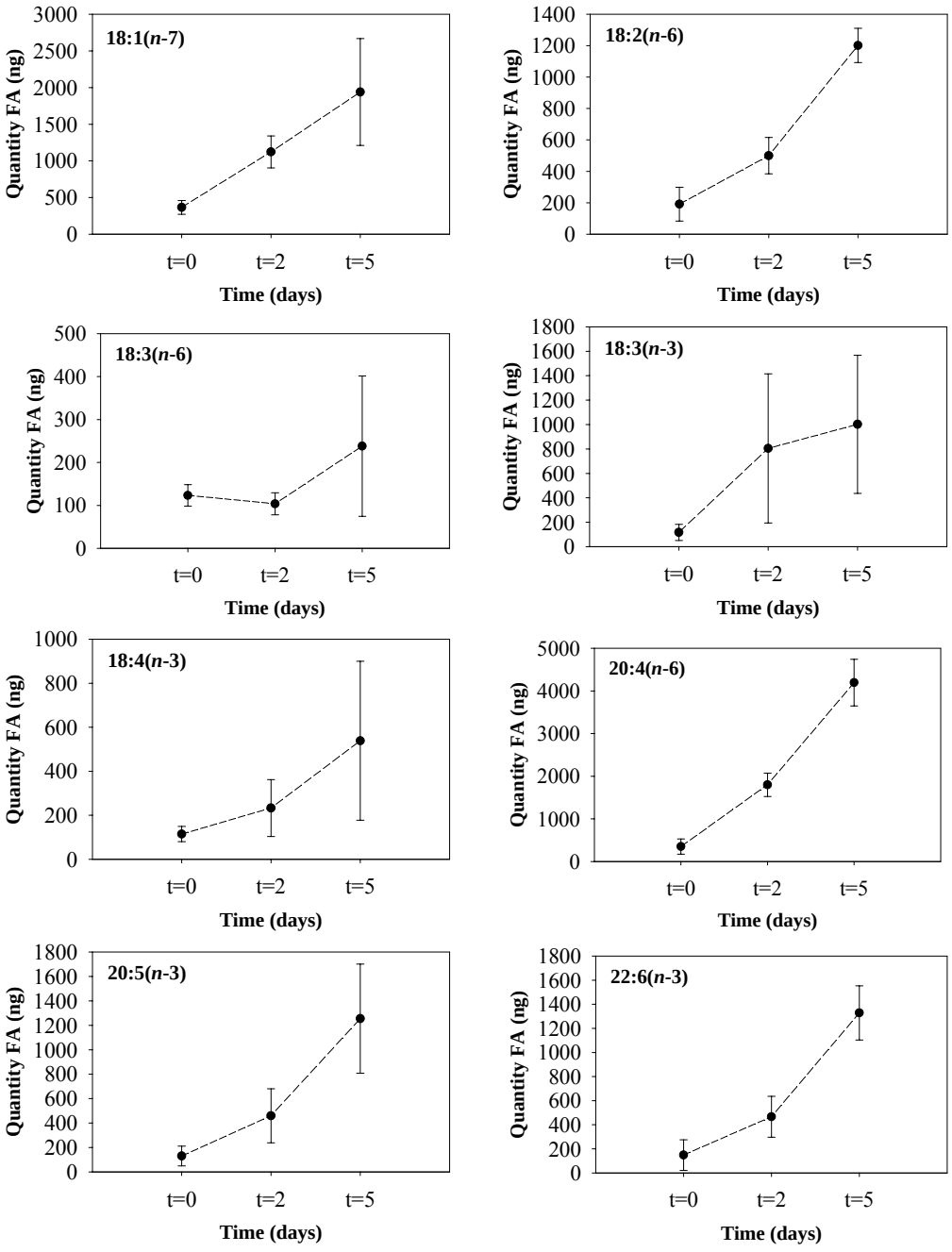


Figure 6.9a Quantities of selected individual fatty acids (FA) in the foraminiferan *Uvigerina* ex. gr. *semiornata* at time points t=0 (natural) and t=2.5 days of an *in situ* ^{13}C-labelled diatom feeding experiment at 140 m, SW monsoon. Data are average quantity (ng per 30 Foraminifera) (mean of 4 replicate samples). 95% Confidence Intervals are given.

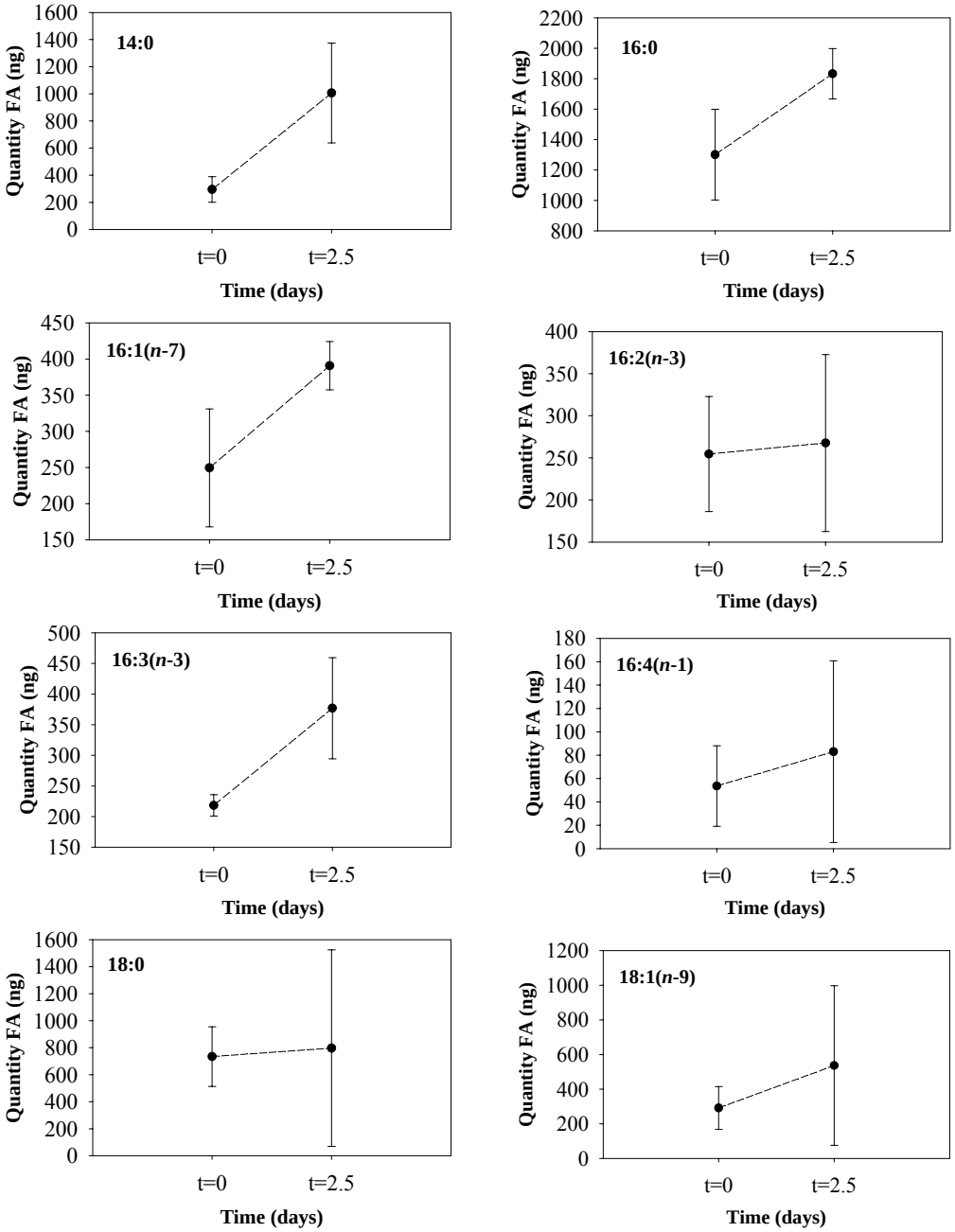
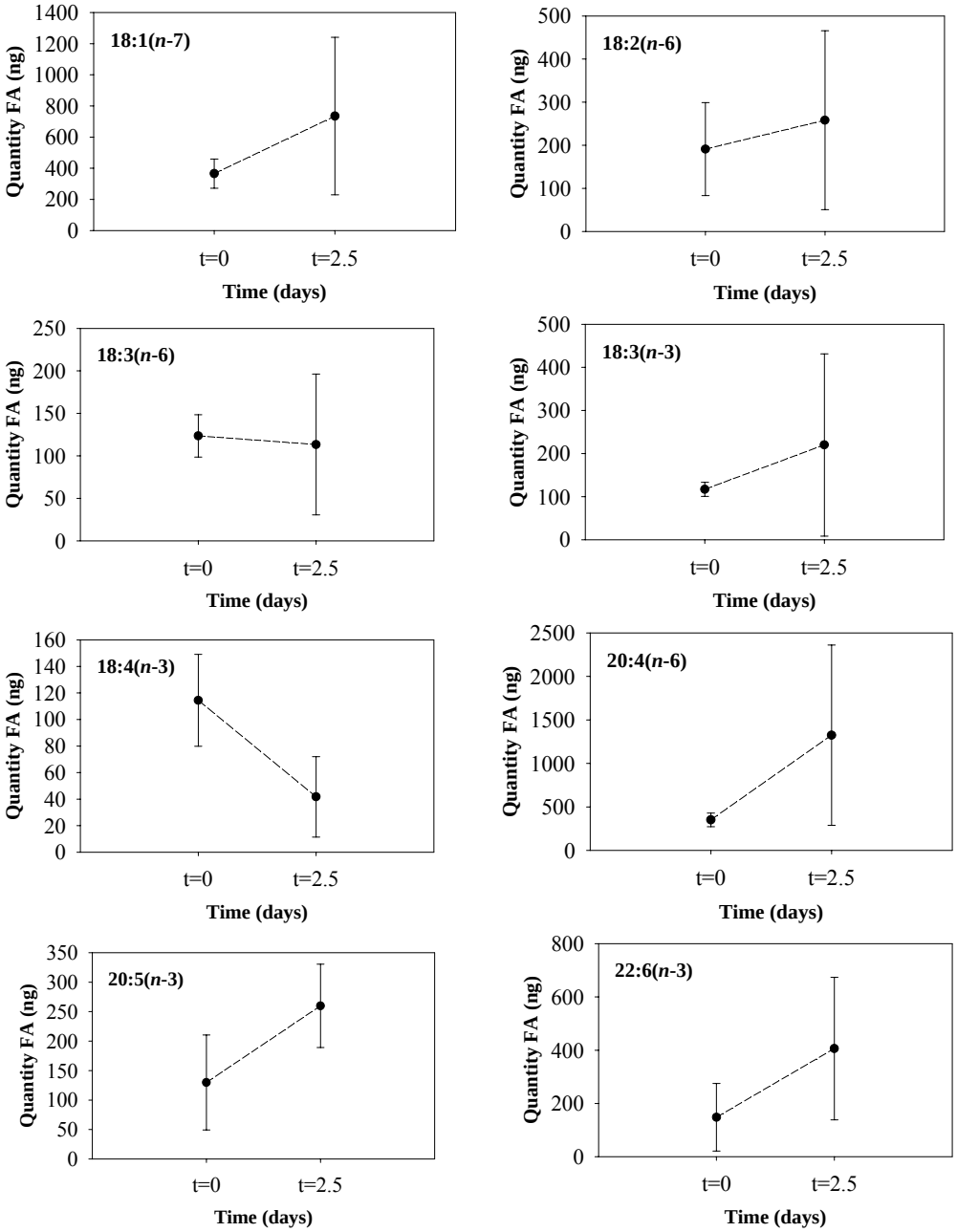


Figure 6.9b Quantities of selected individual fatty acids (FA) in the foraminiferan *Uvigerina* ex. gr. *semiornata* at time points t=0 (natural) and t=2.5 days of an *in situ* ^{13}C-labelled diatom feeding experiment at 140 m, SW monsoon. Data are average quantity (ng per 30 Foraminifera) (mean of 4 replicate samples). 95% Confidence Intervals are given.



The amounts of three polyunsaturated fatty acids (PUFAs), 16:2(*n*-3), 16:3(*n*-3) and 20:5(*n*-3), and the monounsaturated fatty acid (MUFA) 16:1(*n*-7) (all diatom fatty acid biomarkers), increased significantly ($P < 0.05$, 2-sample t-test) between natural Foraminifera (t=0) and the experimental Foraminifera exposed to the diatom food source in both the shipboard (t = 2 day and t = 5 day) and *in situ* (t=2.5 day) experiments. All four of these fatty acids were highly abundant in the diatom monoculture (*Thalassiosira weisflogii*) (Figure 6.4) and were only present in small amounts in the natural (t=0) Foraminifera (Figure 6.8a,b and Figure 6.9a,b), indicating that diatoms were being consumed over the duration of the feeding experiment. The monounsaturated fatty acids 14:0 and 16:0 (dominant in the diatom food source) also increased significantly ($P < 0.05$, 2-sample t-test) in foraminiferan samples from the start to the endpoint of both the shipboard and *in situ* feeding experiments (Figure 6.8a,b and Figure 6.9a,b).

Other fatty acids that increased (although not significantly) in the experimental Foraminifera over the course of both ^{13}C-labelled feeding experiments included the monounsaturated fatty acids (MUFAs) 18:1(*n*-9) and 18:1(*n*-7) and the polyunsaturated fatty acids (PUFAs) 16:4(*n*-1), 18:2(*n*-6), 18:3(*n*-3), 20:4(*n*-6) and 22:6(*n*-3). All of the aforementioned fatty acids were only present in small amounts in the diatom food source, indicating that the increase of these fatty acids may be a result of ingestion of other food sources other than the diatoms. The PUFAs 18:3(*n*-6) and 18:4(*n*-3) displayed different trends in the change in quantity (ng) over the duration of each experiment. In the shipboard experiment, 18:3(*n*-6) initially decreased in average quantity (ng) (t=0 to t=2 days) then increased to the endpoint of the experiment (t=2 days to t=5 days). This initial decrease was also evident in the *in situ* feeding experiment, where the average quantity (ng) of 18:3(*n*-6) decreased from t=0 to t=2.5 days. The PUFA 18:4(*n*-3) increased in average quantity (ng) over the entire duration of the shipboard experiment (t=0 to t=5 days), but decreased in average quantity (ng) from the start to the endpoint of the *in situ* feeding experiment.

6.3.4 ^{13}C-enrichment of individual fatty acids

The percentage ^{13}C labelling of thirteen dominant fatty acids in *Uvigerina* ex. gr. *semiornata* over the duration of both the shipboard (5 days) and *in situ* (2.5 days) feeding experiments is summarised in Figures 6.10 and Figure 6.11. The percentage of ^{13}C in all fatty acids analysed in natural Foraminifera before exposure to the ^{13}C-labelled diatom food source was very low (≤ 1.5 % ^{13}C). In both experimental set-ups, the percentage of ^{13}C present in the thirteen fatty acids from t=0 to t=2 days (shipboard) and from natural samples to t=2.5 (*in situ*), indicating a rapid ingestion of ^{13}C-labelled diatoms into the foraminiferan cell. However, the percentage of ^{13}C varied considerably between each individual fatty acid analysed. Fatty acids displaying the highest degree of ^{13}C labelling at the endpoints of both shipboard (5 days) and *in situ* (2.5 days) feeding experiments included the four diatom fatty acid biomarkers 16:1(*n*-7), (16:2(*n*-3), 16:3(*n*-3) and 20:5(*n*-3) (all present in high quantities in the diatom food source). Of these fatty acids, 16:1(*n*-7) and 16:2(*n*-3) exhibited the highest percentage of ^{13}C of all fatty acids analysed, with 78.3-95.9 % ^{13}C in 16:1(*n*-7) and 94-94.1 % ^{13}C in 16:2(*n*-3) in Foraminifera sampled at the endpoints of both feeding experiments. In all cases, the percentage of ^{13}C increased with the increase in the quantity of the fatty acid in the Foraminifera, clearly demonstrating that the increase in quantity of these fatty acids was due to ingestion of the ^{13}C-labelled diatoms. One surprising exception was the fatty acid 20:5(*n*-3), sampled in Foraminifera at the endpoint of the 2.5 day *in situ* feeding experiment. Whilst Foraminifera at an equivalent time point (t=2 days) during the shipboard experiments exhibited a high (78.9 %) level of ^{13}C-enrichment, 20:5(n-3) in Foraminifera sampled at the end of the *in situ* feeding experiment (2.5 days) displayed only a low (2.9%) level of ^{13}C-enrichment. This may reflect analytical error, or it may be due to the Foraminifera obtaining 20:5(*n*-3) during the experiment from a food source other than the ^{13}C-labelled diatoms.

The bacterial biomarker 18:1(*n*-7) increased in percentage ^{13}C in *U.* ex. gr. *semiornata* over the duration of the feeding experiment, despite being present in low amounts in the diatom food source. However, the level of ^{13}C-enrichment in 18:1(*n*-7) at the endpoint of both feeding experiments was much less than for other fatty acids and less than 30 % of this fatty acid was labelled in the Foraminifera even after the longest exposure to the ^{13}C-labelled diatom food source (t=5 day, shipboard). Other minor fatty acids in the natural Foraminifera (e.g. 18:2(*n*-3), 18:3(*n*-3), 18:4(*n*-3), 20:4(*n*-6) and 22:6(*n*-3)) exhibited an increased percentage of ^{13}C over the duration of the experiment, despite being minor components of the diatom food source.

Three fatty acids (14:0, 16:0 and 20:5(*n*-3)) analysed in *U*. ex. gr. *semiornata* at the end point of the longer shipboard experiment (t=5 days) displayed a decline in percentage ^{13}C between the time points t=2 days and t=5 days, despite a corresponding increase in their quantities over the course of the feeding experiment. This suggests that the increased quantities of these fatty acids may be derived from the uptake of non-labelled food sources rather than of ^{13}C-labelled diatoms. An alternative explanation is that these fatty acids are synthesized in the foraminiferal cell from other non-labelled fatty acids.

Figure 6.10 Shipboard laboratory ^{13}C-labelled feeding experiments at 140 m, SW monsoon (October 2003). Percentage ^{13}C in selected fatty acids of the foraminiferan *Uvigerina* ex. gr. *semiornata* sampled at time points t=0, t=2 days and t=5 days of exposure to a ^{13}C-labelled diatom food source. In each bar, percentage ^{13}C (label) is shown in grey and percentage ^{12}C (natural) is shown in white. Data are average values of 4 replicate samples (each of 30 Foraminifera). 95% Confidence Intervals are given for ^{13}C values.

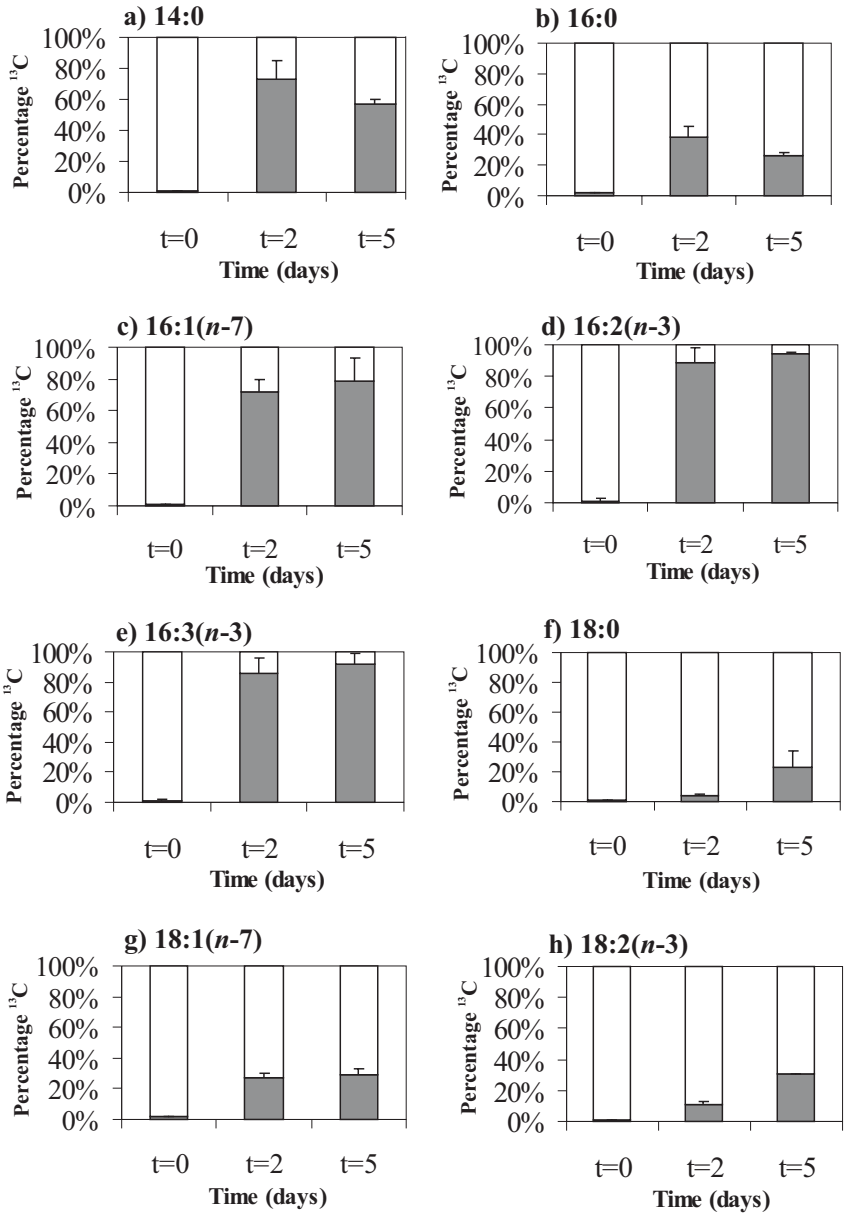


Figure 6.10 continued.

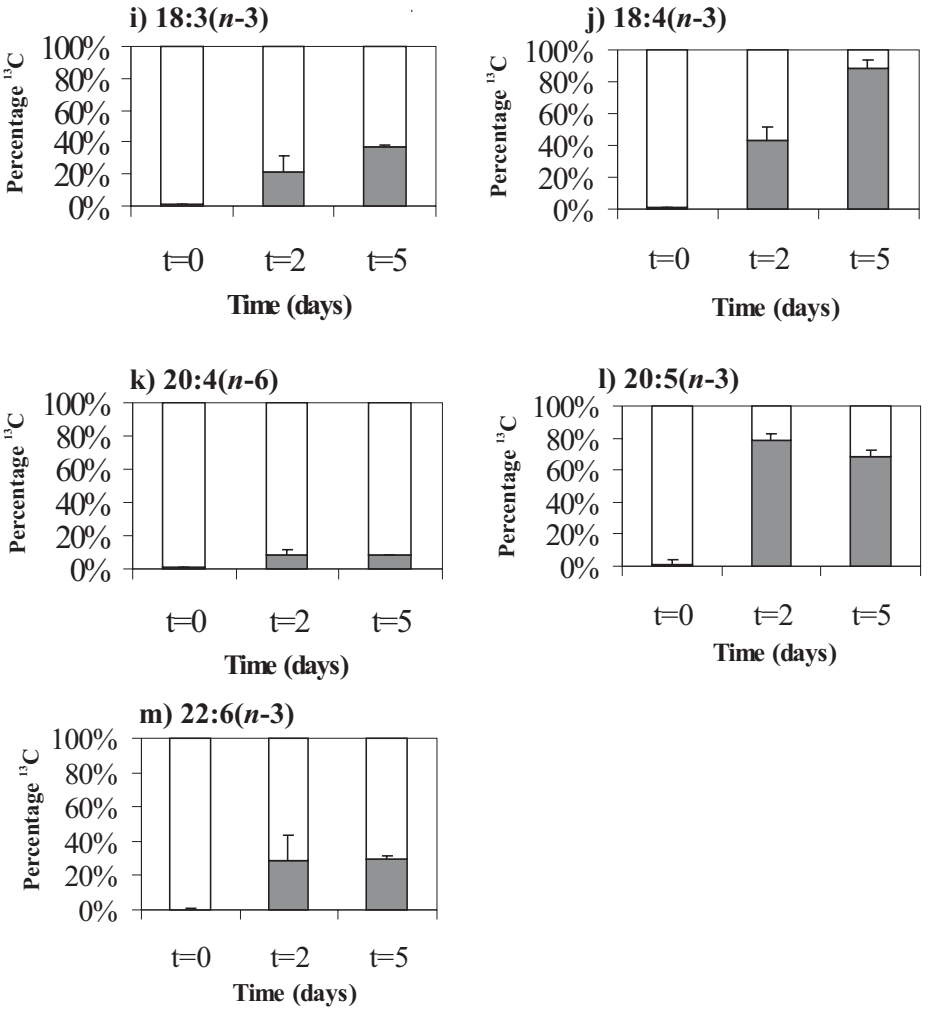


Figure 6.11 *In situ* ^{13}C-labelled diatom feeding experiments at 140 m, SW monsoon (October 2003). Percentage ^{13}C in selected individual fatty acids of the foraminiferan *Uvigerina* ex. gr. *semiornata* sampled at t=0 days, t=2.5 days of exposure to a ^{13}C-labelled diatom food source. In each bar, percentage ^{13}C (label) is shown in grey and percentage ^{12}C (natural) is shown in white. Data are average values of 4 replicate samples (each of 30 Foraminifera). 95% Confidence Intervals are shown for ^{13}C values.

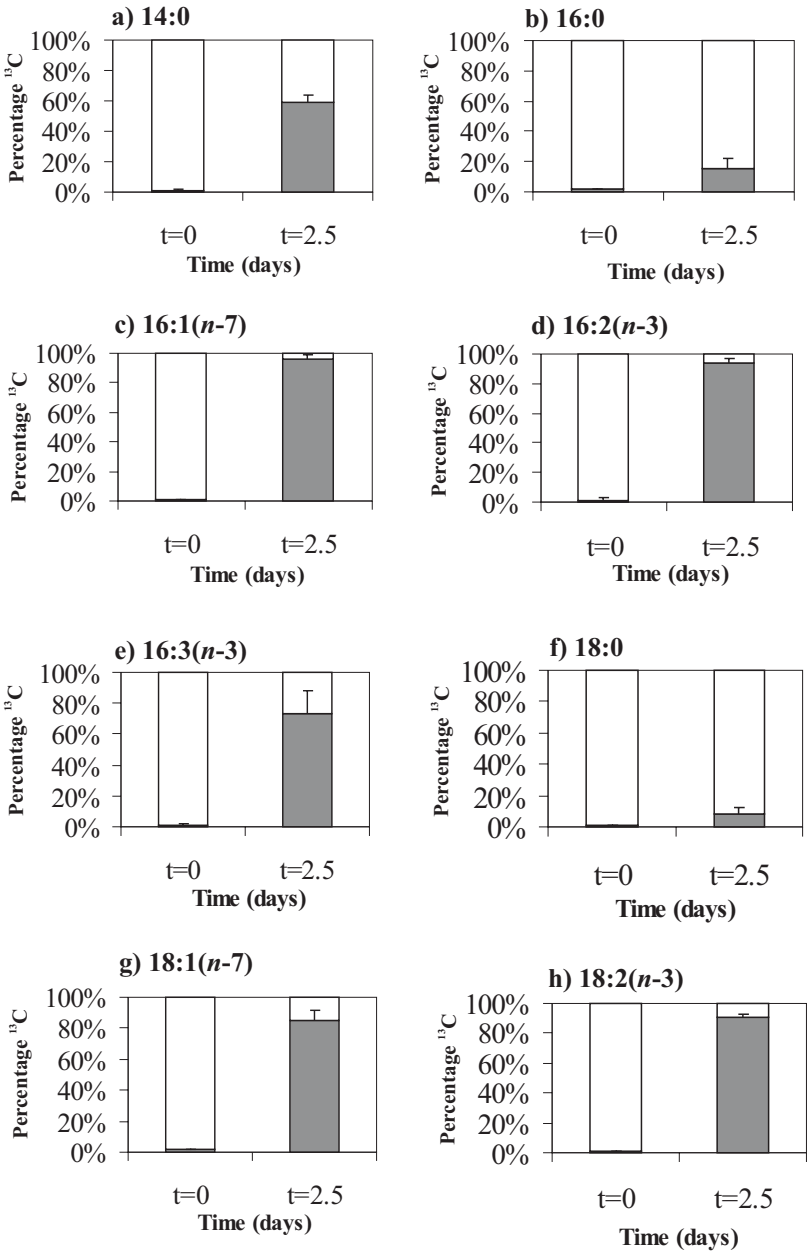
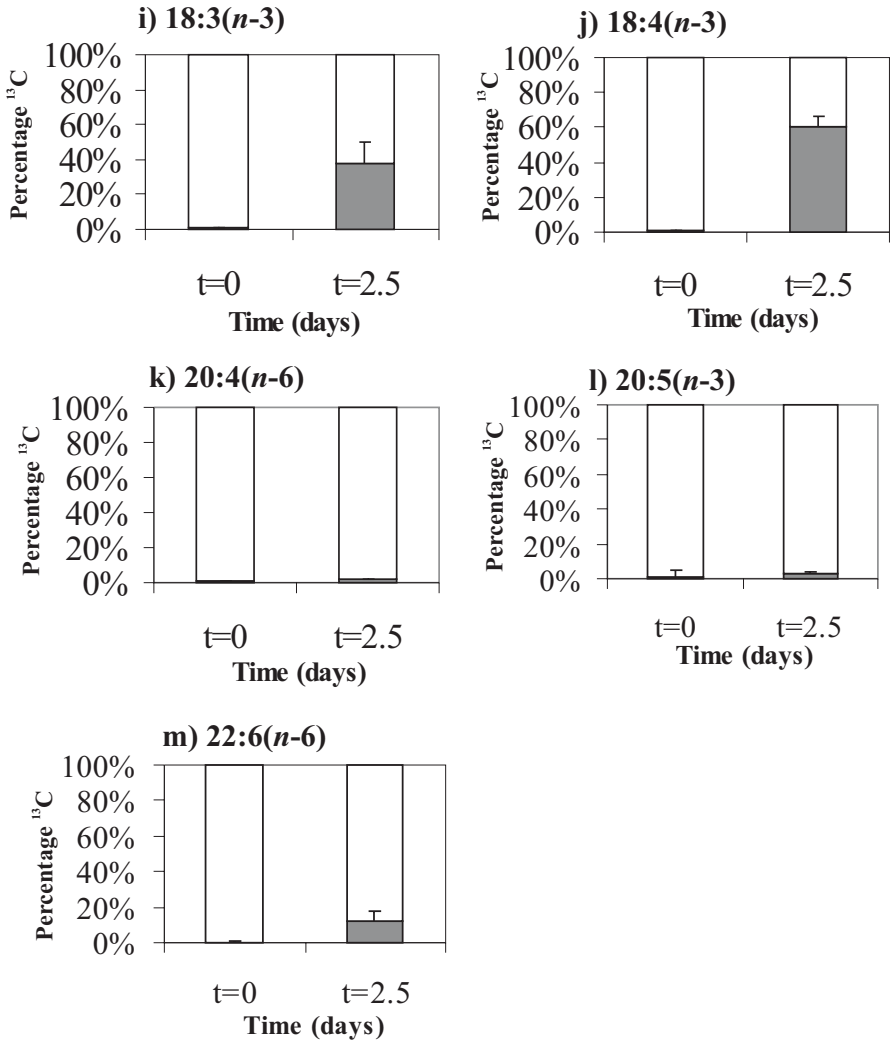


Figure 6.11 continued.



6.4 General Discussion

6.4.1 Evidence for ingestion of diatoms by *Uvigerina* ex. gr. *semiornata*.

There was an increase in diatom fatty acid biomarkers, particularly 16:1(*n*-7), 16:2(*n*-3), 16:3(*n*-3) and 20:5(*n*-3), in *Uvigerina* ex. gr. *semiornata* between the start and the end of both shipboard (5 days duration) and *in situ* (2.5 days duration) feeding experiments. The percentage of ^{13}C in all four of these fatty acids increased correspondingly, indicating that ^{13}C-labelled diatoms were being consumed throughout the experiment. This is consistent with an increase in cytoplasmic δ^{13}C values for the total Foraminifera over the course of both feeding experiments (Woulds et al. in prep).

Many previous studies provide evidence for the consumption of diatoms by deep-sea Foraminifera and in particular by calcareous species. Nomaki et al. (2005a, 2006) reported that the shallow-infaunal, calcareous species *Uvigerina akitaensis* rapidly consumed algae, particularly the marine diatom *Chaetoceros sociale*, during *in situ* ^{13}C-labelled feeding experiments carried out at a deep-water site (1450 m water depth) in Sagami Bay, Japan. Goldstein and Corliss (1994) analysed the ultrastructure of *Uvigerina peregrina* from 710 m water depth in the San Pedro Basin (California Borderland) and found a variety of food items in the food vacuoles of *Uvigerina peregrina*. These included numerous aggregates of sediment, organic detritus and diatom frustules. Heeger (1990) concluded that phytodetritus was important in the diet of some calcareous species from the deep Greenland-Norwegian Sea, based on the occurrence of pennate diatoms in their food vacuoles. Experimental work by Ernst and van der Zwaan (2004) showed that an input of diatoms and other algae can maintain or lead to increased populations of opportunistic species such as *Epistominella exigua* and *Adercotryma glomeratum*. Finally, a higher foraminiferal population density was recorded 21 days after the

addition of an algal food source to deep-sea sediments (from 919 m water depth, western Mediterranean) in laboratory culture experiments (Heinz et al. 2002).

The changes in quantity and ^{13}C content of other fatty acids indicate that *Uvigerina* ex. gr. *semiornata* was also consuming other food over the duration of the feeding experiment. For example, the increase in the quantity (ng) of 18:1(*n*-7) in this species over the course of both the *in situ* and shipboard experiments (Figures 6.7a,b, Figure 6.8a,b and Figure 6.9a,b) is surprising, since this fatty acid is not known to be produced in significant amounts by eukaryotes (Gurr and Harwood 1991) and constituted a very low percentage of the total fatty acids in the diatom food source (1.7%) (raw data in Appendix C). This suggests that the 18:1(*n*-7) in the foraminiferan cell may derive from a bacterial (prokaryotic) food source. It is therefore likely that *U*. ex. gr. *semiornata* ingested natural bacteria from the sediment over the duration of the feeding experiment. This is supported by the low ^{13}C content of 18:1(*n*-7) (< 30 % labelled, Figure 6.8g) at the endpoint of the five day shipboard experiment. However, there was a substantial increase in the percentage of ^{13}C in 18:1(*n*-7) at the endpoint of the *in situ* feeding experiment (2.5 days). This suggests the possibility that Foraminifera may have ingested bacteria from the sediment that had already assimilated dissolved organic carbon derived from the ^{13}C-labelled diatom food source and had synthesized other fatty acids *de novo*, therefore incorporating some ^{13}C-label into other fatty acids.

The increase in the amount of 18:1(*n*-9), a possible storage fatty acid (Lewis 1967; Morris 1971a; Morris 1971b; Albers et al. 1996; Parrish and Wangersky 1990; Kattner and Hagen 1998; Pond et al. 2000a), in *Uvigerina* ex. gr. *semiornata* at the endpoint of both feeding experiments suggests that the foraminiferan was rapidly consuming the diatom food source at the start of the experiments and not relying on storage fatty acids. During the course of the experiment, however, the foraminiferan increased the amount of 18:1(*n*-9). Since there are no data for the ^{13}C content of this particular fatty acid, its origin remains unclear. However, the low amounts of

18:1(*n*-9) in the diatom food source suggest either that the high amounts in the Foraminifera were obtained from ingestion of other food items in the sediment, or that this fatty acid was synthesized *de novo* in the foraminiferal cell.

6.4.2. Does *Uvigerina* ex. gr. *semiornata* synthesize fatty acids *de novo*?

There is no direct evidence for *de novo* intracellular synthesis of fatty acids by any foraminiferal species. However, results from this study suggest that *U.* ex. gr. *semiornata* may have been synthesising some long-chain *n*-3 polyunsaturated fatty acids (PUFAs). There was an increase in quantity (ng) of the PUFAs 18:2(*n*-6), 18:3(*n*-3), 18:3(*n*-6), 18:4(*n*-3) and 20:4(*n*-6) in *Uvigerina* ex. gr. *semiornata* over the duration of both shipboard and *in situ* feeding experiments. This was unexpected, because these fatty acids were scarce in both the food source and Foraminifera at the start of the experiment. In addition, in three of these fatty acids (18:3(*n*-3), 18:4(*n*-3) and 20:4(*n*-6)) the percentage of ^{13}C increased during both the shipboard and the *in situ* feeding experiments, indicating that they originated from the ^{13}C-labelled diatom food source, and not primarily from other unlabelled food sources available in the sediment. There are two possible explanations for these observations. Either Foraminifera were ingesting natural bacteria that had already consumed dissolved organic matter (DOM) from the ^{13}C-labelled food source and synthesized *n*-6 fatty acids that incorporated some ^{13}C, or the Foraminifera themselves were synthesizing these fatty acids. It has been hypothesized (Bowles et al. 1999) that some marine eukaryotes, including protists, may be synthesizing *n*-6 PUFAs such as 18:2(*n*-6). If this is the case, it is possible that other fatty acids, including *n*-3 PUFAs may also be synthesized by the foraminiferal cell.

6.4.3 A comparison of shipboard and *in situ* ^{13}C-labelled diatom feeding experiments

The fatty acid data for *Uvigerina* ex. gr. *semiornata* from the shipboard and *in situ* experiments (2 day and 2.5 day incubations respectively) were very similar, suggesting that the Foraminifera in the shipboard experiments were behaving in a similar way to those living on the seafloor. However, the increase in the average quantity (ng) of fatty acids and the percentage of ^{13}C-enrichment in fatty acids, was much lower in Foraminifera analysed from the *in situ* experiment than in the shipboard experiment. This may be because the algae did not spread out evenly on the surface of the sediment enclosed in the boxcore resulting in a patchy distribution of the food source and reducing potential uptake by the Foraminifera.

6.4.4 Future directions for this study

The combination of fatty acid biomarker analysis with ultrastructural work, using Transmission Electron Microscopy (TEM), would allow further investigation into the uptake and retention times of the algal food source in the food vacuoles of the foraminiferal cell. Feeding experiments using a monoculture of an individual fatty acid (labelled with ^{13}C) as a food source would enable a more controlled study of fatty acid biosynthesis in Foraminifera. This would allow the assimilation and metabolic pathways of the foraminiferal cell to be investigated further and would enhance knowledge on the capabilities of the foraminiferal cell for *de novo* synthesis of fatty acids. Experiments of longer duration and more sampling time points over the course of the experiments would allow the uptake and assimilation of food by the foraminiferal cell to be examined in more detail. The comparison between shipboard laboratory and *in situ* experimental approaches would be enhanced by conducting *in situ* experiments using megacores (instead of a larger sediment chamber). This would allow the same dosing of the algal food source to be administered in each experiment, which would facilitate a direct comparison between these two techniques.

6.5 Conclusions

This study has resulted in the first tracking at a molecular level, using mass spectrometry, of distinct ^{13}C-enriched mass fragments derived from a ^{13}C-labelled food source in individual fatty acids in a foraminiferan species. *Uvigerina* ex. gr. *semiornata* responded rapidly to the introduction of ^{13}C-labelled diatom detritus in pulse-chase feeding experiments. After only two days, rapid ingestion of diatoms into the foraminiferal cell had occurred and this ingestion continued over the duration of the feeding experiment (between 0 and 5 days). Food uptake was clearly evident in the bright green colouration of the cytoplasm in *U*. ex. gr. *semiornata*. At a molecular level, the ingestion of the diatom food source was indicated by both the increase in quantity of diatom biomarker fatty acids in the Foraminifera during the feeding experiments, and the high percentage of ^{13}C in many of the fatty acids present in Foraminifera at the endpoint of both *in situ* and laboratory-based experiments. These results clearly demonstrate that the fatty acids were derived from the ^{13}C-labelled diatom food source. However, there is evidence that *U*. ex. gr. *semiornata* also consumed other non-labelled food and may even be capable of synthesizing certain fatty acids *de novo.*

This shallow infaunal, calcareous species dominated the macrofaunal (>300 μm) foraminiferal assemblage in the centre (300-m site) and the upper boundary (140-m site) of the oxygen minimum zone and responded rapidly and extensively to an input of fresh labile organic matter resulting from the natural flux of phytodetritus following the SW monsoon. Observations made on natural populations, together with the results from shipboard and *in situ* feeding experiments, indicate that *Uvigerina* ex. gr. *semiornata* plays a key role in short-term benthic organic matter cycling on the Pakistan margin.

7 Conclusions and Future Directions

7.1 Conclusions

The overarching aim of this study was to investigate the impact of environmental variables and ecological factors, particularly bottom-water oxygen concentration and organic matter availability, on the abundance, diversity and taxonomic composition of the benthic foraminiferal community and the ecological and trophic responses of individual species to these factors. The main conclusions are listed below.

- Foraminifera dominate the macrofaunal (> 300 µm) organisms in terms of abundance (and presumably biomass) in the upper boundary (140 m) and core (300 m) of the Pakistan margin OMZ**,** and are therefore of ecological significance in this oxygen-deficient benthic environment (see Chapter 4).
- Low bottom-water oxygen concentrations in the Pakistan margin OMZ promote a low-diversity foraminiferal assemblage dominated (>60 %) by a few opportunistic calcareous species. A total of 36 species was found at 140 m and 300 m and diversity was not greatly affected by water depth or season. *Uvigerina* ex. gr. *semiornata* overwhelmingly dominates the foraminiferal assemblage at both sites (see Chapter 4).
- Live agglutinated and monothalamous (including soft-shelled) taxa are present, but rare at 140 m and 300 m, except for the genus *Reophax* which is relatively abundant, particularly in the core of the OMZ. The overall low abundance of these forms may be because agglutinated and monothalamous species are generally less tolerant of hypoxia than calcareous species and are consequently out-competed by a few highly successful calcareous Foraminifera in such a stressful environment (see Chapter 4).
- Food appears to be the main factor controlling the abundance of Foraminifera on the Pakistan margin. A seasonal increase in the total foraminiferal

standing stock at both the 140-m site (74 to 153 individuals per 10 cm^2) and 300-m site (86 to 122 individuals per 10 cm^2) from the spring intermonsoon to the SW monsoon is driven by the increase in abundance of a few opportunistic species, probably as a response to a presumed pulse of phytodetritus to the seafloor. For example, *Uvigerina* ex. gr. *semiornata* increases significantly in standing stock at both sites following the SW monsoon (140 m, 54 to 118 individuals per 10 cm^2; 300 m, 41 to 69 individuals per 10 cm^2) (see Chapter 4).

- Oxygen and food appear to be the main factors controlling the vertical distribution (microhabitat) of Foraminifera on the Pakistan margin. At both sites, most Foraminifera (>86 %) are restricted to the upper 0-1 cm layer of sediment. This probably reflects the generally hypoxic conditions. A further shallowing of the Average Living Depth is observed from the spring intermonsoon to the SW monsoon, driven by the vertical migration of a few dominant species, particularly *U*. ex. gr. *semiornata*. At the 300-m site, this upwards migration occurs despite the relatively stable hypoxic bottom-water conditions during both seasons, suggesting that it may be a response to an increase in food availability on the sediment surface following the SW monsoon (see Chapter 4).
- Foraminifera and metazoans display contrasting temporal patterns. In particular, at the 140-m site, Metazoa and Foraminifera were present in larger numbers during the spring intermonsoon when bottom-water oxygen concentrations are 2.05 ml^{-1}. However, following the SW monsoon, when oxygen concentrations fall to low values (~ 0.11 ml^{-1}), Metazoa decline in abundance wheras foraminiferal populations increase. Metazoan numbers at 300 m were too small to show any conclusions (see Chapter 4).
- Two main dietary types are evident among the six foraminiferal species analysed. The more “primitive” monothalamous and polythalamous agglutinated forms (*Ammodiscus* aff. *cretaceus*, *Bathysiphon* sp. nov. 1, *Reophax dentaliniformis*) are suggested to be unselective omnivores, whilst

the more "advanced" calcareous forms (*Uvigerina* ex. gr. *semiornata, Globobulimina* cf. *G. pyrula* and *Bolivina* aff. *dilatata*) are suggested to feed selectively on phytodetritus (see Chapter 5). These trophic differences probably facilitate resource partitioning at the two study sites.

- Foraminifera respond rapidly to labile organic matter. *Uvigerina* ex. gr. *semiornata* rapidly ingests (within two days) ^{13}C-labelled diatoms in shipboard laboratory and *in situ* pulse-chase experiments at the 140-m site following the SW monsoon (see Chapter 6).
- *Uvigerina* ex. gr. *semiornata* may be capable of synthesizing certain fatty acids (such as long-chain *n*-3 polyunsaturated fatty acids) *de novo* in the foraminiferal cell (see Chapter 6).
- The rapid ingestion of labile organic matter (phytodetritus) by *U*. ex. gr. *semiornata*, in combination with the dominance of this species at the 140-m and 300-m sites, its increase in both absolute and relative abundance following the SW monsoon (Chapter 4), and evidence for selective feeding on phytodetritus in the natural environment (see Chapter 5), all suggest that *U*. ex. gr. *semiornata* is a key player in carbon cycling on the Pakistan margin.

7.2 Answers to hypotheses of this study

The conclusions listed above provide answers to the hypotheses stated in Chapter 1:

1) *Bottom-water oxygen concentrations influence benthic foraminiferal abundances, species diversity and dominance.* Hypothesis accepted.

Bottom-water oxygen concentrations do influence the diversity and dominance of the entire live foraminiferal assemblage. However, whilst there is evidence that some species (particularly agglutinated and monothalamous taxa), are less tolerant to hypoxia and decline as bottom-water oxygen concentration decreases, there is no

evidence that abundances of other opportunistic, predominantly calcareous species, notably *Uvigerina* ex. gr. *semiornata* are influenced by bottom-water oxygen concentrations at the levels recorded during the study (0.1 $ml l^{-1}$).

2) *Bottom-water oxygen concentrations influence the microhabitat (vertical distribution) of the benthic foraminiferal assemblage.* Hypothesis accepted.
Bottom-water oxygen concentrations appear to provide the overarching control on the vertical distribution of benthic Foraminifera, restricting them to the upper 0-1 cm layer of the sediment at the boundary (140 m) and core (300 m) of the OMZ. However, the small-scale vertical migrations within the 0-1 cm sediment layer observed in some species appear to be controlled by food availability.

3) Food availability is an important factor controlling the abundance of benthic Foraminifera. Hypothesis accepted.
Food availability is suggested to be the main factor controlling the abundance of live benthic Foraminifera in the upper boundary and core of the Pakistan margin.

4) Benthic Foraminifera and Metazoa exhibit contrasting responses to environmental gradients in oxygen concentration and organic enrichment. Hypothesis accepted.
Foraminifera (as a group) seem to be little affected by hypoxia and are abundant at both sites during both seasons. Metazoans, on the other hand, are less abundant at the permanently hypoxic (300 m) site than at the seasonally hypoxic (140 m) site. This contrasting response is likely to be because each group exhibits a different minimum threshold for oxygen concentration, with Foraminifera displaying a lower minimum threshold and therefore a higher tolerance to hypoxia compared to Metazoa.

5) Benthic Foraminifera are unselective deposit feeders and there are no trophic differences between individual species. Hypothesis rejected.
This study clearly shows that some species of Foraminifera feed selectively on phytodetritus, and that individual species in the same environment may feed on somewhat different components of the food sources available.

6) Benthic Foraminifera respond rapidly to labile organic matter. Hypothesis accepted.
Some species of Foraminifera, particularly *Uvigerina* ex. gr. *semiornata*, do respond rapidly (within two days) to labile organic matter (diatom food source) during feeding experiments.

7) Foraminifera are important in benthic carbon cycling within an oxygen minimum zone (OMZ). Hypothesis accepted.
Foraminifera, in particular a few calcareous species, feed on labile organic material, and since they are abundant at 140 m and 300 m, they must be important in benthic carbon cycling within the Pakistan margin OMZ.

7.3 Future directions

A range of modern techniques, in addition to traditional faunal approaches, are now available to investigate foraminiferal ecology. The combination of new techniques together with an interdisciplinary approach should lead to a better understanding of foraminiferal ecology. The following are some examples of approaches that could be applied in environments such as the Pakistan Margin OMZ and other deep-water hypoxic settings.

- There is a need to analyse foraminiferal ecology at much finer spatial scales within the sediment, in order to gain a better understanding of the vertical

distribution patterns and microhabitats of Foraminifera and their relationships to sedimentary and biogenic structures, as well as the small-scale biotic interactions between Foraminifera and other organisms. This is particularly important in OMZ settings where most of the Foraminifera are concentrated in the sediment layer close to the surface and vertical zonation is therefore compressed.

- Resin impregnation of sediments is one technique that enables the life positions of Foraminifera in sediments to be examined in detail at a submillimetre resolution. Observations using this technique were first carried out by Frankel in the 1970s (Frankel 1970; 1972; 1974; 1975a,b) on estuarine and marine sediments, using an Epon 812 epoxy resin mixture (Frankel 1970). This method was further developed by Bernhard and Bowser (1996) and Bernhard et al. (2003), who added an aldehyde-fixable fluorescent probe (Cell Tracker Green CMFDA) to the sediment before resin impregnation of laminated sediments of the Santa Barbara Basin and sandy sediments around Antarctica. This fluorescently labelled embedded core technique enables small-scale spatial relationships between Foraminifera, their food sources and other organisms and their structures, such as burrows (metazoans) and prokaryotic biofilms in the sediment to be analysed. It also offers a novel way to examine the morphology, configuration and extent of the pseudopodial network of Foraminifera, previously analysed using glass slides (Travis and Bowser 1991). A limitation of this method is that the resin will only penetrate silty and sandy sediment. However, this technique worked well on laminated sediments within the hypoxic Santa Barbara Basin (Bernhard et al. 2003) and may therefore be applicable to other hypoxic environments. For example, at 300 m on the Pakistan Margin, the top 0.5 cm sediment layer is a porous surface crust, which may be amenable to this method.
- The recent advances in microelectrode and planar optode techniques, such as those described by Glud et al. (2005) and Oguri et al. (2006), are enabling the effects of foraminiferal activity on oxygen concentrations at the sediment-

water interface to be assessed at previously unresolved microscale resolutions. This approach may be particularly appropriate in the case of Foraminifera in oxygen-deficient benthic environments, where species are generally limited to the upper 1-2 centimetres because of oxygen depletion in sediment pore waters and therefore inhabit narrower microhabitats than in oxygenated settings.

- The trophic ecology of Foraminifera can be investigated using pigment analysis (High Performance Liquid Chromatography, HPLC) to identify the food sources ingested with Transmission Electron Microscopy (TEM) being used to visualise ingested food particles and any organisms living symbiotically in the foraminiferal cell. These techniques can reveal information on diets and ingestion rates and assimilation of food particles by Foraminifera that are not provided by fatty acid biomarker analysis alone.
- Single-time point studies offer only snapshots of interactions that are complex and highly variable, temporally and spatially. Time-series studies including high resolution data on environmental parameters such as oxygen, temperature, salinity, together with sediment traps to assess organic matter flux, would help to improve knowledge of temporal changes in the upper OMZ boundary on the Pakistan margin and the responses of benthic organisms to these changes over time scales of years and decades. A Eulerian (fixed-point) observatory in the Arabian Sea, with both pelagic and benthic components, is required to realise these aims.
- Pressure aquaria used to conduct experiments and make observations of deep-sea metazoan organisms under *in situ* pressures as well as temperatures are under development (e.g. Bird et al. 2004; Miwa et al. 2006). Such a system would allow experiments on Foraminifera, similar to those described in this thesis, to be carried out in a laboratory under ambient environmental conditions. The incorporation of a microscope into a pressure aquarium (already developed by the Japanese, H. Kitazato pers. comm.) would allow

comparisons of pseudopodial activity under *in situ* and atmospheric pressures.

- At present, most of the *in situ* feeding experiments conducted in the benthic environment have involved benthic landers. Exceptions are the recent studies conducted by Kitazato et al. (2003), and Nomaki et al. (2005a), which used Submersibles and Remotely Operated Vehicles (ROVs). Submersibles are very expensive and not widely available. ROV technology, on the other hand, is becoming increasingly accessible and offers many advantages compared to landers. In particular, experiments can be placed and manipulated precisely on the seafloor, and, can be used in confined and heterogeneous environments such as canyons.

7.4 Concluding remarks

As emphasised in the Introduction to this thesis, the current spread of hypoxia in the World Ocean, accentuated by anthropogenic organic pollution of coastal areas, may have a devastating impact on marine biodiversity. This has important societal implications. For example, the expansion of oxygen minimum zones onto the shelf, may impact commercial fishstocks and cause shifts in the location of fish populations. Benthic environments, generally and in particular the deep sea, are also at risk. The deep sea constitutes one of the world's largest reservoirs of biodiversity (Thistle et al. 2005). Already, changes in the spatial distributions of species are being observed. How will these changes affect the long-term ecosystem functioning of the oceans? This study suggests that Foraminifera dominate the eukaryotic biomass on the seafloor in some oxygen-deficient environments. As areas of hypoxia increase in the World Ocean, the structure and function of benthic communities and the biogeochemistry of sedimentary environments may alter considerably as Foraminifera become more important in benthic organic matter cycling across increasing areas of the sea-floor. This may have implications for the uptake, cycling

and burial of organic matter in benthic environments and the carbon budget of the ocean system as a whole. There is clearly an increasing need to understand the ecology and trophic responses of Foraminifera and the role of these protists in the utilisation of organic matter on the seafloor.

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Appendices

A taxonomic survey of live benthic macrofaunal (>300 µm) Foraminifera from 140 m and 300 m on the Pakistan Continental Margin, northeast Arabian Sea.

Reference to plates and figures in this thesis are given in bold immediately below the species name. For described species, a reference is given to a representative description and illustration in the literature. Undescribed species are briefly characterised. The suprageneric classification follows Loeblich and Tappan (1987). As far as possible, I have followed the species names assigned by Schumacher et al. (in press).

A.1 Allogromiida

Foraminifera with an entirely or predominantly organic wall (both mono – and polythalamous forms), which appears more or less transparent under the stereomicroscope. Many have a single aperture.

Allogromiid sp. 1

Pl. 1, fig. 1.

This species has a relatively elongate, slightly irregular transparent organic test, 400-670 µm in length. The tests tapers into a short neck, ending in a single terminal aperture. The cytoplasm is clear, with no obvious mineral grains or stercomata. This species was found only at 140 m.

Allogromiid sp. 2

Pl. 1, fig. 2.

A morphologically simple form, 320-550 µm long with an oval to elongate, transparent test. It is very similar to Allogromiid sp. 1, but lacks a neck and instead has a much smaller, indistinct single terminal aperture. The test interior is full of stained cytoplasm, but no visible stercomata. Detritus collects over the entire test surface. This species was found only at 300 m.

Allogromiid sp. 3

Pl. 1, fig. 3.

This species is large, with an elongate, transparent, test 600-1000 µm in length, with many constrictions. It has a short fluted neck with a single terminal aperture. Detritus is often found collecting on the test surface. This species was found predominantly at 300 m.

Allogromiid sp. 4

Pl. 1, fig. 4.

This species is small and oval, 320-460 µm in length, with a thin transparent organic wall and broadly rounded proximal and apertural ends. The cytoplasmic body is finely granular and occupies only part of the test interior. Stercomata are absent. A single, clearly-defined, terminal aperture is present. This species was found only at 300 m.

Allogromiid sp. 5

Pl. 1, fig. 6.

This species has an elongate, transparent test, 480-730 µm in length, with a single aperture. It is very similar to Allogromiid sp. 1, but has an organic wall that is clearly separated from the cytoplasm. This species was very rare in Pakistan margin samples and only one live specimen was found at 140 m.

A.2 Saccamminidae

Monothalamous foraminifera in which the test wall is composed mainly of agglutinated particles. In some species, the wall is soft and flexible.

Saccamminid sp. 1

Pl. 1, fig. 5.

This species displays a range of morphologies from oval to more elongate, varying in length between 300 µm and 700 µm. The agglutinated wall is not completely opaque

and the cytoplasm, which contains dark mineral grains and stercomata, can be seen through it. Some detritus commonly collects around the two terminal apertures, which lack necks. This species was found at both 140 m and 300 m.

Saccamminid sp. 2

Pl. 1, fig. 7a-c.

This species is similar to Saccamminid sp. 1, but has an opaque, soft wall with a brown metallic sheen. The wall becomes transluscent in glycerol. Specimens are elongate tubular and range greatly in size, from 600 µm to 2600 µm in length and 120-200 µm in width. Detritus commonly collects around the two terminal apertures, which lack necks. This species was found only at 300 m.

Saccamminid sp. 3

Pl. 1, fig. 8a-b.

This species is characterised by an opaque, white, soft wall. Specimens are elongate, tubular, between 530 µm and 1000 µm in length and sometimes have a kink. This species was found only at 300 m.

A.3 Psammosphaeridae

Psammosphaerid sp. 1

Pl. 2, fig. 2.

This species lacks apertures and is similar to *Psammosphaera testacea* Flint 1899 in being composed of dead foraminiferal shells. However, it is almost tubular in form rather than being spherical. The test is between 470µm and 630µm in length. This species is rare and present only at 140 m.

A.4 Other Astrorhizacea

Monothalamous foraminifera with one or more apertures in which the test wall is composed mainly of agglutinated particles. In some species the wall is soft and flexible.

***Bathysiphon* sp. nov. 1**

Pl. 1, fig. 9; Pl. 2, fig. 4a-b.

This species has a finely agglutinated, very smooth tubular test, varying in length between 500 µm and 870 µm, with a white/silver metallic sheen. This species was found at both 140 m and 300 m. It probably represents a new species.

***Bathysiphon* sp. nov. 2**

Pl. 2, fig. 5a-b.

This rare species has a thick, elongate test, 600-920 µm length, with a coarse agglutinated surface which is dull orange/white without a metallic sheen. It is present at 300 m only and it probably represents a new species.

Lagenammina arenulata (Skinner 1961)

Pl. 2, fig. 1.

Reophax difflugiformis Brady subsp. *arenulata* Skinner 1961, p. 1239.

I consider the Pakistan margin species to be conspecific with *Reophax difflugiformis* of Brady (1884, Pl. 30, Fig. 5) = *Lagenammina arenulata* according to Jones (1994), described from 988 m in the North Atlantic. The specimens are 450-570 µm in length and use calcareous benthic and planktonic Foraminifera, including small *Bolivina* tests, to construct the test wall. The monothalamous test has a terminal aperture and is therefore placed in the genus *Lagenammina*. Test length is 350-470 µm. This species was present at 140 m only.

***Pelosina* sp. 1**

Pl. 1, fig. 10.

This species has a muddy bulb 420-710 µm in length from which develop thin, delicate dendritic branches up to 910 µm in length.

A.5 Hyperamminacea

***Hyperammina* sp. nov. 1**

Pl. 2, fig. 3a-b.

The Pakistan margin species has a thin, delicate wall and is silvery-grey in colour with a metallic surface sheen. The slightly enlarged proloculus which merges smoothly with the rest of the test resembles several of the species illustrated by Zheng and Fu (2001), for example *Hyperammina elongata* Brady (Zheng and Fu, 2001, Pl. VIII, Fig. 11-14). The test is up to 490-760 µm long; the proloculus is 110 µm wide and the tubular part up to 80 µm wide. This species was found at 140 m and 300 m.

A.6 Ammodiscacea

Ammodiscus* aff. *cretaceus (Reuss 1845) sensu Maas

Pl. 3, fig. 1a-d; Pl. 4, figs. 11-12.

Specimens were usually small, with a diameter of 300-350 µm, and with a tendency to uncoil. The uncoiled portion, when present, is long and bends away from the test at an angle to the previous direction of coiling. This species is similar to *Ammodiscus cretaceus* Reuss (1845, Pl. 13, Figs. 64-65). The original *Ammodiscus cretaceus* of Reuss was a fossil species of late Cretaceus age from northern Bohemia (Czech Republic). The Pakistan margin species differs from the original *Ammodiscus cretaceus* in the slightly more irregular coiling of the last whorl and the tendency to uncoil. Maas (2000, Pl. 1, Fig. 2) illustrated a similar species from the northern Arabian Sea as *Ammodiscus cretaceus*. However, Maas' species does not uncoil, and the last whorl is more regular.

The characteristics of irregularity in the last whorl and a tendency to uncoil are seen in some other fossil *Ammodiscus* species such as *Ammodiscus latus* Grzybowski (1898, Pl. 10, Figs. 27-28) and *Ammodiscus nagyi* Kaminski (1989, Pl. 2, figs. 2-3) (see Kaminski and Gradstein 2005 for a systematic treatment of Palaeogene Ammodiscina). It is also exhibited in an extant species *Trochammina (Ammodiscus) tenuis* of Brady (1881, Pl. 38, Fig. 4-6) = *Ammodiscus tenuis* according to Jones (1994), first described from 2461 m in the North Atlantic and 2005 m off NE New Zealand. However, this is a deep-water species and is not likely to be the same as the upper bathyal Pakistan margin form, which may therefore represent a new species. It was found mainly at 300m.

A.7 Hormosinacea

***Reophax* sp. 1**

Pl. 4, fig. 1.

This species consists of two chambers and has a distinct neck. The specimens are 430-650 µm in length and the test is constructed primarily of biogenic particles, which obscure the chamber arrangement. A number of similar species have been described, e.g. *Reophax fusiformis* of Brady (1884, Pl. 30, Figs. 7-10) and *Reophax agglutinatus* Cushman (1913, p. 637, Pl. 79, Fig. 6). However, the Pakistan margin form has a more protuberant neck. This *Reophax* species was present at 140 m only.

***Reophax* sp. 2**

Pl. 3, fig. 4a-b; Pl. 4, figs. 3-4.

This species most closely resembles *Reophax bicameratus* Earland (1934, p. 83, Pl. 2, Fig. 27), described from 580 m in the Bellingshausen Sea, Antarctica. However, the Pakistan margin form differs in having a test composed of muddy agglutinated particles, three (instead of two) elongate-oval chambers, the second with a slightly tapering apertural end. The Pakistan margin species is 390-610 µm in length. It was rare at 140m, but the second most common *Reophax* species at 300 m.

Reophax bilocularis Flint 1899

Pl. 4, fig. 2.

Reophax bilocularis Flint 1899, p. 273, Pl. 17, Fig. 2.

This species is very similar to the illustrations of *Reophax bilocularis* given by Zheng and Fu (2001, Pl. XIV, Fig. 8-9, 11). The Pakistan margin specimens are finely agglutinated with a test length of 370-640 µm. *Reophax bilocularis* was common at 140 m, but very rare at 300 m.

Reophax dentaliniformis (Brady 1881)

Pl. 3, fig. 5; Pl. 4, figs. 5-7.

Lituola (Reophax) dentaliniformis Brady 1881, p.49.

Nodulina dentaliniformis (Brady). Zheng and Fu 2001, Pl. XIII, Figs. 4-6.

This species is very similar to *Reophax dentaliniformis* as illustrated by Brady (1884, Pl. 30, Figs. 21-22). Like the syntypes of *Reophax dentaliniformis* in the Natural History Museum, London (registration number ZF 2266) it exhibits substantial intraspecific morphological variability of the test, which range from straight to strongly curvature. Test is 700-1200 µm long and 240-410 µm wide. *Reophax dentaliniformis* was common at 300 m, but rare at 140 m.

A.8 Other Multilocular Agglutinated

Veleroninoides crassimargo (Norman 1892)

Pl. 3, fig. 2; Pl. 4, fig. 8a-b, 9.

Haplophragmium crassimargo Norman 1892, p.17.

Labrospira crassimargo (Norman). Höglund 1947, p.141-144, Pl. 11, Fig. 1, text – figs. 121-125.

The Pakistan margin specimens are similar to *Haplophragmium canariensis* d'Orbigny of Brady (1884, Pl. 35, Fig. 4). This was re-identified by Jones (1994) as *Veleroninoides crassimargo*, a species first described from 73-91 m off Scarborough,

North Sea. Test length is between 340-590 µm. This species was present only at 300 m.

Veleroninoides wiesneri (Parr 1950)

Pl. 3, fig. 3; Pl. 4, fig. 10a-b.

Labrospira wiesneri Parr 1950, p.272, Pl. 4, Figs. 25-26.

The Pakistan margin specimens resemble *Trochammina trullissata* of Brady (1884, Pl. 40, Figs. 14-15) = *Veleroninoides wiesneri* according to Jones (1994). Brady's specimens came from 437 m in the Indian Ocean off Antarctica. The Pakistan margin specimens are 310-520 µm long. This species was present only at 300 m.

A.9 Miliolina

Quinqueloculina* aff. *venusta (Karrer 1868)

Pl. 5, fig. 3.

This species is similar to the fossil species *Quinqueloculina venusta*, as illustrated by Zobel (1973, Pl. 2, Fig. 65). Maas (2000, Pl. 1, Fig. 9) illustrated the same species as *Quinqueloculina* sp. 2. Test length is up to 670µm. This species was present only at 140m.

A.10 Lagenina

Amphicoryna* aff. *scalaris (Batsch 1791)

Pl. 5, fig. 7.

The Pakistan margin species is very similar to *Nautilus (Orthoceras) scalaris* Batsch (1791, pp. 1-4. Pl. 2, Fig. 4a-b). Brady (1884, Pl. 63, Figs. 28-31) refers to this species as *Nodosaria scalaris = Amphicoryna scalaris* according to Jones (1994).

Brady's material came from 171 m in the Philippines area. The Pakistan margin species differs from *Amphicoryna scalaris* in having fewer longitudinal costae on the

surface of the test and it is lacking a proximal spine. Test length is 390-480 µm. This species was found only at 140 m.

Dentalina* aff. *flintii (Cushman 1923)

Pl. 5, fig. 9.

The Pakistan margin species is similar to *Nodosaria flintii* Cushman (1923, p. 85, Pl. 14, Fig. 1) = *Dentalina flintii* of Brady (Pl. 64, Fig. 20-22) but has fewer longitudinal costae. Test length is 570-760 µm. This species was found only at 140 m.

Laevidentalina aphelis (Loeblich and Tappan 1986)

Pl. 5, fig. 10.

Nodosaria (*Dentalina*) *communis* d'Orbigny 1826, p.254.

Laevidentalina aphelis Loeblich and Tappan 1986, Pl. 439, Figs. 22-24.

I consider this species to be conspecific with *Nodosaria (Dentalina) communis* d'Orbigny 1826, as illustrated by Brady (1884, Pl. 62, Figs. 21-22) = *Dentalina aphelis* according to Jones (1994). However, it differs from members of the genus *Dentalina* in lacking longitudinal costae and having an even curvature of the test. I therefore follow Loeblich and Tappan (1986) in placing it in the genus *Laevidentalina*. Test length is 480-770 µm. This species was found only at 140 m.

Lenticulina* aff. *iota (Cushman 1923)

Pl. 5, fig. 5.

The present material is identical to *Lenticulina articulata* of Maas (2000, Pl.2, Fig. 10) and *Lenticulina iota* of Hermelin and Shimmield (1990, Pl. 2, Figs. 1-2). It is also similar to *Cristellaria cultrata* Brady (1884, Pl. 70, Figs. 4-6) = *Lenticulina iota* according to Jones (1994). However, it is clearly a different species as it has a less pronounced keel around the edge of the test. Specimens are commonly large and test diameter is 390-550 µm. This species was found live at 140 m only and was the most common *Lenticulina* sp. in the Pakistan margin samples.

Neolenticulina variabilis (Reuss 1850)

Pl. 5, fig. 6.

Cristellaria variabilis Reuss 1850, p. 369, Pl. 46, Figs. 15-16.

I consider the Pakistan margin specimens to be conspecific with *Neolenticulina variabilis* of Brady (1884, Pl. 68, Figs 11-16; particularly Fig.11). A possible synonym is *Neolenticulina chathamensis* McCulloch (1977, Pl. 447, Fig. 9-16, particularly Figs. 14-15) as illustrated by Loeblich and Tappan (1987). Test length is 300-390 µm. This species was very rare in the Pakistan margin samples. Three live specimens were found at 140 m.

***Nodosaria* aff. *pyrula* (**d'Orbigny 1826)

Pl. 5, fig. 8.

The Pakistan margin species is similar to *Nodosaria pyrula* d'Orbigny (1826) = *Nodosaria pyrula* according Loeblich and Tappan (1986, Pl. 441, Figs, 1-5; particularly Fig. 5). However, *Nodosaria pyrula* exhibits a wide variety of morphologies. The Pakistan margin species has fewer chambers and lacks the large elongate basal spine and longitudinal costae of *Nodosaria pyrula*. Test length is 410-480 µm. This species was represented in the Pakistan margin samples by a single live specimen found at 140 m.

Saracenaria italica Defrance 1824

Pl. 5, fig. 4.

Saracenaria italica Defrance 1824, p. 176, Pl. 13, Fig. 6.

Cristellaria sp. Brady 1884, Pl. 68, Fig. 18, 20-23; particularly Figs. 18 and 21.

This species is identical to *Cristellaria* sp. of Brady (1884) = *Saracenaria italica* according to Jones (1994). The original *Saracenaria italica* is a fossil species from Italy (type level not given). The first extant specimens were those of Brady (1884) from 383 m off Fiji, Pacific. Test length is 420-500 µm. This species was rare and only present at 140 m.

A.11 Rotaliida

Baggina philippinensis (Cushman 1921)

Pl. 6, fig. 3.

Pulvinulina hauerii d'Orbigny. Brady 1884, Pl. 106, Fig. 7.

Pulvinulina philippinensis Cushman 1921, p.331.

I consider this species to be conspecific with *Pulvinulina hauerii* d'Orbigny of Brady (1884) = *Baggina philippinensis* according to Jones (1994), described from 232 m near the Ki Islands, Pacific. The number and shape of the chambers of the Pakistan margin specimens are identical to those found in *Baggina philippinensis*. Test length is 300-370 µm. This species was rare, but found at both 140 m and 300 m.

Bolivina* aff. *dilatata (Reuss 1850)

Pl. 6, figs. 4-6; Pl. 7, fig. 3.

This species is identical to *Bolivina dilatata* of Maas (2000, Pl. 2, Fig. 5-6) and *Brizalina* sp. of Zobel (1973, Pl. 2, Figs 20-21). The original *Bolivina dilatata* of Reuss was a fossil species from the Tertiary Vienna basin. The Pakistan margin species differs from the fossil species in having a less inflated and apiculate test. The original material of *Bolivina dilatata* of Brady (1884, Pl. 52 Figs 20-21), in the Natural History Museum (registration number 64.2.5.422-488) collected off SW Ireland, has been re-examined and clearly belongs to a different species. Brady's specimens have a sharper margin and the test is serrated in some specimens. Jones (1994) identifies Brady's form as *Brizalina spathulata.* The Pakistan margin specimens are 300-710 µm long and 90-240 µm wide. This form was present at 140 m and 300 m and may represent a new species.

Cancris auriculus (Fichtel and Moll 1798)

Pl. 6, figs. 1-2; Pl. 7, fig. 4.

Nautilus auricula Fichtel and Moll 1798, p.108.

Pulvinulina oblonga Williamson. Brady 1884, Pl. 106, Fig. 4.

This species is identical to *Pulvinulina oblonga* Williamson of Brady (1884) = *Cancris auriculus* according to Jones (1994), described from 273m off S. Africa in the South Atlantic. Maas (2000, Pl. 2, Fig. 9) illustrated the same species as *Cancris auriculus*. The Pakistan margin specimens exhibit a flaring trochospiral coil, characteristic of the genus *Cancris*. The test length is 350-590 µm. This species was found at both 140 m and 300 m.

Cassidulina laevigata d'Orbigny 1826

Pl. 5, fig. 2; Pl. 7, fig. 5.

Cassidulina laevigata d'Orbigny 1826, p.282, Pl. 15, Figs. 4-5.

This species is identical to *Cassidulina laevigata* of Zobel (1973, Pl. 2, Fig. 44). Some specimens (in the 0 - 0.5 cm vertical fraction at 300m only) display a slightly deformed test, similar to the illustration of *Cassidulina laevigata* in Loeblich and Tappan (1987, Pl. 555, Fig. 8). The test diameter is 310-470 µm. This species was found at both 140 m and 300 m.

Cibicides **sp. 1**

Pl. 5, fig. 1a-b.

This species somewhat resembles *Nautilus lobatulus* Walker and Jacob 1798. Brady (1884, Pl. 92, Fig. 10) referred to it as *Truncatulina lobatulus* = *Cibicides lobatulus* according to Jones (1994). However, the Pakistan margin form lacks the clearly defined ridge around the edge of the test, characteristic of *Cibicides lobatulus*. Test diameter is 300-350 µm. This species was found at 140 m and 300 m, but was rare at 300 m.

Globobulimina cf. G. pyrula (d'Orbigny 1846)

Pl. 6, figs. 12-14; Pl. 7, fig. 1a-b.

I include in this species forms with a pointed proximal end and others with a rounded proximal end. The former resemble *Globobulimina affinis* (d'Orbigny, 1839) of Maas (2000, Pl. 2, Fig. 8) and the latter *Globobulimina turgida* (Bailey, 1851) of Maas (2000, Pl. 2, Fig. 7). However, my material also includes specimens that are intermediate between these two morphotypes, which I therefore consider conspecific. The *G.turgida*-like form also resembles *Globobulimina pyrula* of Fontainier (2003, Pl.1, Figs. A-E) although it has shorter, more inflated chambers, with a pronounced apertural lip and larger pores. I consider it to be more similar to, but not conspecific with, *Globobulimina pyrula*. I therefore follow Schumacher et al. (in press) in calling this species *Globobulimina* cf. *G. pyrula*. Test length is 380-520 µm. The Pakistan margin form was found at 140 m and 300 m.

Saidovina amygdalaeformis (Brady 1881)

Pl. 6, fig. 7.

Bulimina (Bolivina) amygdalaeformis Brady 1881, p. 59.

This species resembles *Bolivina amygdalaeformis* of Brady (1884, Pl. 53, Figs. 28-29) = *Saidovina amygdalaeformis* according to Jones (1994), first described from 171-180 m in the Philippines area, Pacific. Zobel (1973, Plate 1, Fig. 63) illustrated the same species as *Bolivina* ?*amygdalaeformis.* The Pakistan margin specimens exhibit the prominent longitudinal costae and nearly smooth, perforated terminal chamber that are characteristic of the genus *Saidovina.* This species is up to 350 µm in length and was rare at 140m and 300m.

Uvigerina* ex gr. *semiornata (d'Orbigny 1846)

Pl. 6, figs. 8-11; Pl. 7, fig. 2a-b.

The Pakistan margin species is identical to *Uvigerina* ex. gr. *semiornata* (d'Orbigny, 1846) of Maas (2000, Pl. 2, Figs 1-3). This species was identified by Zobel (1973) as *U*. sp. ("*U. peregrina*"). It is similar to *U. mediterranea* but differs in the following

features. Costae are present on the test surface except for the final chamber of some specimens. Costae sometimes cross the sutures and there is a short apertural neck in a prominent depression. I follow Schumacher et al. (in press) in calling it *Uvigerina* ex. gr. *semiornata*. The test is 600-1300 µm long and 350-550 µm wide. This was the dominant species at 140 m and 300 m, rising in abundance following the summer SW monsoon at both sites.

Plate 1

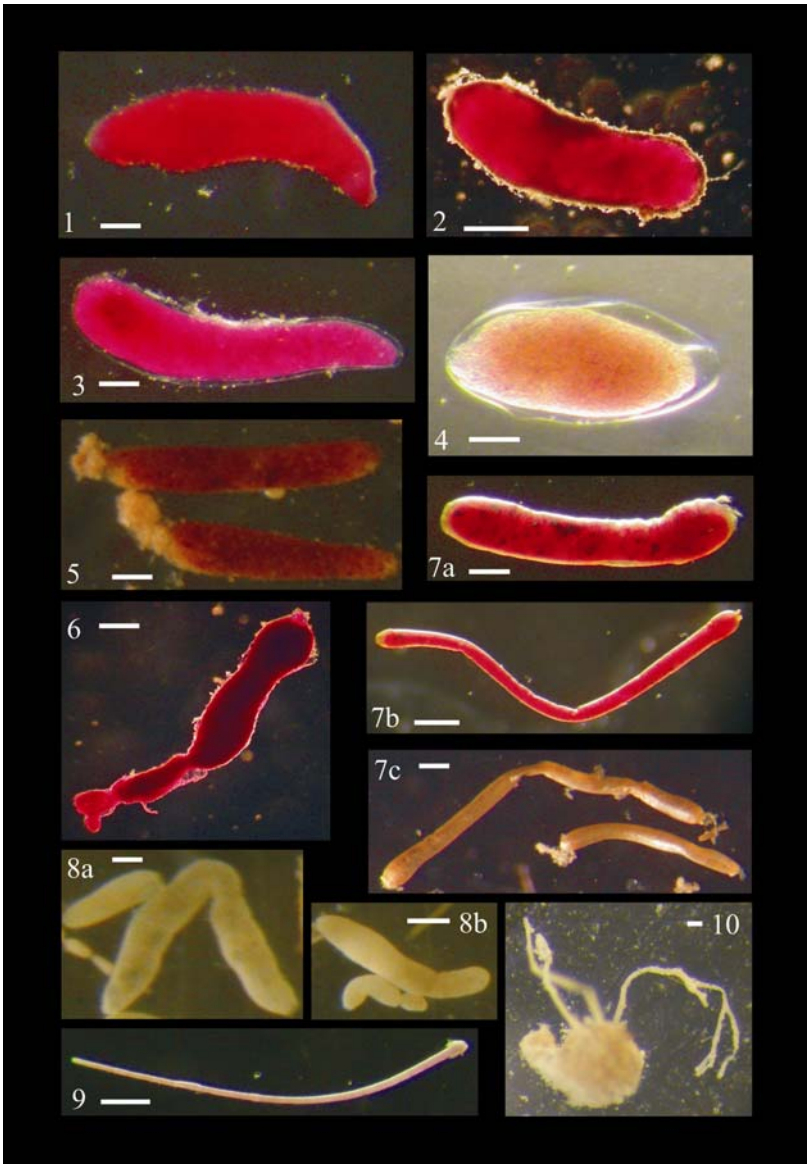

Plate 1. Light photographs of "live" stained macrofaunal (>300 µm) monothalamous foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm. **Fig.1,** Allogromiid sp. 1. **Fig.2,** Allogromiid sp. 2. **Fig.3,** Allogromiid sp. 3. **Fig.4,** Allogromiid sp. 4. **Fig.5,** Saccamminid sp. 1. **Fig.6,** Allogromiid sp. 5. **Fig.7a-c,** Saccamminid sp. 2. **Fig.8a-b,** Saccamminid sp. 3. **Fig.9,** *Bathysiphon* sp. 1. **Fig.10,** *Pelosina* sp. 1. Figures 1-7b and 9 are photographs of fixed specimens stained with rose Bengal. Figures 7c, 8a-b and 10 are shipboard photographs of fresh, unstained specimens.

Plate 2

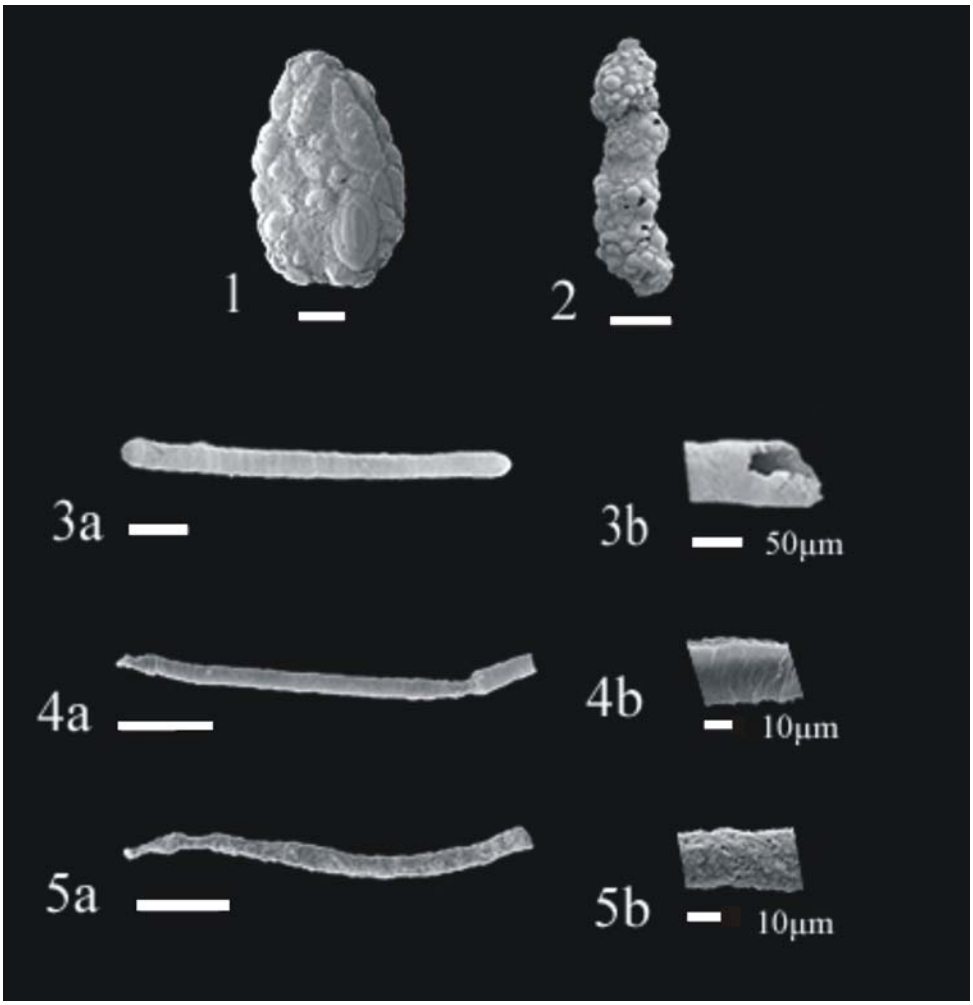

Plate 2. Scanning electron micrographs of monothalamous foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm unless otherwise stated. **Fig.1,** *Lagenammina arenulata*. **Fig.2,** *Psammosphaera* aff. *fusca*. **Fig.3a-b,** *Hyperammina* sp. nov. 1. **Fig.4a-b,** *Bathysiphon* sp. nov. 1. **Fig.5a-b,** *Bathysiphon* sp. nov. 2.

Plate 3

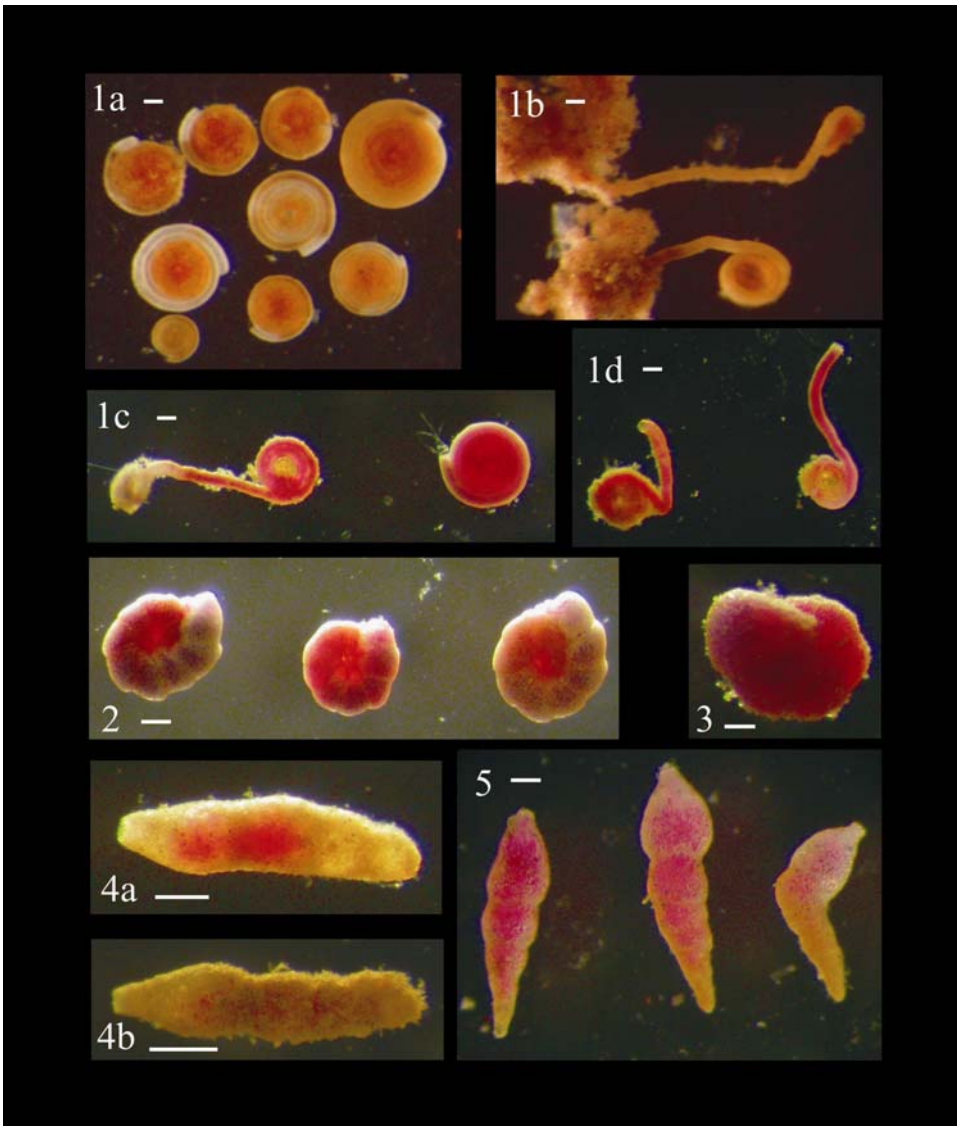

Plate 3. Light photographs of "live" macrofaunal (>300µm) agglutinated foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm. **Fig.1a-d,** *Ammodiscus* aff**.** *cretaceous* (Reuss, 1845). **Fig.2,** *Veleroninoides crassimargo* (Norman 1892). **Fig.3,** *Veleroninoides wiesneri* (Parr 1950). **Fig.4a-b,** *Reophax* sp. 2. **Fig.5,** *Reophax dentaliniformis* (Brady 1881). Figures 1a and 1b are shipboard photographs of fresh, unstained specimens. Other photographs are of fixed specimens stained with Rose Bengal.

Plate 4

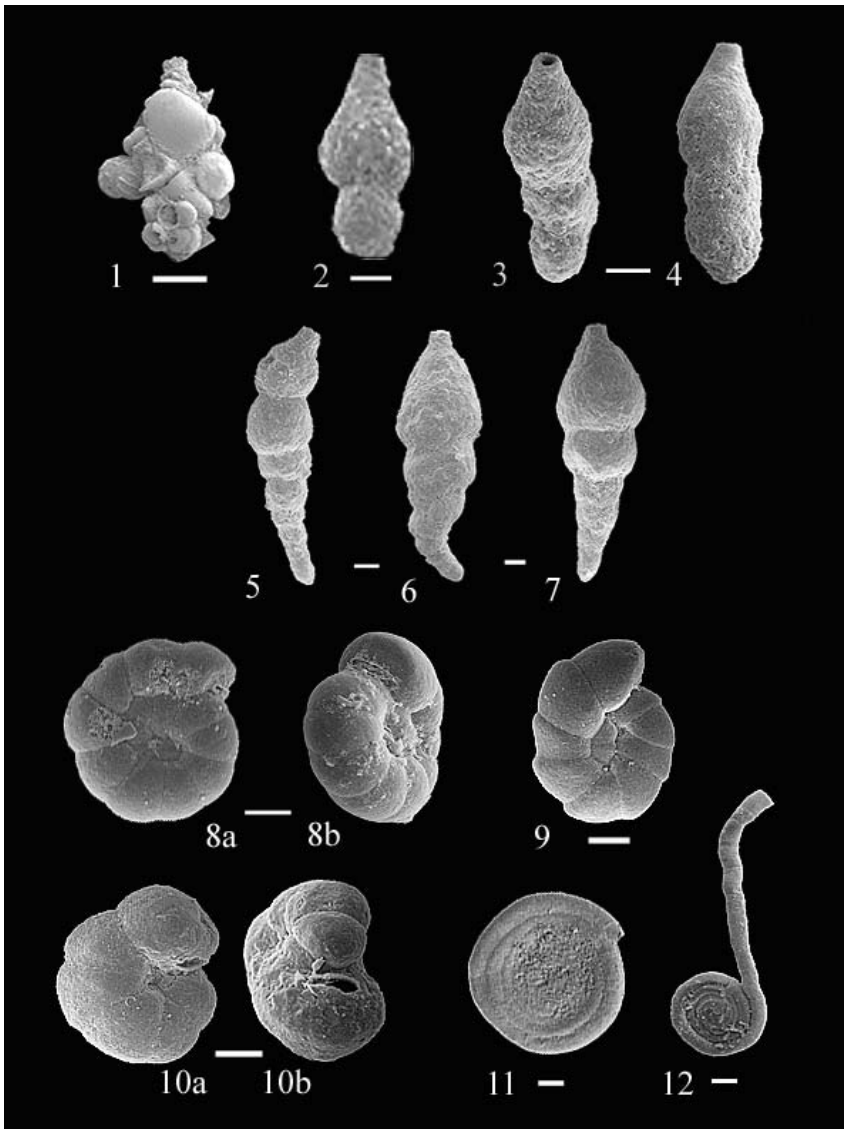

Plate 4. Scanning electron micrographs of agglutinated foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm. **Fig.1,** *Reophax* sp. 1. **Fig.2,** *Reophax bilocularis* Flint 1899. **Figs.3-4,** *Reophax* sp. 2. **Figs.5-7**, *Reophax dentaliniformis* (Brady 1881). **Figs.8a-b, 9,** *Veleroninoides crassimargo* (Norman 1892). **Fig.10a-b,** *Veleroninoides wiesneri* (Parr 1950). **Figs.11-12,** *Ammodiscus* aff. *cretaceus* (Fig.11, coiled, Fig.12, uncoiled).

Plate 5

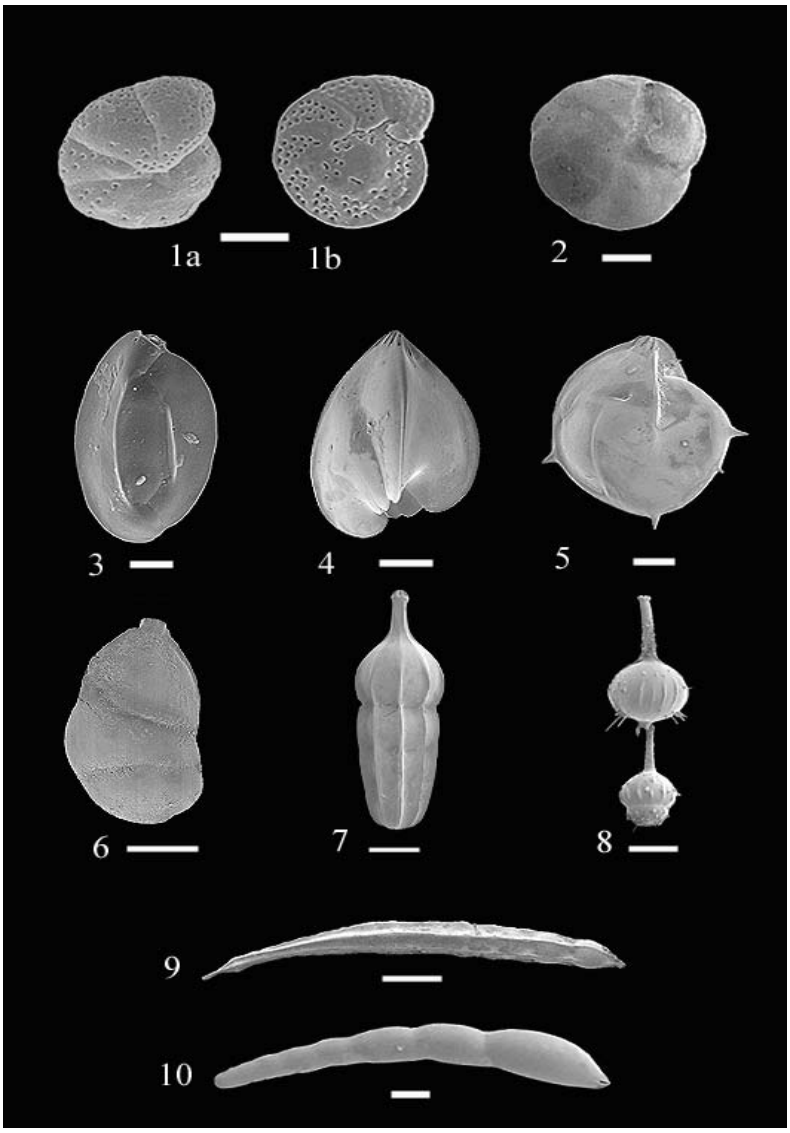

Plate 5. Scanning electron micrographs of calcareous foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm. **Fig.1a-b,** *Cibicides* sp. 1. **Fig.2,** *Cassidulina laevigata* (d'Orbigny 1826). **Fig.3,** *Quinqueloculina* aff. *venusta* (Karrer 1868). **Fig.4,** *Saracenaria italica* (Defrance 1824). **Fig.5,** *Lenticulina* aff. *iota* (Cushman 1923). **Fig.6,** *Neolenticulina variabilis* (Reuss 1850). **Fig.7,** *Amphicoryna* aff. *scalaris* (Batsch 1791). **Fig.8.** *Nodosaria* aff. *pyrula* (d'Orbigny 1826). **Fig.9,** *Dentalina* aff. *flintii* (Cushman 1923). **Fig.10,** *Laevidentalina aphelis* (Loeblich and Tappan 1986).

Plate 6

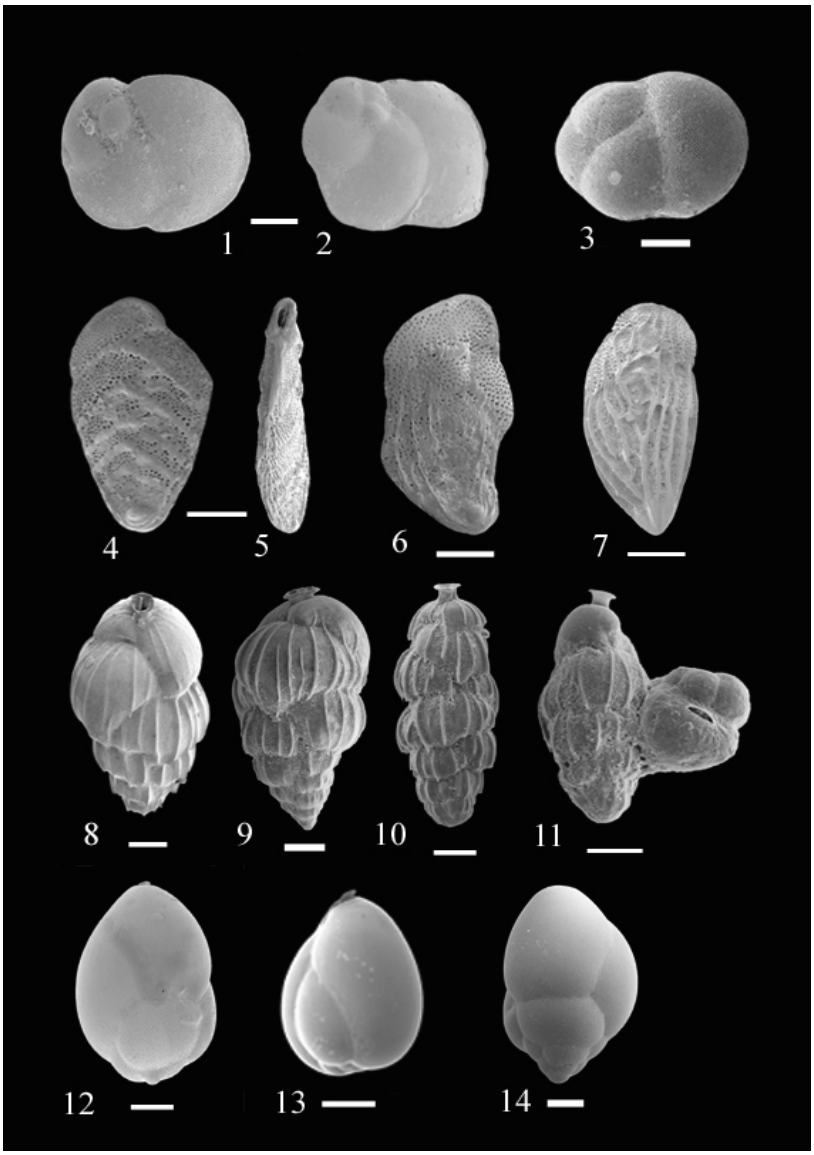

Plate 6. Scanning electron micrographs of calcareous foraminifera from 140 m and 300 m, Pakistan Margin. Scale bars = 100 µm. **Figs.1-2,** *Cancris auriculus* (Fitchel and Moll 1798). **Fig.3,** *Baggina philippinensis* (Cusman 1921). **Figs.4-6,** *Bolivina* aff. *dilatata* (Reuss 1850). **Fig.7,** *Saidovina amygdalaeformis* (Brady 1881). **Figs.8-11,** *Uvigerina* ex. gr. *semiornata* (d'Orbigny 1846). **Figs.12-14,** *Globobulimina* cf. *G. pyrula* (d'Orbigny 1846).

Plate 7

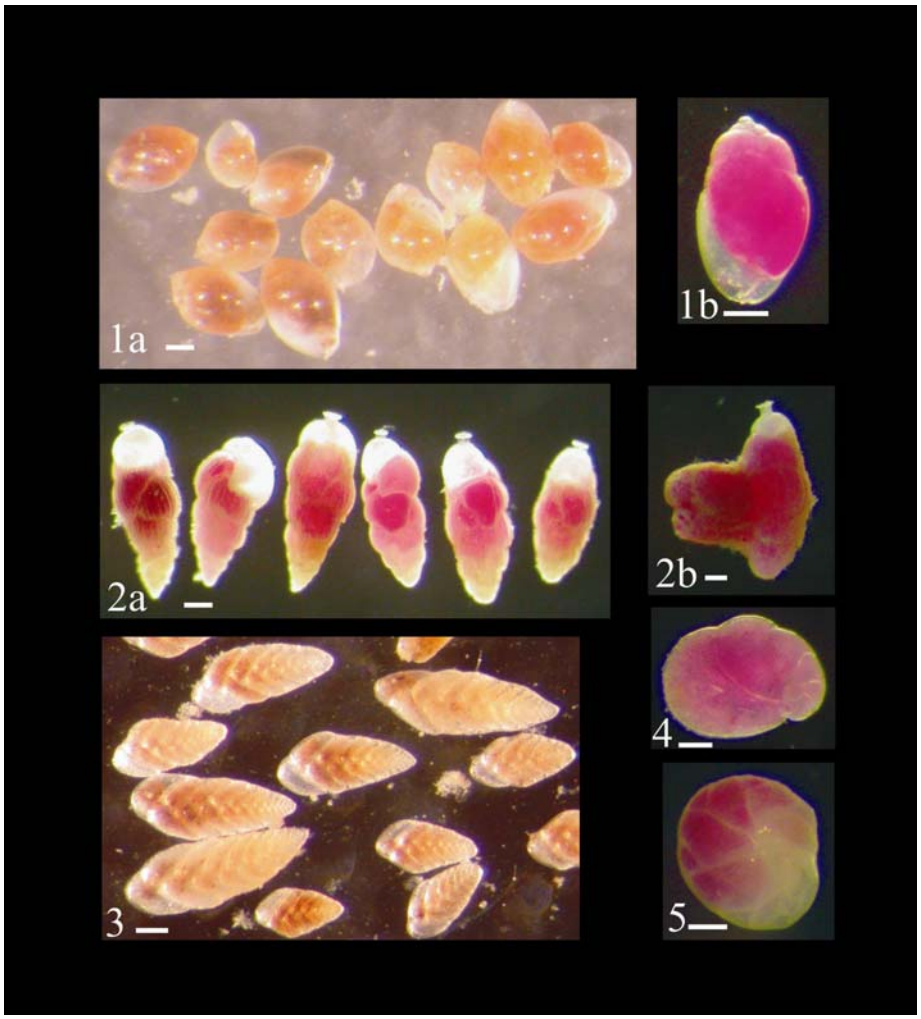

Plate 7. Light photographs of "live" macrofaunal (>300 µm) calcareous foraminifera from 140 m and 300 m. Scale bars = 100 µm. **Fig.1a-b,** *Globobulimina* cf. *G. pyrula* (d'Orbigny 1846). **Fig.2a-b,** *Uvigerina* ex. gr. *semiornata* (d'Orbigny 1846) (2b. specimen with 'live' attached agglutinated *Veleroninoides wiesneri* (Parr 1950). **Fig.3,** *Bolivina* aff. *dilatata* (Reuss 1850). **Fig.4,** *Cancris auriculus* (Fitchtel and Moll 1798). **Fig.5,** *Cassidulina laevigata* (d'Orbigny 1826). Figures 1a and 3 are shipboard photographs of fresh, unstained specimens. Others are laboratory photographs of fixed specimens stained with Rose Bengal.

Figure 1. Biomarker fatty acids, their sources and references in the literature

Fatty acid	Source of fatty acid	References
14:0	Flagellates (Coccolithophorida), polar calanoid copepods	11,21
15:0	Bacteria	2
16:0	Substantial biomass in prokaryotes and eukaryotes, bacteria cyanobacteria, Chlorophyceae, dinoflagellates and flagellates copepods (storage substance)	12,14,18,20
16:1(*n*-9)	Present in many organisms. Synthesised *de novo* by some eukaryotic cells via chain shortening of 18:1(*n*-9) and desaturation of 18:0	12
16:1(*n*-7)	Synthesised *de novo* by eukaryotic cells, bacteria and cyanobacteria	1,13
	Algae e.g. diatoms if present in high amountsand in association with high 16:0 and low 16:1(*n*-9), Prymnesiophyceae, Eustigmatophyceae	3
16:1(*n*-5)	Bacteria (if present in high amounts)	4
16:2(*n*-3)	Algae e.g. Bacillariophyceae (diatoms)	1,12,15
16:3(*n*-3)	Algae e.g. Bacillariophyceae (diatoms)	1,12,15
17:0	Bacteria	13
17:1	Bacteria and Chlorophyceae	13
16:4(*n*-1)	Algae e.g. Bacillariophyceae (diatoms)	1,12,15
18:0	Bacteria and detritus	13,26
18:1(n-9)	Many algal classes (Chlorophyceae, dinoflagellates), storage reserves in foraminifera	1,3,4,13,15,27
18:1(*n*-7)	Bacteria, cyanobacteria (blue-green algae)	5,13
18:1(*n*-9): 18:1(*n*-7)	Bacteria only when ratio is low i.e. high amounts of 18:1(*n*-7)	26,27
18:2(*n*-6)	Seed oils, micro-algae (especially cyanobacteria = blue-green algae), benthic eukaryotes	5,10,12,13
18:3(*n*-6)	Chlorophyceae	1,17,19,23
18:3(*n*-3)	Chlorophyceae, cyanobacteria, flagellates	1,13,23
18:4(*n*-3)	Micro-algae, flagellates (especially Cryptophyceae, Chrysophyceae, Prasinophyceae, Prymneisophyceae), dinoflagellates	1,9,12,23
20:1(*n*-9)	Zooplankton	1,13
20:1(*n*-7)	Algae e.g. Bacillariophyceae (diatoms), zooplankton	1,12,13
20:4(*n*-6)	Seed oils, micro-algae, benthic eukaryotes	11,13,27
20:4(*n*-3)	Algae e.g. Bacillariophyceae (diatoms)	1,12,15
20:5(*n*-3) (EPA)	Bacillariophyceae (Diatoms), flagellates including Cryptophyceae, Chrysophyceae, Prasinophyceae) eustigmatophyceae, marine yeasts, copepods	1,7,12,13,23
22:1(*n*-11)	Copepods (storage), deep ocean zooplankton	7,12,13,27
21:5(*n*-3)	Algae e.g. Bacillariophyceae (diatoms)	1,12,15
22:6(*n*-3) (DHA)	Flagellates (especially Crytophycea, Coccolithophorida, Chrysophyceae, Haptophyceae, Prymnesiophyceae) dinoflagellates, marine yeasts, copepods	1,13,15,21,23

EPA = Eicosapentaenoic Acid, DHA = Docosahexaenoic acid

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(See Bibliography for full references)

Figure 1. Live Foraminifera and metazoans (>300 µm) at 140 m, spring intermonsoon.

Site, sample, (cruise) season		140 m, 55901#5, (CD146) spring intermonsoon						140 m, 55901#7, (CD146) spring intermonsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1	2											
	Allogromiid sp. 2												
	Allogromiid sp. 3												
	Allogromiid sp. 4												
	Allogromiid sp. 5							1					
	Bathysiphon sp. nov. 1		1					3					
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1		1					2	1				
	Lagenammina arenulata		2										
	Pelosina sp. 1	3	2					1	1				
	Psammosphaerid sp. 1		1					1					
	Saccamminid sp. 1							2					
	Saccamminid sp. 2												
	Saccamminid sp. 3												
	Ammodiscus aff. *cretaceus*		1					1					
	Reophax bilocularis	2	3	1	2			1	4	2			
	Reophax dentaliniformis												
	Reophax sp.1		6						1				
	Reophax sp.2												
	Veleroninoides crassimargo												
	Veleroninoides wiesneri												
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis	1	1										
	Bolivina aff. *dilatata*							1					
	Cancris auriculus	20	4	4				3	5	1			
	Cassidulina laevigata								1				
	Cibicides sp. 1		2					1	2				
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*		7	1				1	1				
	Laevidentalina aphelis							1					
	Lenticulina aff. *iota*	1											
	Neolenticulina variabilis	1						1					
	Nodosaria aff. *pyrula*	1											
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis												
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	86	68	21	3			92	12	12	3	1	
	Indeterminate attached												
	Total monothalamous	5	7					10	2				
	Total other agglutinated	2	10	1	2			2	5	2			
	Total calcareous	110	82	26	3			100	21	13	3	1	
	Total forams 25 cm^{-2}	117	99	27	5			112	28	15	3	1	
	Total forams 10 cm^{-2}	46	39	11	2			44	11	6	1		
Metazoa	Amphipoda								1				
	Bivalvia		2										
	Copepoda	3	3	1									
	Echinodermata	2											
	Gastropoda		2					2	5				
	Nematoda							5	1	3	1	1	
	Ostracoda	1	5						1				
	Polychaeta	8	7	5	8			7	6	10	9	5	5
	Total metazoans 25 cm^{-2}	14	19	6	8			14	14	13	10	6	5
	Total metazoans 10 cm^{-2}	5	7	2	3			5	5	5	4	2	2

Figure 1. (continued)

Site, sample, (cruise) season		140 m, 55901#13, (CD146) spring intermonsoon						140 m, 55901#11 (CD146) spring intermonsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1	1											
	Allogromiid sp. 2												
	Allogromiid sp. 3												
	Allogromiid sp. 4												
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1	2	1										
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1							3					
	Lagenammina arenulata							5					
	Pelosina sp. 1	1						1					
	Psammosphaerid sp. 1	1	2										
	Saccamminid sp. 1	1											
	Saccamminid sp. 2												
	Saccamminid sp. 3												
	Ammodiscus aff. *cretaceus*							1	1				
	Reophax bilocularis	1	5					2					
	Reophax dentaliniformis												
	Reophax sp.1	1											
	Reophax sp.2												
	Veleroninoides crassimargo												
	Veleroninoides wiesneri												
	Amphicoryna aff. *scalaris*	4						1					
	Baggina philippinensis												
	Bolivina aff. *dilatata*	4	2					3					
	Cancris auriculus	10	1					2	1	3		1	1
	Cassidulina laevigata	3	2										
	Cibicides sp. 1	4						8	1	1			
	Dentalina aff. *flintii*							1					
	Globobulimina cf. *G. pyrula*	5	3	2				2		1			
	Laevidentalina aphelis							1					
	Lenticulina aff. *iota*	2											
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis												
	Saracenaria italica							1					
	Uvigerina ex. gr. *semiornata*	84	65	10	2			72	6	7	1		3
	Indeterminate attached							1					
	Total monothalamous	6	3					9					
	Total other agglutinated	2	5					3	1				
	Total calcareous	116	73	12	2			92	8	12	1	1	4
	Total forams 25 cm^{-2}	124	81	12	2			104	9	12	1	1	4
	Total forams 10 cm^{-2}	49	32	5	1			41	4	5			2
Metazoa	Amphipoda												
	Bivalvia	1						1					
	Copepoda	5	1					2					
	Echinodermata							1					
	Gastropoda							2					
	Nematoda	5	5	2				2		3	3	1	1
	Ostracoda	6	2							3			1
	Polychaeta	19	12	3	1			6	2	3	3	3	3
	Total metazoans 25 cm^{-2}	36	20	5	1			14	2	9	6	4	5
	Total metazoans 10 cm^{-2}	14	8	2				5	1	4	2	2	2

Figure 2. Live Foraminifera and metazoans (>300 µm) at 140 m, SW monsoon.

Site, sample, (cruise) season		140 m, 56033#1, (CD150) SW monsoon						140 m, 56036#4, (CD150) SW monsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1	3						1					
	Allogromiid sp. 2												
	Allogromiid sp. 3												
	Allogromiid sp. 4												
	Allogromiid sp. 5	1											
	Bathysiphon sp. nov. 1												
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1	1						4					
	Lagenammina arenulata							1	1				
	Pelosina sp. 1							2					
	Psammosphaerid sp. 1	1											
	Saccamminid sp. 1							2	1	1			
	Saccamminid sp. 2												
	Saccamminid sp. 3												
	Ammodiscus aff. *cretaceus*							1					
	Reophax bilocularis	1						2					
	Reophax dentaliniformis												
	Reophax sp.1												
	Reophax sp.2												
	Veleroninoides crassimargo												
	Veleroninoides wiesneri												
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis												
	Bolivina aff. *dilatata*	15						23					
	Cancris auriculus	40						20					
	Cassidulina laevigata												
	Cibicides sp. 1												
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*	1											
	Laevidentalina aphelis							1					
	Lenticulina aff. *iota*							1	1				
	Neolenticulina variabilis								1				
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*							1					
	Saidovina amygdalaeformis							1					
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	238	1					263		1	1		
	Indeterminate attached												
	Total monothalamous	6						10	2	1			
	Total other agglutinated	1						3					
	Total calcareous	294	1					310	2	1	1		
	Total forams 25 cm^{-2}	301	1					323	4	2	1		
	Total forams 10 cm^{-2}	118						127	2	1			
Metazoa	Amphipoda								1				
	Bivalvia								1				
	Copepoda	3							1				
	Echinodermata	2											
	Gastropoda												
	Nematoda			1				3	3	1	1		
	Ostracoda	1							1		2		
	Polychaeta	8	2	5	3			6	4	2	2		
	Total metazoans 25 cm^{-2}	14	2	6	3			9	11	3	5		
	Total metazoans 10 cm^{-2}	5	1	2	1			4	4	1	2		

Figure 2. (continued)

Site, sample, (cruise) season		140 m, 56101#7, (CD151) SW monsoon						140 m, 56101#27, (CD151) SW monsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1												
	Allogromiid sp. 2												
	Allogromiid sp. 3												
	Allogromiid sp. 4												
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1												
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1	3						3					
	Lagenammina arenulata							6	1				
	Pelosina sp. 1	5											
	Psammosphaerid sp. 1												
	Saccamminid sp. 1												
	Saccamminid sp. 2												
	Saccamminid sp. 3												
	Ammodiscus aff. *cretaceus*												
	Reophax bilocularis	1						1					
	Reophax dentaliniformis												
	Reophax sp.1	1						3					
	Reophax sp.2												
	Veleroninoides crassimargo												
	Veleroninoides wiesneri												
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis												
	Bolivina aff. *dilatata*	28	3					27	2				
	Cancris auriculus	57	2	9	2			36					
	Cassidulina laevigata							2					
	Cibicides sp. 1		6										
	Dentalina aff. *flintii*	1											
	Globobulimina cf. *G. pyrula*	3	3	3	2			2					
	Laevidentalina aphelis	1	1										
	Lenticulina aff. *iota*												
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*							2					
	Saidovina amygdalaeformis	5	3	2				1					
	Saracenaria italica	1											
	Uvigerina ex. gr. *semiornata*	221	52	31	2			362	32	1			
	Indeterminate attached												
	Total monothalamous	8						9	1				
	Total other agglutinated	2						4					
	Total calcareous	317	70	45	6			432	34	1			
	Total forams 25 cm^{-2}	327	70	45	6			445	35	1			
	Total forams 10 cm^{-2}	128	27	18	2			175	14				
Metazoa	Amphipoda												
	Bivalvia												
	Copepoda	2		3				2					1
	Echinodermata												
	Gastropoda							2	2				
	Nematoda	2		3	1	1		4	3	2			1
	Ostracoda	2		1	1	1	1	1					
	Polychaeta	5	3	4	1	1		2	3	1	2		
	Total metazoans 25 cm^{-2}	11	3	11	3	3	1	11	8	3	2		2
	Total metazoans 10 cm^{-2}	4	1	4	1	1		4	3	1	1		1

Figure 3. Live Foraminifera and metazoans (>300 µm) at 300 m, spring intermonsoon.

Site, sample, (cruise)		300 m, 55803#5, (CD145)						300 m, 55902#5, (CD146)					
season		spring intermonsoon						spring intermonsoon					
sediment depth		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1												
	Allogromiid sp. 2												
	Allogromiid sp. 3							3					
	Allogromiid sp. 4												
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1	5						10	3	1			
	Bathysiphon sp. nov. 2	6						2	1				
	Hyperammina sp. nov. 1	2											
	Lagenammina arenulata												
	Pelosina sp. 1												
	Psammosphaerid sp. 1												
	Saccamminid sp. 1	1						1					
	Saccamminid sp. 2	1											
	Saccamminid sp. 3	2						4					
	Ammodiscus aff. *cretaceus*	13	1	1				19	1				
	Reophax bilocularis												
	Reophax dentaliniformis	24	4	7	2			34	6	3	1		
	Reophax sp.1												
	Reophax sp.2	2	5	2				1	3	1			
	Veleroninoides crassimargo	4											
	Veleroninoides wiesneri	1	1					1					
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis							1					
	Bolivina aff. *dilatata*	1						3					
	Cancris auriculus	2						9					
	Cassidulina laevigata	6						1	2				
	Cibicides sp. 1												
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*	8	4	1	2			7	2	2			
	Laevidentalina aphelis												
	Lenticulina aff. *iota*												
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis												
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	68	1	5				75	8	1			
	Indeterminate attached												
	Total monothalamous	17						20	4	1			
	Total other agglutinated	44	11	10	2			55	10	4	1		
	Total calcareous	85	5	6	2			96	12	3			
	Total forams 25 cm^{-2}	146	16	16	4			171	26	8	1		
	Total forams 10 cm^{-2}	49	5	6	2			57	10	3			
Metazoa	Amphipoda												
	Bivalvia												
	Copepoda												
	Echinodermata												
	Gastropoda												
	Nematoda	19	2	1	2			8	3				
	Ostracoda												
	Polychaeta		1					2	1				
	Total metazoans 25 cm^{-2}	19	3	1	2			10	4				
	Total metazoans 10 cm^{-2}	7	1		1			4	2				

Figure 3 (continued)

Site, sample, (cruise)		300 m, 55902#12, (CD146)						300 m, 55902#26, (CD146)					
season		spring intermonsoon						spring intermonsoon					
sediment depth		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1	0											
	Allogromiid sp. 2	1	3										
	Allogromiid sp. 3								1				
	Allogromiid sp. 4	1											
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1							10	6	2			
	Bathysiphon sp. nov. 2	1											
	Hyperammina sp. nov. 1	1						5					
	Lagenammina arenulata												
	Pelosina sp. 1												
	Psammosphaerid sp. 1												
	Saccamminid sp. 1							2					
	Saccamminid sp. 2												
	Saccamminid sp. 3	2						1					
	Ammodiscus aff. *cretaceus*	21	1					4	3	1			
	Reophax bilocularis									2			
	Reophax dentaliniformis	26	5	2				32	7	7	1		
	Reophax sp.1												
	Reophax sp.2	3	5					1	1				
	Veleroninoides crassimargo	3	2					1					
	Veleroninoides wiesneri	2											
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis												
	Bolivina aff. *dilatata*	14							2				
	Cancris auriculus								3				
	Cassidulina laevigata	2											
	Cibicides sp. 1		1										
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*	12	2					1	12	9	2		
	Laevidentalina aphelis												
	Lenticulina aff. *iota*												
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis												
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	147	5					97	8	2			
	Indeterminate attached												
	Total monothalamous	6	3					18	7	2			
	Total other agglutinated	55	13	2				38	11	10	1		
	Total calcareous	175	8					98	25	11	2		
	Total forams 25 cm^{-2}	236	24	2				154	43	23	3		
	Total forams 10 cm^{-2}	93	9	1				58	16	9	1		
Metazoa	Amphipoda												
	Bivalvia												
	Copepoda												
	Echinodermata												
	Gastropoda												
	Nematoda	3	2						3	3	1	1	
	Ostracoda												
	Polychaeta		3					3	2				
	Total metazoans 25 cm^{-2}	3	5					3	5	3	1	1	
	Total metazoans 10 cm^{-2}	1	2					1	2	1			

Figure 4. Live Foraminifera and metazoans (>300 µm) at 300 m, SW monsoon.

Site, sample, (cruise)		300 m, 56037#1, (CD150)						300 m, 56115#2, (CD151)					
season		SW monsoon						SW monsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1												
	Allogromiid sp. 2	4						1					
	Allogromiid sp. 3												
	Allogromiid sp. 4		1										
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1	1	2	1				3	2				
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1												
	Lagenammina arenulata												
	Pelosina sp. 1												
	Psammosphaerid sp. 1												
	Saccamminid sp. 1	1											
	Saccamminid sp. 2	1											
	Saccamminid sp. 3	2						6					
	Ammodiscus aff. *cretaceus*	2						4	1				
	Reophax bilocularis												
	Reophax dentaliniformis	45	1	1	16	1	1	19	6	3	1		
	Reophax sp.1												
	Reophax sp.2	1	3	2	1			2	1				
	Veleroninoides crassimargo	3						5	1				
	Veleroninoides wiesneri	1						2					
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis	0											
	Bolivina aff. *dilatata*	29						8					
	Cancris auriculus	6						2					
	Cassidulina laevigata		1					5	1				
	Cibicides sp. 1												
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*	13	5					5	3	2	1		
	Laevidentalina aphelis												
	Lenticulina aff. *iota*												
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis												
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	135	2		1			194	19				
	Indeterminate attached												
	Total monothalamous	9	3	1				10	2				
	Total other agglutinated	52	4	3	17	1	1	32	9	3	1		
	Total calcareous	183	8		1			214	23	2	1		
	Total forams 25 cm^{-2}	244	15	4	18	1	1	256	34	5	2		
	Total forams 10 cm^{-2}	93	6	2	7			94	13	2	1		
Metazoa	Amphipoda												
	Bivalvia												
	Copepoda												
	Echinodermata												
	Gastropoda												
	Nematoda	17	3					16	1	2			
	Ostracoda												
	Polychaeta	1	1					2	1				
	Total metazoans 25 cm^{-2}	18	4					18	2	2			
	Total metazoans 10 cm^{-2}	7	1					7		1			

Figure 4 (continued).

Site, sample, (cruise)		300 m, 56105#7, (CD151)						300 m, 56107#6, (CD151)					
season		SW monsoon						SW monsoon					
sediment depth (cm)		0-0.5	0.5-1	1-2	2-3	3-4	4-5	0-0.5	0.5-1	1-2	2-3	3-4	4-5
Foraminifera	Allogromiid sp. 1												
	Allogromiid sp. 2	3	1					1					
	Allogromiid sp. 3							1					
	Allogromiid sp. 4							1					
	Allogromiid sp. 5												
	Bathysiphon sp. nov. 1	11							1				
	Bathysiphon sp. nov. 2												
	Hyperammina sp. nov. 1												
	Lagenammina arenulata												
	Pelosina sp. 1												
	Psammosphaerid sp. 1												
	Saccamminid sp. 1												
	Saccamminid sp. 2	2											
	Saccamminid sp. 3	3						2					
	Ammodiscus aff. *cretaceus*	7						12	2	1	1		
	Reophax bilocularis												
	Reophax dentaliniformis	44	16	4	2	2		44	3		1	1	
	Reophax sp.1												
	Reophax sp.2	7	1					19	2				
	Veleroninoides crassimargo	7	2					8					
	Veleroninoides wiesneri	1						4					
	Amphicoryna aff. *scalaris*												
	Baggina philippinensis												
	Bolivina aff. *dilatata*	10						15	3				
	Cancris auriculus	2	2					6					
	Cassidulina laevigata	16											
	Cibicides sp. 1							2					
	Dentalina aff. *flintii*												
	Globobulimina cf. *G. pyrula*	11	2	1				13	5	1			
	Laevidentalina aphelis												
	Lenticulina aff. *iota*												
	Neolenticulina variabilis												
	Nodosaria aff. *pyrula*												
	Quinqueloculina aff. *venusta*												
	Saidovina amygdalaeformis							2					
	Saracenaria italica												
	Uvigerina ex. gr. *semiornata*	146	4	1				202	2	1			
	Indeterminate attached												
	Total monothalamous	19	1					5	1				
	Total other agglutinated	66	19	4	2	2		87	7	1	2	1	
	Total calcareous	185	8	2				240	10	2			
	Total forams 25 cm^{-2}	270	28	6	2	2		332	18	3	2	1	
	Total forams 10 cm^{-2}	99	10	2	1	1		120	6	1			
Metazoa	Amphipoda												
	Bivalvia												
	Copepoda												
	Echinodermata												
	Gastropoda												
	Nematoda	19	8	2		1		20	1				
	Ostracoda												
	Polychaeta							2					
	Total metazoans 25 cm^{-2}	19	8	2		1		22	1				
	Total metazoans 10 cm^{-2}	7	3	1				8					

Table 5. 300 m, spring intermonsoon (April 2003). Percentage composition (Mol %) of total fatty acids in six dominant species of Foraminifera. Data are average values of four replicates. C = 95% Confidence Intervals. (see Chapter 5)

	Bathysiphon sp. 1		*Ammodiscus* aff. *cretaceus*		*Reophax dentaliniformis*		*Bolivina* aff. *dilatata*		*Globobulimina* cf. *G. pyrula*		*Uvigerina* ex. gr. *semiornata*	
	Mol %	C	Mol %	C	Mol %	C	Mol %	C	Mol %	C	Mol %	C
14:0	3.9	0.2	5.3	2.1	3.1	0.3	3.8	2.5	2.6	0.2	2.3	0.6
14:1	1.3	0.3	2.2	1.1	1.1	0.3	0.7	0.5	0.8	0.3	0.6	0.2
15:0	5.1	0.6	7.6	4.3	4.2	0.3	2.5	1.1	3.6	0.4	3.7	0.3
16:0	19.7	6.5	23.2	6.1	12.8	1.3	21.8	4.7	17.8	4.7	22.2	2.4
16:1(*n*-9)	3.4	5.3	1.4	1.0	1.1	1.4	3.0	0.7	2.0	0.3	2.4	2.1
16:1(*n*-7)	4.2	2.2	4.1	2.1	3.2	2.4	2.1	0.4	2.4	0.2	3.3	1.9
16:1(*n*-5)	-	-	-	-	-	-	0.6	0.4	0.5	0.6	0.9	0.8
16:2	1.4	0.3	0.9	0.2	1.9	0.7	2.0	1.1	1.1	0.9	2.3	0.7
16:3	1.6	0.4	0.5	0.4	0.7	1.2	1.3	2.0	1.1	0.9	2.3	1.0
17:0	1.9	0.7	3.2	1.8	2.4	0.7	1.1	0.2	1.6	0.6	1.0	0.2
17:1	1.1	0.6	0.6	0.7	1.2	0.2	0.8	0.2	0.6	0.3	1.1	0.1
16:4(*n*-1)	-	-	-	-	-	-	0.6	0.1	0.6	1.1	1.0	1.0
18:0	13.9	5.9	14.5	3.5	7.8	1.2	17.1	3.5	13.4	2.9	13.3	2.9
18:1(*n*-9)	6.0	1.5	8.7	1.8	15.5	0.8	11.4	1.7	11.8	2.4	12.0	2.2
18:1(*n*-7)	19.2	0.9	11.9	0.8	18.9	3.2	10.4	4.0	11.6	0.8	8.3	1.5
18:2(*n*-6)	1.8	0.4	1.1	1.0	0.5	0.4	2.3	1.1	0.7	0.5	2.5	0.9
18:3(*n*-6)	0.5	0.9	-	-	0.3	0.1	0.5	0.2	1.3	1.1	0.8	0.5
18:3(*n*-3)	-	-	0.5	0.6	0.9	0.7	1.8	3.4	1.4	1.1	2.7	2.3
18:4(*n*-3)	0.5	1.0	0.7	0.5	0.5	0.3	0.8	0.7	1.2	0.8	0.9	0.8
20:0	0.2	0.4	0.1	0.3	0.7	0.6	0.3	0.3	0.2	0.3	0.2	0.3
20:1(*n*-9)	2.7	2.7	3.1	1.2	3.5	1.2	1.3	1.2	5.8	3.9	0.2	0.3
20:1(*n*-7)	1.6	1.6	1.7	1.0	2.5	0.2	2.0	1.4	2.6	0.9	1.0	0.9
20:4(*n*-6)	5.7	1.8	6.8	3.4	9.2	2.2	6.8	0.8	7.3	0.9	5.8	1.2
20:4(*n*-3)	0.3	0.5	-	-	0.9	1.1	0.2	0.4	0.7	0.6	1.9	1.1
20:5(*n*-3)	0.8	0.6	-	-	1.0	0.3	1.1	0.2	0.7	0.4	1.6	0.2
22:0	-	-	0.3	0.2	-	-	0.8	0.4	0.7	0.3	1.1	0.2
22:1(*n*-11)	1.4	0.4	0.4	0.3	2.9	0.3	0.9	0.2	1.6	1.2	1.1	1.0
21:5(*n*-3)	-	-	-	-	-	-	0.5	0.5	1.0	0.2	1.1	0.5
22:5(*n*-3)	0.4	0.8	0.1	0.4	0.2	0.4	0.5	0.2	0.9	0.2	1.2	0.5
22:6(*n*-3)	1.2	0.2	1.0	0.4	2.8	0.2	1.4	0.2	2.1	0.9	1.4	0.4

Table 6. 300-m site, SW monsoon (October 2003). Percentage composition (Mol %) of total fatty acids in six dominant species of Foraminifera. Data are average values of four replicates. C = 95% Confidence Intervals. (see Chapter 5).

	Bathysiphon sp. 1		*Ammodiscus* aff. *cretaceus*		*Reophax dentaliniformis*		*Bolivina* aff. *dilatata*		*Globobulimina* cf. *G. pyrula*		*Uvigerina* ex. gr. *semiornata*	
	Mol %	C	Mol %	C	Mol %	C	Mol %	C	Mol %	C	Mol %	C
14:0	3.8	0.5	3.3	0.9	2.6	1.0	2.6	0.7	1.5	0.2	1.6	0.3
14:1	1.2	1.0	1.7	1.3	1.7	0.4	1.4	0.6	0.7	0.3	1.2	0.8
15:0	5.4	0.1	5.5	1.7	4.6	3.0	2.3	1.4	1.6	0.9	2.7	0.2
16:0	19.0	2.6	28.5	0.8	14.4	2.3	13.6	2.9	17.4	3.1	13.9	1.4
16:1(*n*-9)	1.8	1.2	0.9	0.9	1.8	0.3	2.7	2.7	1.9	0.2	3.9	1.4
16:1(*n*-7)	1.2	0.6	4.0	2.9	6.0	1.9	3.4	1.7	1.9	0.3	5.2	2.4
16:1(*n*-5)	0.2	0.4	-	-	1.1	0.5	1.1	0.4	1.2	0.1	2.9	0.3
16:2	0.8	0.9	1.3	2.0	3.1	0.8	5.4	2.5	2.5	0.7	6.6	0.8
16:3	0.4	0.3	0.3	0.4	2.7	0.8	4.9	1.8	2.3	0.3	6.6	1.0
17:0	2.0	0.7	3.4	1.2	1.9	0.5	0.7	0.5	1.7	0.2	1.2	0.0
17:1	1.0	0.3	1.3	1.0	1.4	0.4	0.4	0.3	1.1	0.1	0.8	0.3
16:4(*n*-1)	0.3	0.5	-	-	1.2	0.3	2.0	0.9	2.2	0.1	2.7	0.9
18:0	12.2	3.9	23.1	4.9	5.7	1.3	10.0	1.9	16.1	5.0	9.2	1.8
18:1(*n*-9)	4.2	0.8	4.4	0.4	3.0	0.7	10.5	2.1	10.2	2.5	2.7	0.6
18:1(*n*-7)	22.1	1.9	15.3	3.7	24.4	2.7	11.4	2.2	9.3	1.8	5.2	0.8
18:2(*n*-6)	0.4	0.3	1.4	0.6	2.1	1.0	2.3	1.6	2.3	0.7	4.7	0.2
18:3(*n*-6)	1.1	1.0	-	-	1.6	0.7	2.1	1.4	1.5	1.6	3.4	1.2
18:3(*n*-3)	1.0	1.0	0.2	0.4	1.8	1.0	1.6	0.8	2.2	0.7	3.6	0.4
18:4(*n*-3)	0.8	0.7	0.2	0.4	1.9	0.6	1.2	0.6	1.7	0.5	3.1	0.7
20:0	0.4	0.4	-	-	0.7	0.1	0.5	0.3	0.6	0.2	1.0	0.2
20:1(*n*-9)	3.9	3.2	0.2	0.4	2.2	0.7	3.3	5.0	2.4	1.6	1.7	0.2
20:1(*n*-7)	3.0	1.9	0.9	1.0	3.5	0.6	3.3	4.2	1.8	0.8	1.1	0.5
20:4(*n*-6)	4.5	3.1	2.0	1.2	2.2	1.1	2.5	0.0	5.2	1.3	2.9	0.6
20:4(*n*-3)	0.8	1.0	-	-	0.9	0.5	1.8	0.7	1.6	0.6	2.7	0.2
20:5(*n*-3)	0.9	0.8	-	-	1.6	0.6	2.9	0.4	2.3	0.3	3.9	1.2
22:0	1.1	1.1	0.4	1.1	0.8	0.6	0.7	0.3	0.7	1.1	1.0	0.1
22:1(*n*-11)	2.8	0.6	0.3	0.4	2.9	2.2	1.0	0.7	1.3	0.8	0.8	0.1
21:5(*n*-3)	0.6	0.7	-	-	0.8	0.1	1.8	0.8	1.5	0.5	1.2	0.4
22:5(*n*-3)	0.8	0.8	-	-	0.8	0.2	1.6	1.4	1.4	0.3	1.2	0.3
22:6(*n*-3)	2.2	0.9	1.4	0.6	0.8	0.1	1.0	0.5	1.7	0.4	1.3	0.3

Table 7. Percentage composition (Mol %) of total fatty acids in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites during spring intermonsoon (April 2003) and SW monsoon (October 2003). Data are average values of four replicates (to 1 d.p.). C = 95% Confidence Intervals. (see Chapter 5)

	Uvigerina ex. gr. *semiornata*							
	140-m site				300-m site			
	intermonsoon		monsoon		intermonsoon		monsoon	
	Mol %	C	Mol %	C	Mol %	C	Mol %	C
14:0	4.4	1.1	4.9	1.3	2.3	0.6	1.6	0.3
14:1	2.1	0.4	1.6	0.6	0.6	0.2	1.2	0.8
15:0	4.6	0.6	6.3	2.9	3.7	0.3	2.7	0.2
16:0	21.9	2.3	19.1	3.7	22.2	2.4	13.9	1.4
16:1(*n*-9)	2.9	1.1	4.4	1.5	2.4	2.1	3.9	1.4
16:1(*n*-7)	2.3	0.5	4.3	1.0	3.3	1.9	5.2	2.4
16:1(*n*-5)	1.8	0.2	1.5	0.5	0.9	0.8	2.9	0.3
16:2	5.4	6.4	5.6	0.7	2.3	0.7	6.6	0.8
16:3	0.8	0.1	4.8	1.1	2.3	1.0	6.6	1.0
17:0	3.8	0.3	1.4	0.3	1.0	0.2	1.2	0.0
17:1	1.7	0.4	0.7	0.2	1.1	0.1	0.8	0.3
16:4(*n*-1)	0.7	0.3	0.8	0.4	1.0	1.0	2.7	0.9
18:0	10.3	3.2	9.6	2.0	13.3	2.9	9.2	1.8
18:1(*n*-9)	12.2	1.9	3.9	1.3	12.0	2.2	2.7	0.6
18:1(*n*-7)	1.8	1.4	4.9	1.0	8.3	1.5	5.2	0.8
18:2(*n*-6)	0.7	0.1	2.6	1.2	2.5	0.9	4.7	0.2
18:3(*n*-6)	0.6	0.1	1.7	0.3	0.8	0.5	3.4	1.2
18:3(*n*-3)	0.8	0.2	1.6	0.1	2.7	2.3	3.6	0.4
18:4(*n*-3)	0.9	0.4	1.6	0.4	0.9	0.8	3.1	0.7
20:0	1.0	0.2	1.1	0.2	0.2	0.3	1.0	0.2
20:1(*n*-9)	1.3	0.2	0.9	0.5	0.2	0.3	1.7	0.2
20:1(*n*-7)	2.7	3.0	2.9	4.0	1.0	0.9	1.1	0.5
20:4(*n*-6)	5.9	1.1	4.4	1.0	5.8	1.2	2.9	0.6
20:4(*n*-3)	0.5	0.2	1.7	0.5	1.9	1.1	2.7	0.2
20:5(*n*-3)	0.6	0.2	1.6	0.7	1.6	0.2	3.9	1.2
22:0	0.4	0.4	1.0	0.8	1.1	0.2	1.0	0.1
22:1(*n*-11)	4.6	0.9	1.6	0.8	1.1	1.0	0.8	0.1
21:5(*n*-3)	1.0	0.2	1.0	0.8	1.1	0.5	1.2	0.4
22:5(*n*-3)	0.7	0.1	1.3	1.2	1.2	0.5	1.2	0.3
22:6(*n*-3)	1.6	0.7	1.7	1.1	1.4	0.4	1.3	0.3

Table 8. ^{13}C-labelled diatom feeding experiment: average percentage composition (Mol %) of total fatty acids in the diatom monoculture *Thalassiosira weisflogii* (food source) and the foraminiferan *Uvigerina* ex. gr. *semiornata* during laboratory experiments (T=0, T=2 days, T=5 days) and *in situ* experiments (T=2.5 days). Data are average Mol % of four replicates per foraminiferan samples and two replicates for the diatom sample. (see Chapter 6)

	diatom monoculture		*Uvigerina* ex. gr. *semiornata* Laboratory experiments						*in situ* experiment	
			T=0 days		T=2 days		T=5 days		T=2.5 days	
	Mol %	C	Mol %	C	Mol %	C	Mol %	C	Mol %	C
14:0	8.5	0.8	5.1	1.3	9.6	2.2	11.8	1.0	11.6	3.1
14:1	0.6	0.1	1.7	0.6	0.8	0.3	1.0	0.3	1.4	0.8
15:0	1.8	0.5	6.5	2.9	3.3	0.7	3.7	0.4	3.8	1.0
16:0	10.8	0.5	19.8	3.5	18.5	2.8	17.6	2.1	18.9	1.9
16:1(*n*-9)	0.6	0.2	4.6	1.4	1.1	0.2	1.3	0.2	1.5	0.8
16:1(*n*-7)	11.0	0.8	3.8	1.0	4.7	1.1	4.6	0.3	4.0	0.2
16:1(*n*-5)	2.3	0.3	1.5	0.5	1.2	1.3	0.5	0.1	1.6	1.4
16:2	11.8	1.1	4.0	1.0	2.0	0.5	2.5	1.0	2.8	1.0
16:3	21.8	6.6	3.4	0.2	4.3	3.1	5.9	0.8	4.0	0.7
17:0	1.0	0.1	1.4	0.3	2.2	2.1	0.9	0.4	1.8	1.4
17:1	0.0	0.0	0.7	0.2	0.6	0.2	0.6	0.3	0.5	0.1
16:4(*n*-1)	1.5	0.9	0.8	0.4	0.5	0.2	1.1	0.3	0.9	0.6
18:0	0.9	0.3	10.1	2.4	5.8	2.6	4.0	0.0	7.6	5.4
18:1(*n*-9)	3.9	2.0	4.0	1.3	3.9	1.2	3.5	0.3	4.8	2.8
18:1(*n*-7)	1.7	0.4	5.1	1.0	7.7	1.7	6.4	1.8	6.7	3.2
18:2(*n*-6)	1.6	0.1	2.7	1.2	3.4	0.6	4.0	0.4	2.4	1.4
18:3(*n*-6)	0.1	0.1	1.7	0.3	0.7	0.2	0.8	0.4	1.0	0.8
18:3(*n*-3)	3.1	0.8	1.6	0.1	5.3	3.7	3.3	1.2	2.1	1.5
18:4(*n*-3)	0.9	0.5	1.6	0.4	1.6	1.5	1.9	2.0	0.4	0.2
20:0	0.3	0.6	1.1	0.2	0.5	0.3	0.2	0.0	0.2	0.1
20:1(*n*-9)	0.4	0.8	0.9	0.6	0.8	1.3	0.3	0.1	0.4	0.4
20:1(*n*-7)	0.3	0.5	3.0	4.0	1.0	1.1	0.3	0.2	0.7	0.5
20:4(*n*-6)	0.9	0.1	4.5	0.9	11.6	2.7	12.8	0.9	11.1	6.1
20:4(*n*-3)	0.4	0.9	1.8	0.6	1.4	1.3	1.1	0.4	1.1	0.6
20:5(*n*-3)	11.6	0.9	1.7	0.8	2.9	1.3	3.9	1.1	2.3	0.6
22:0	0.0	0.0	1.0	0.9	0.4	0.3	0.5	0.1	0.8	0.6
22:1(*n*-11)	0.0	0.0	1.7	0.9	0.4	0.3	0.5	0.3	0.8	0.8
21:5(*n*-3)	0.6	0.0	1.0	0.9	0.4	0.1	0.4	0.0	0.5	0.2
22:5(*n*-3)	0.0	0.0	1.4	1.3	0.8	0.2	0.9	0.1	0.9	0.3
22:6(*n*-3)	1.7	0.2	1.7	1.2	2.7	1.0	3.8	0.6	3.2	1.4

Table 9. ^{13}C-labelled diatom feeding experiment: average weight (ng per 30 Foraminifera) of total fatty acids in the diatom monoculture *Thalassiosira weisflogii* (food source) and the foraminiferan *Uvigerina* ex. gr. *semiornata* during laboratory experiments (T=0, T=2 days, T=5 days) and *in situ* experiments (T=2.5 days). Data are averages (to 1 d.p.) of four replicates per foraminiferan samples and two replicates for the diatom sample. Total[1] = total average weight (ng) in 30 Foraminifera, Total[2] = total average weight (ng) in 1 foraminiferan. (see Chapter 6).

	diatom monoculture		*Uvigerina* ex. gr. *semiornata* Laboratory experiments						*in situ* experiment	
			T=0 days		T=2 days		T=5 days		T=2.5 days	
	weight (ng)	C	weight (ng)	C	weight (ng)	C	weight (ng)	C	weight (ng)	C
14:0	872	64.2	295	94.2	1147	294	2886	296	1006	368
14:1	57.3	15.8	98.7	43.3	86.3	36.2	232	96	113	82.0
15:0	196	51.7	399	206	421	105	956	166	341	96.4
16:0	1254	42.8	1301	298	2473	488	4873	1081	1832	166
16:1(*n*-9)	66.5	19.0	299	117	154	32.5	355	71	145	94.2
16:1(*n*-7)	1258	68.6	250	81.5	624	176	1256	83	391	3.3
16:1(*n*-5)	262	32.8	98.7	37.6	144	126	127	34	166	205
16:2	1345	102	255	68.3	265	59.3	699	414	268	105
16:3	2469	787	219	17.4	571	419	1593	231	377	82.5
17:0	124	8.0	98.8	30.4	320	327	254	141	180	190
17:1	-	-	46.4	16.3	89.1	38.2	167	119	52.4	15.3
16:4(*n*-1)	183	110	53.6	34.5	58.0	22.2	232	231	83.0	77.8
18:0	116	34.0	734	221	877	449	1250	707	797	728
18:1(*n*-9)	486	261	292	124	555	106	1063	188	537	461
18:1(*n*-7)	214	52.1	366	93.8	1122	219	1940	730	735	506
18:2(*n*-6)	196	9.8	191	108	500	116	1202	109	258	208
18:3(*n*-6)	7.5	14.7	124	24.9	104	25.7	238	163	113	123
18:3(*n*-3)	391	96.3	117	16.2	805	611	1002	566	220	212
18:4(*n*-3)	113	56.4	114	34.6	233	229	539	761	41.7	30.3
20:0	37.1	72.7	88.8	18.5	76.8	45.9	55.0	12.7	27.7	18
20:1(*n*-9)	51.7	101	73.6	56.4	134	233	88.6	63.3	52.0	75
20:1(*n*-7)	31.7	62.1	230	367	154	181	100	102	86.1	89.2
20:4(*n*-6)	111	15.0	351	77.5	1799	275	4195	546	1324	1036
20:4(*n*-3)	56.7	111	140	57.9	235	227	354	185	130	81
20:5(*n*-3)	1493	92.0	130	80.6	460	221	1255	447	260	71
22:0	-	-	93	102	62.3	43.2	186	76.4	103	103
22:1(*n*-11)	-	-	145	101	65.5	48.2	186	179	97.9	131
21:5(*n*-3)	84.4	5.0	83	93	66.4	10.5	146	20.7	59.3	40
22:5(*n*-3)	-	-	117	139	143	27.7	327	35.2	117	62
22:6(*n*-3)	224	16.4	148	127	467	170	1329	225	406	268
Total[1]	11700	146	10425	399	15139	515	36306	1605	12901	1056
Total[2]	n/a	n/a	348	5.4	505	17.2	1210	166	430	49.4

Results of statistical analysis

1. One-way analysis of similarity (ANOSIM)

The ANOSIM statistical test was conducted in PRIMER (v. 5.2.1) (Clarke and Warwick, 1994). A value of P < 3 % represents a significant difference between samples (P values highlighted in grey) and a value of P < 1 % represents a strong significant difference between samples Inter = spring intermonsoon sample, Mons = SW monsoon sample.

Chapter 4: Testing the similarity between different sediment layers. Bray-Curtis similarity matrix based on the full live macrofaunal (>300 µm) foraminiferal species in each sediment layer (square-root transformed data).

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Inter 0.5-1, Inter 0-0.5	0.073	34.3	35	35	12
Inter 1-2, Inter 0-0.5	0.87	2.9	35	35	1
Inter 1-2, Inter 0.5-1	0.5	5.7	35	35	2
Inter 1-2, Inter 2-3	0.796	2.9	35	35	1
Inter 2-3, Inter 0-0.5	1	2.9	35	35	1
Inter 2-3, Inter 0.5-1	0.948	2.9	35	35	1

Table 1. ANOSIM results: 140 m, spring intermonsoon. Complete species list data. Sediment layers 0-3 cm (see Chapter 4)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Mons 0.5-1, Mons 0-0.5	0.594	2.9	35	35	1
Mons 1-2, Mons 0-0.5	0.823	2.9	35	35	1
Mons 1-2, Mons 0.5-1	-0.073	62.9	35	35	22
Mons 1-2, Mons 2-3	-0.093	54.3	35	35	19
Mons 2-3, Mons 0-0.5	0.63	2.9	35	35	1
Mons 2-3, Mons 0.5-1	0.056	40	35	35	14

Table 2. ANOSIM results: 140 m , SW monsoon. Complete species list data. Sediment layers 0-3 cm. (see Chapter 4)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Same sediment layer					
Inter 0-0.5, Mons 0-0.5	0.469	2.9	35	35	1
Inter 0.5-1, Mons 0.5-1	0.469	5.7	35	35	2
Inter 1-2, Mons 1-2	-0.046	45.7	35	35	16
Inter 2-3, Mons 2-3	0.241	14.3	35	35	5
Different sediment layers					
Inter 1-2, Mons 0-0.5	0.981	2.9	35	35	1
Inter 1-2, Mons 0.5-1	0.111	28.6	35	35	10
Inter 2-3, Mons 0-0.5	1	2.9	35	35	1
Inter 2-3, Mons 0.5-1	0.26	14.3	35	35	5
Mons 0-0.5, Inter 0.5-1	0.719	2.9	35	35	1
Mons 0.5-1, Inter 0-0.5	0.51	5.7	35	35	2
Mons 1-2, Inter 0-0.5	0.698	2.9	35	35	1
Mons 1-2, Inter 0.5-1	0.438	5.7	35	35	2
Mons 1-2, Inter 2-3	0.031	28.6	35	35	10
Mons 2-3, Inter 0-0.5	0.63	2.9	35	35	1
Mons 2-3, Inter 0.5-1	0.5	2.9	35	35	1

Table 3. ANOSIM results: 140 m. Seasonal comparison between samples collected in spring intermonsoon and SW monsoon. Complete species list data. Sediment layers 0-3 cm. (see Chapter 4)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Inter 0.5-1, Inter 0-0.5	0.594	2.9	35	35	1
Inter 1-2, Inter 0-0.5	0.635	2.9	35	35	1
Inter 1-2, Inter0.5-1	-0.135	80	35	35	28
Inter 1-2, Inter 2-3	0.306	11.4	35	35	4
Inter 2-3, Inter 0-0.5	1	2.9	35	35	1
Inter 2-3, Inter 0.5-1	0.028	40	35	35	14

Table 4. ANOSIM results: 300 m, spring intermonsoon. Complete species list data. Sediment layers 0-3 cm. (see Chapter 4).

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Mons 0.5-1, Mons 0-0.5	0.802	2.9	35	35	1
Mons 1-2, Mons 0-0.5	0.833	2.9	35	35	1
Mons 1-2, Mons 0.5-1	0.313	8.6	35	35	3
Mons 1-2, Mons 2-3	-0.125	77.1	35	35	27
Mons 1-2, Mons 3-4	0.296	8.6	35	35	3
Mons 2-3, Mons 0-0.5	1	2.9	35	35	1
Mons 2-3, Mons 0.5-1	0.792	2.9	35	35	1
Mons 2-3, Mons 3-4	-0.185	100	35	35	35
Mons 3-4, Mons 0-0.5	1	2.9	35	35	1
Mons 3-4, Mons 0.5-1	1	2.9	35	35	1

Table 5. ANOSIM results: 300m, SW monsoon. Complete species list data. 0-4 cm sediment layers. (see Chapter 4).

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Same sediment layer					
Inter 0-0.5, Mons 0-0.5	0.198	14.3	35	35	5
Inter 0.5-1, Mons 0.5-1	0.167	25.7	35	35	9
Inter 1-2, Mons 1-2	-0.156	77.1	35	35	27
Inter 2-3, Mons 2-3	-0.12	71.4	35	35	25
Different sediment layer					
Inter 0-0.5, Mons 0.5-1	0.813	2.9	35	35	1
Inter 0.5-1, Mons 0-0.5	0.604	2.9	35	35	1
Inter 1-2, Mons 0-0.5	0.656	2.9	35	35	1
Inter 1-2, Mons 0.5-1	-0.021	57.1	35	35	20
Inter 1-2, Mons 2-3	0.01	42.9	35	35	15
Inter 1-2, Mons 3-4	0.426	8.6	35	35	3
Inter 2-3, Mons 0-0.5	1	2.9	35	35	1
Inter 2-3, Mons 0.5-1	1	2.9	35	35	1
Mons 1-2, Inter 0-0.5	0.813	2.9	35	35	1
Mons 1-2, Inter 0.5-1	-0.167	71.4	35	35	25
Mons 1-2, Inter 2-3	-0.102	62.9	35	35	22
Mons 2-3, Inter 0-0.5	1	2.9	35	35	1
Mons 2-3, Inter 0.5-1	-0.089	60	35	35	21
Mons 3-4, Inter 0-0.5	1	2.9	35	35	1
Mons 3-4, Inter 0.5-1	0.167	20	35	35	7

Table 6. ANOSIM results: 300 m. Seasonal comparison between spring intermonsoon and SW monsoon. Complete species list data. 0-4 cm sediment layers. (see Chapter 4).

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Same sediment layer, season					
140m-Inter 0-0.5, 300m-Inter 0-0.5	0.906	2.9	35	35	1
140m-Inter 0.5-1, 300m-Inter 0.5-1	0.719	2.9	35	35	1
140m-Mons 0-0.5, 300m-Mons 0-0.5	1	2.9	35	35	1
140m-Mons 0.5-1, 300m Mons 0.5-1	0.667	2.9	35	35	1
Same sediment layer, diff. season					
140m-Inter 0-0.5, 300m-Mons 0-0.5	1	2.9	35	35	1
140m-Mons 0-0.5, 300m Inter 0-0.5	1	2.9	35	35	1
140m-Inter 0.5-1, 300m-Mons 0.5-1	0.865	2.9	35	35	1
140m-Mons 0.5-1, 300m-Inter 0.5-1	0.719	2.9	35	35	1
Diff. sediment layer, same season					
140m-Inter 0-0.5, 300m-Inter 0.5-1	0.958	2.9	35	35	1
140m-Mons 0-0.5, 300m Mons 0.5-1	1	2.9	35	35	1
140m-Inter 0.5-1, 300m-Inter 0-0.5	0.885	2.9	35	35	1
140m-Mons 0.5-1, 300m-Mons 0-0.5	0.719	2.9	35	35	1
Diff. sediment layer, season					
140m-Inter 0-0.5, 300m-Mons 0-0.5	0.896	2.9	35	35	1
140m-Mons 0-0.5, 300m Inter 0.5-1	1	2.9	35	35	1
140m-Inter 0.5-1, 300m-Mons 0-0.5	0.896	2.9	35	35	1
140m-Mons 0.5-1, 300m-Inter 0-0.5	0.74	2.9	35	35	1

Table 7. ANOSIM results: 140 m and 300 m – Comparison between sites. Complete species list data.0-0.5 cm, 0.5-1 cm sediment layers. (see Chapter 4)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
300 m spring intermonsoon					
Uvigerina sp., *Bolivina* sp.	0.188	11.4	35	35	4
Uvigerina sp., *Globobulimina* sp.	0.583	2.9	35	35	1
Uvigerina sp., *Ammodiscus* sp.	0.917	2.9	35	35	1
Uvigerina sp., *Bathysiphon* sp.	0.896	2.9	35	35	1
Uvigerina sp., *Reophax* sp.	1	2.9	35	35	1
Bolivina sp., *Globobulimina* sp.	0.458	5.7	35	35	2
Bolivina sp., *Ammodiscus* sp.	0.698	2.9	35	35	1
Bolivina sp., *Bathysiphon* sp.	0.729	2.9	35	35	1
Bolivina sp., *Reophax* sp.	1	2.9	35	35	1
Globobulimina sp., *Ammodiscus* sp.	0.688	2.9	35	35	1
Globobulimina sp., *Bathysiphon* sp.	0.813	2.9	35	35	1
Globobulimina sp., *Reophax* sp.	0.958	2.9	35	35	1
Ammodiscus sp., *Bathysiphon* sp.	531	2.9	35	35	1
Ammodiscus sp., *Reophax* sp.	1	2.9	35	35	1
Bathysiphon sp., *Reophax* sp.	0.854	2.9	35	35	1
300m sw monsoon					
Uvigerina sp., *Bolivina* sp.	0.729	2.9	35	35	1
Uvigerina sp., *Globobulimina* sp.	1	2.9	35	35	1
Uvigerina sp., *Ammodiscus* sp.	1	2.9	35	35	1
Uvigerina sp., *Bathysiphon* sp.	1	2.9	35	35	1
Uvigerina sp., *Reophax* sp.	1	5.7	35	35	2
Bolivina sp., *Globobulimina* sp.	0.615	2.9	35	35	1
Bolivina sp., *Ammodiscus* sp.	1	2.9	35	35	1
Bolivina sp., *Bathysiphon* sp.	0.958	2.9	35	35	1
Bolivina sp., *Reophax* sp.	0.854	2.9	35	35	1
Globobulimina sp., *Ammodiscus* sp.	1	2.9	35	35	1
Globobulimina sp., *Bathysiphon* sp.	1	2.9	35	35	1
Globobulimina sp., *Reophax* sp.	1	2.9	35	35	1
Ammodiscus sp., *Bathysiphon* sp.	1	2.9	35	35	1
Ammodiscus sp., *Reophax* sp.	1	2.9	35	35	1
Bathysiphon sp., *Reophax* sp.	0.938	2.9	35	35	1

Table 8. 300 m. Comparison of total fatty acid composition (Mol % data; Appendix C) in six dominant species of Foraminifera during each season sampled. (see Chapter 5)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Polyunsaturated fatty acids (PUFAs)					
spring intermonsoon					
Uvi inter, Bol inter	0.229	5.7	35	35	2
Uvi inter, Globo inter	0.083	31.4	35	35	11
Uvi inter, Ammo inter	0.948	2.9	35	35	1
Uvi inter, Bathy inter	0.833	2.9	35	35	1
Uvi inter, Reo inter	0.531	5.7	35	35	2
Bol inter, Globo inter	-0.115	68.6	35	35	24
Bol inter,Ammo inter	0.594	2.9	35	35	1
Bol inter, Bathy inter	0.125	11.4	35	35	4
Bol inter, Reo inter	0.052	28.6	35	35	10
Globo inter, Ammo inter	0.583	5.7	35	35	2
Globo inter, Bathy inter	0.281	14.3	35	35	5
Globo inter, Reo inter	0.146	11.4	35	35	4
Ammo inter, Bathy inter	0.031	42.9	35	35	15
Ammo inter, Reo inter	0.917	2.9	35	35	1
Bathy inter, Reo inter	0.635	2.9	35	35	1
sw monsoon					
Uvi mons Bol mons	0.885	2.9	35	35	1
Uvi mons, Globo mons	1	2.9	35	35	1
Uvi mons, Ammo mons	1	2.9	35	35	1
Uvi mons, Bathy mons	1	2.9	35	35	1
Uvi mons, Reo mons	1	2.9	35	35	1
Bol mons, Globo mons	-0.021	42.9	35	35	15
Bol mons,Ammo mons	1	2.9	35	35	1
Bol mons, Bathy mons	0.917	2.9	35	35	1
Bol mons, Reo mons	0.677	2.9	35	35	1
Globo mons, Ammo mons	1	2.9	35	35	1
Globo mons, Bathy mons	0.833	2.9	35	35	1
Globo mons, Reo mons	0.531	2.9	35	35	1
Ammo mons, Bathy mons	0.771	2.9	35	35	1
Ammo mons, Reo mons	1	2.9	35	35	1
Bathy mons, Reo mons	0.299	8.6	35	35	3
seasonal comparison of each species					
Uvi inter, Uvi mons	1	2.9	35	35	1
Bol inter, Bol mons	0.677	2.9	35	35	1
Globo inter, Globo mons	0.458	2.9	35	35	1
Ammo inter, Ammo mons	0.74	2.9	35	35	1
Bathy inter, Bathy mons	-0.135	74.3	35	35	26
Reo inter, Reo mons	-0.094	74.3	35	35	26

Table 9. 300 m. Comparison of polyunsaturated fatty acids (PUFAs) (Mol %) in six dominant species of Foraminifera during each season sampled. (see Chapter 5)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Algal biomarkers					
spring intermonsoon					
Uvi inter, Bol inter	0.219	11.4	35	35	4
Uvi inter, Globo inter	0.406	14.3	35	35	5
Uvi inter, Ammo inter	0.948	2.9	35	35	2
Uvi inter, Bathy inter	0.542	5.7	35	35	5
Uvi inter, Reo inter	0.24	14.3	35	35	1
Bol inter, Globo inter	-0.167	88.6	35	35	31
Bol inter,Ammo inter	0.958	2.9	35	35	1
Bol inter, Bathy inter	0.292	14.3	35	35	5
Bol inter, Reo inter	-0.156	68.6	35	35	24
Globo inter, Ammo inter	0.979	2.9	35	35	1
Globo inter, Bathy inter	0.313	11.4	35	35	4
Globo inter, Reo inter	-0.146	74.3	35	35	26
Ammo inter, Bathy inter	-0.063	65.7	35	35	23
Ammo inter, Reo inter	0.917	2.9	35	35	1
Bathy inter, Reo inter	0.271	14.3	35	35	5
sw monsoon					
Uvi mons Bol mons	0.552	2.9	35	35	1
Uvi mons, Globo mons	0.979	2.9	35	35	1
Uvi mons, Ammo mons	1	2.9	35	35	1
Uvi mons, Bathy mons	1	2.9	35	35	1
Uvi mons, Reo mons	1	2.9	35	35	1
Bol mons, Globo mons	0.698	2.9	35	35	1
Bol mons,Ammo mons	1	2.9	35	35	1
Bol mons, Bathy mons	1	2.9	35	35	1
Bol mons, Reo mons	1	2.9	35	35	1
Globo mons, Ammo mons	1	2.9	35	35	1
Globo mons, Bathy mons	0.948	2.9	35	35	1
Globo mons, Reo mons	0.719	2.9	35	35	1
Ammo mons, Bathy mons	0.135	28.6	35	35	10
Ammo mons, Reo mons	1	2.9	35	35	1
Bathy mons, Reo mons	0.771	2.9	35	35	1
seasonal comparison of each species					
Uvi inter, Uvi mons	0.646	2.9	35	35	1
Bol inter, Bol mons	0.938	2.9	35	35	1
Globo inter, Globo mons	0.698	2.9	35	35	1
Ammo inter, Ammo mons	0.656	2.9	35	35	1
Bathy inter, Bathy mons	-0.156	97.1	35	35	34
Reo inter, Reo mons	-0.146	80	35	35	28

Table 10. 300 m. Comparison of algal biomarker groups (Mol %) in six dominant species of Foraminifera during each season sampled. (see Chapter 5)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
bacterial biomarkers					
spring intermonsoon					
Uvi inter, Bol inter	0.51	5.7	35	35	2
Uvi inter, Globo inter	0.26	14.3	35	35	5
Uvi inter, Ammo inter	0.885	2.9	35	35	1
Uvi inter, Bathy inter	1	2.9	35	35	1
Uvi inter, Reo inter	0.635	2.9	35	35	1
Bol inter, Globo inter	0	48.6	35	35	17
Bol inter,Ammo inter	0.698	2.9	35	35	1
Bol inter, Bathy inter	1	2.9	35	35	1
Bol inter, Reo inter	-0.115	77.1	35	35	27
Globo inter, Ammo inter	0.792	2.9	35	35	1
Globo inter, Bathy inter	1	2.9	35	35	1
Globo inter, Reo inter	0.354	14.3	35	35	5
Ammo inter, Bathy inter	0.729	2.9	35	35	1
Ammo inter, Reo inter	0.635	5.7	35	35	2
Bathy inter, Reo inter	1	2.9	35	35	1
sw monsoon					
Uvi mons Bol mons	0.021	28.6	35	35	10
Uvi mons, Globo mons	0.833	2.9	35	35	1
Uvi mons, Ammo mons	1	2.9	35	35	1
Uvi mons, Bathy mons	1	2.9	35	35	1
Uvi mons, Reo mons	1	14.3	35	35	1
Bol mons, Globo mons	0.156	2.9	35	35	5
Bol mons,Ammo mons	1	2.9	35	35	1
Bol mons, Bathy mons	1	2.9	35	35	1
Bol mons, Reo mons	0.99	2.9	35	35	1
Globo mons, Ammo mons	1	2.9	35	35	1
Globo mons, Bathy mons	1	2.9	35	35	1
Globo mons, Reo mons	0.927	2.9	35	35	1
Ammo mons, Bathy mons	0.802	2.9	35	35	1
Ammo mons, Reo mons	0.979	2.9	35	35	1
Bathy mons, Reo mons	0.229	8.6	35	35	3
seasonal comparison of each species					
Uvi inter, Uvi mons	0.24	5.7	35	35	2
Bol inter, Bol mons	0.646	2.9	35	35	1
Globo inter, Globo mons	-0.219	91.4	35	35	32
Ammo inter, Ammo mons	1	2.9	35	35	1
Bathy inter, Bathy mons	0.052	31.4	35	35	11
Reo inter, Reo mons	0.875	2.9	35	35	1

Table 11. 300 m. Comparison of bacterial biomarker groups (Mol %) in six dominant species of Foraminifera during each season sampled. (see Chapter 5)

Uvigerina* ex. gr. *semiornata

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
140-m intermonsoon, 140-m monsoon	1	2.9	35	35	1
300-m intermonsoon, 300-m monsoon	0.906	2.9	35	35	1
140-m intermonsoon, 300-m intermonsoon	0.906	2.9	35	35	1
300-m monsoon, 140-m monsoon	0.792	2.9	35	35	1

Table 12. 300 m. Comparison of percentage composition (Mol %) of fatty acids in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites during each season sampled. (see Chapter 5)

Groups observed	R Statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number observed
Polyunsaturated Fatty acids (PUFAs)					
140-m intermonsoon, 140-m monsoon	0.427	14.3	35	35	5
140-m intermonsoon, 300-m intermonsoon	0.219	11.4	35	35	4
140-m monsoon, 300-m monsoon	-0.052	2.9	35	35	1
300-m intermonsoon, 300-m monsoon	0.938	2.9	35	35	1
bacteria					
140-m intermonsoon, 140-m monsoon	-0.125	62.9	35	35	22
140-m intermonsoon, 300-m intermonsoon	-0.052	48.6	35	35	17
140-m monsoon, 300-m monsoon	0.219	14.3	35	35	5
300-m intermonsoon, 300-m monsoon	0.24	5.7	35	35	2
zooplankton					
140-m intermonsoon, 140-m monsoon	0.583	2.9	35	35	1
140-m intermonsoon, 300-m intermonsoon	0.5	2.9	35	35	1
140-m monsoon, 300-m monsoon	0.021	37.1	35	35	13
300-m intermonsoon, 300-m monsoon	0.125	8.6	35	35	3
Algae					
140-m intermonsoon, 140-m monsoon	0.083	31.4	35	35	11
140-m intermonsoon, 300-m intermonsoon	0.073	37.1	35	35	13
140-m monsoon, 300-m monsoon	0.594	2.9	35	35	1
300-m intermonsoon, 300-m monsoon	0.469	2.9	35	35	1

Table 13. 300 m. Comparison of fatty acid biomarker groups (Mol %) of fatty acids in *Uvigerina* ex. gr. *semiornata* at the 140-m and 300-m sites during each season sampled. (see Chapter 5)

Groups observed	R statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number Observed
		Level P (%)			
t=0, t=2 days	0.906	2.9	35	35	1
t=0, t=5 days	1	2.9	35	35	1
t=2 days, t=5 days	1	2.9	35	35	1

Table 14. ANOSIM results for the fatty acid data (average quantity) of *Uvigerina* ex. gr. *semiornata* from shipboard ^{13}C-labelled diatom feeding experiments, sampled at t=0, t=2 days and t=5 days (see Chapter 6 and Appendix C)

Groups observed	R statistic	Significance Level P (%)	Possible Permutations	Actual Permutations	Number Observed
		Level P (%)			
t=0, t=2.5 days	0.583	5.7	35	35	1

Table 15. ANOSIM results for the fatty acid data (average quantity) of *Uvigerina* ex. gr. *semiornata* from *in situ* ^{13}C-labelled diatom feeding experiments, sampled at t=0 (natural), and t=2.5 days (see Chapter 6 and Appendix C)

2. 2 sample t-test assuming unequal variance

The 2 sample t-test (assuming unequal variance) was conducted in excel.

Values of P < 0.05 indicate a significant difference (grey highlighted values)

	Probability (P)
Allogromiid sp. 1	0.780872253
Allogromiid sp. 5	1
Bathysiphon sp. nov. 1	0.10183797
Hyperammina sp. nov. 1	0.347557663
Lagenammina arenulata	0.814575091
Psammosphaerid sp. 1	0.215036147
Pelosina sp. 1	0.752926814
Saccamminid sp. 1	0.831896843
Ammodiscus aff. *cretaceus*	0.178284932
Reophax bilocularis	0.039343975
Reophax sp.1	0.544501874
Amphicoryna aff. *scalaris*	0.278319356
Baggina philippinensis	0.391002218
Bolivina aff. *dilatata*	0.005323372
Cancris auriculus	0.071552251
Cassidulina laevigata	0.481546965
Cibicides sp. 1	0.215857505
Dentalina aff. *flintii*	1
Globobulimina cf. *G. pyrula*	0.508225332
Laevidentalina aphelis	0.67369441
Lenticulina sp. 1	0.730380442
Neolenticulina variabilis	0.537440344
Nodosaria aff. *pyrula*	0.391002218
Quinqueloculina aff. *venusta*	0.215169942
Saidovina amygdalaeformis	0.290794958
Saracenaria italica	1
Uvigerina ex. gr. *semiornata*	0.009538129
Indeterminate attached	0.391002218
Total live (per sample 25.5 cm2)	0.011343452

Table 19. Results from a 2 sample t-test, assuming unequal variance to test the significance in differences between the total live abundance of individual species from the spring intermonsoon to the SW monsoon. (see Chapter 4 and Appendix C).

	Probability (P)
Ammodiscus aff. *cretaceus*	0.001387453
Bathysiphon sp. 1	0.028813314
Reophax dentaliniformis	0.396729464
Bolivina aff. *dilatata*	0.584028409
Globobulimina cf. *G. pyrula*	0.011400602
Uvigerina ex. gr. *semiornata*	0.006466386

Table 20. Results from a 2 sample t-test, assuming unequal variance to test the significance in differences between average total quantity of fatty acid in 6 species of foraminifera between the spring intermonsoon and monsoon. Data values where $P < 0.05$ indicate a significant change in the average total quantity of fatty acid between seasons and are highlighted in grey. (see Chapter 5)

	t=0 to t=2day	t=2 day to t=5 day	t=0 to t=5 days
14:0	0.019058393	0.081512275	5.02722E-05
14:1	0.062035891	0.01298262	0.054581572
15:0			
16:0	0.120314277	0.003383211	0.002827925
16:1(n-9)			
16:1(n-7)			
16:1(n-5)			
16:2(n-3)	0.107741855	0.063800663	0.100163534
16:3(n-3)	0.001764281	0.000622114	0.000392104
17:0			
17:1			
16:4(n-1)	0.356231777	0.134057832	0.172342535
18:0	0.672650218	0.237363844	0.301201667
18:1(n-9)	0.412550142	0.000900634	0.000426614
18:1(n-7)	0.020948247	0.032677748	0.013868801
18:2(n-6)	0.024127576	1.53316E-05	1.13588E-05
18:3(n-6)	0.013622779	0.105783866	0.271367843
18:3(n-3)	0.128334925	0.522820919	0.116932186
18:4(n-3)	0.532480761	0.390131631	0.287187056
20:0			
20:1(n-9)			
20:1(n-7)			
20:4(n-6)	0.003868361	0.000126477	0.000332456
20:4(n-3)			
20:5(n-3)	0.05185008	0.01244551	0.00749824
22:0			
22:1(n-11)			
21:5(n-3)			
22:5(n-3)			
22:6(n-3)	0.087000293	0.000305463	0.000101242
Total	2.04447E-05	3.81497E-05	3.44867E-05

Table 21. 2 sample t-test results from a 2 sample t-test, assuming unequal variance to test the significance in differences between average total quantity of fatty acid in *Uvigerina* ex. gr. *semiornata* during a shipboard feeding ^{13}C-labelled diatom feeding experiment, sampled at t=0, t=2 days and t=5 days (see Chapter 6 and Appendix C)

	t=0 to t=2.5 days
14:0	0.017881867
14:1	0.905027472
15:0	
16:0	0.169497849
16:1(n-9)	
16:1(n-7)	
16:1(n-5)	
16:2(n-3)	0.517496646
16:3(n-3)	0.020738629
17:0	
17:1	
16:4(n-1)	0.630296784
18:0	0.803858516
18:1(n-9)	0.403152809
18:1(n-7)	0.248262383
18:2(n-6)	0.784932766
18:3(n-6)	0.544343042
18:3(n-3)	0.425107565
18:4(n-3)	0.005269342
20:0	
20:1(n-9)	
20:1(n-7)	
20:4(n-6)	0.37973716
20:4(n-3)	
20:5(n-3)	0.085487482
22:0	
22:1(n-11)	
21:5(n-3)	
22:5(n-3)	
22:6(n-3)	0.133123167
Total	0.013835243

Figure 22. Results from a 2 sample t-test, assuming unequal variance to test the significance in differences between average total quantity of fatty acid in *Uvigerina* ex. gr. *semiornata* during an *in situ* feeding ^{13}C-labelled diatom feeding experiment from natural samples (t=0) to the endpoint (t=2.5 days) (see Chapter 6 and Appendix C)