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FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

National Oceanography Centre
School of Ocean and Earth Sciences

Benthic protozoan community attributes in relation to environmental gradients in the Arabian Sea

By

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Para os meus pais,
Manuel Jorge e Maria Manuela

e avós,
Alexandra, Elísio, Manuel e Marília

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS
NATIONAL OCEANOGRAPHY CENTRE
SCHOOL OF OCEAN AND EARTH SCIENCES

Doctor of Philosophy

BENTHIC PROTOZOAN COMMUNITY ATTRIBUTES IN RELATION TO ENVIRONMENTAL GRADIENTS IN THE ARABIAN SEA

By Ana Aranda da Silva

"Live" (stained) and dead macrofaunal (>300 μm fraction) foraminifera in multicorer samples (0-1 cm and 0-5 cm layers) were analysed at six stations along a transect (100-3400 m water depth) across the Oman margin (Arabian Sea) oxygen minimum zone (OMZ). Very high abundances (2858 per 25.5 cm^2), dominated by *Uvigerina* ex. gr. *semiornata*, were found in the upper 100 m. The 850 m site also had elevated abundances. These peaks probably represented upper and lower OMZ boundary edge effects, respectively. A total of 199 live species was recognized. Diversity was depressed between 100 m and 850 m and relatively higher at the 1250 m and 3400 m sites. Vertical distribution in the sediment reflected responses found across the horizontal gradient, with species concentrated in the top sediment where bottom-water oxygen concentration was low and distributed more evenly through the sediment where concentration was higher. In general foraminifera and metazoan responded similarly to oxygen and food availability, except that the lower boundary of edge effect was located at a shallower depth (700 m) for the metazoans. Live:dead ratios of foraminifera increased with water depth. The second part of the thesis concerns *Gromia*, a large marine protist with filose pseudopodia and an organic test that is abundant in the bathyal Arabian Sea. Deep-water *Gromia*-like morphospecies were discovered in the 1990's but their relation to shallow-water species was not established. Little is known about gromiid diversity, reflecting the fact that these relatively featureless protists have few characters useful for species identification. Consequently, ultrastructural and molecular techniques were used to examine gromiid diversity on the Oman and Pakistan margins of the Arabian Sea (water depths 1000-2000 m). In total, 27 deep-sea gromiid sequences of the SSU rDNA gene and 6 sequences of the ITS rDNA region were obtained. The data confirmed that *Gromia*-like protists from the bathyal deep sea are related to shallow-water gromiids. Among Arabian Sea *Gromia*, seven lineages were identified based on molecular evidence. Five of them form a monophyletic group branching as a sister group to shallow-water species. Four lineages can be defined morphologically, while grape-like morphotypes include 3 lineages that cannot be distinguished morphologically. Each lineage probably represents a separate species, implying that deep-sea gromiid diversity is higher than indicated by their simple morphology. Morphological analysis adds 2 more species, giving a total of 9 deep-sea gromiid species, adding considerably to the number of known marine gromiids, only three of which are currently described.

Declaration of Authorship

I, **Ana Aranda da Silva**, declare that the thesis entitled **Benthic Protozoa community attributes in relation to environmental gradients in the Arabian Sea** 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;
- Chapter 4 is currently in press as
  Aranda da Silva A, Pawlowski J, Gooday A (in press) High diversity of deep-sea *Gromia* from the Arabian Sea revealed by small subunit rDNA sequence analysis. Marine Biology

Signed: …….

Date: …….

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Chapter 1

Introduction

The increase in the extent of bottom water anoxia around the globe is of great importance to science, with possible commercial implications, particularly for the fishery and petroleum industries. A large percentage (80%) of the worlds' petroleum was formed in oxygen-depleted settings. These areas have also been important in the geological history of the oceans and have received considerable attention in paleoceanography (Tyson 1991). Hypoxic and anoxic environments have existed through geological time and were particularly extensive in the deep sea during some periods of earth's history, for example the Cretaceous (Rogers 2000). Estimates of dissolved oxygen levels in ancient oceans can contribute towards understanding the history of ocean circulation, climate, causes of extinctions, and the evolution of marine organisms (Kaiho 1994; Kaiho 1999). Data on dissolved oxygen below 0.2 ml/l (hypoxia) from around the globe, collected between 1905 and 1982 and compiled by the National Oceanographic Data Centre (NODC), Washington, DC, were analysed by Kamykowski and Zentara (1990), in order to obtain information on oxygen distribution to the present day. More recently, a compilation of data on the distribution of areas where bottom-water oxygen concentrations are less than 0.5 ml/l is presented by Helly and Levin (2004). Clearly, understanding how complex marine systems function, and how hypoxia develops in the present day ocean, may reveal how these systems behaved in the past and also how they may behave in future oceans (Kamykowski and Zentara 1990; Helly and Levin 2004).

Biologically, it is important to evaluate the effects of oxygen depletion while at the same time trying to separate possible natural increases from anthropogenic increases due to pollution (Alve 2000). One focus of this thesis concerns the effects of reduced oxygen concentrations on the composition and structure of foraminiferal assemblages. These stressful conditions arise in marine and freshwater environments when organic enrichment leads to the development of large populations of organisms which consume dissolved oxygen, or when the oxygen is not replaced because of bottom-water stagnation, or a combination of all these factors. Oxygen depletion in the bottom water inevitably leads to oxygen depletion in the underlying sediment pore water, so generally there is a close relationship between the two (Hermelin 1992). However, this is not always the case. For example, along a bathymetric transect in the Bay of Biscay, the penetration of free oxygen varied from 8 mm to 6 cm and was influenced by the rate of oxygen

consumption by organisms within the sediment rather than in the bottom water, where the level of oxygenation remained constant (Fontanier et al. 2002).

1.1. Terminology

Oxygen concentration values can be expressed in several different ways, the most common of which are ml/l or μM/kg. The conversion between the two units is roughly 1 ml/l = 45.6 μM/kg, but it depends on salinity and temperature (Bernhard, 2002 pers. comm.). A variety of terms has been used to describe different degrees of oxygen depletion (Tyson 1991; Sen Gupta and Machain-Castillo 1993; Bernhard and Sen Gupta 1999). In this thesis, the following terminology will be adopted. Semantically, anoxia means no oxygen - an, prefix from the Greek that means without or not (Brown 1979) - and the term is only applied to oxygen values equal to zero. The term "anaerobic" is synonymous with anoxic. The word aerobia is used as a biological term referring to respiration using oxygen, even in the case of marine organisms, although the word aerobia comes from aeros, a prefix that in Greek means air. An environment is referred to as oxic, when oxygen values are equal to or exceed 1 ml/l (Tyson 1991; Bernhard and Sen Gupta 1999). Any other values between zero and 1 ml/l characterizes the environment as dysoxic - dys, prefix from the Greek that means with difficulty (Brown 1979). The term dysaerobic is synonymous with dysoxic. Bernhard and Sen Gupta (1999) introduced the term microxic for concentrations ranging from 0 – 0.1 ml/l. The term hypoxic is also widely used in the same context as microxic or dysoxic, but with the implication that conditions are physiologically stressful (Levin et al. 2000). In some cases, hypoxia has been defined as oxygen concentrations below 0.2 ml/l (Kamykowski and Zentara 1990), although the level at which oxygen depletion becomes stressful varies from species to species. Oxygen minimum zones (OMZs) are defined as zones where oxygen concentration is below 0.5 ml/l.

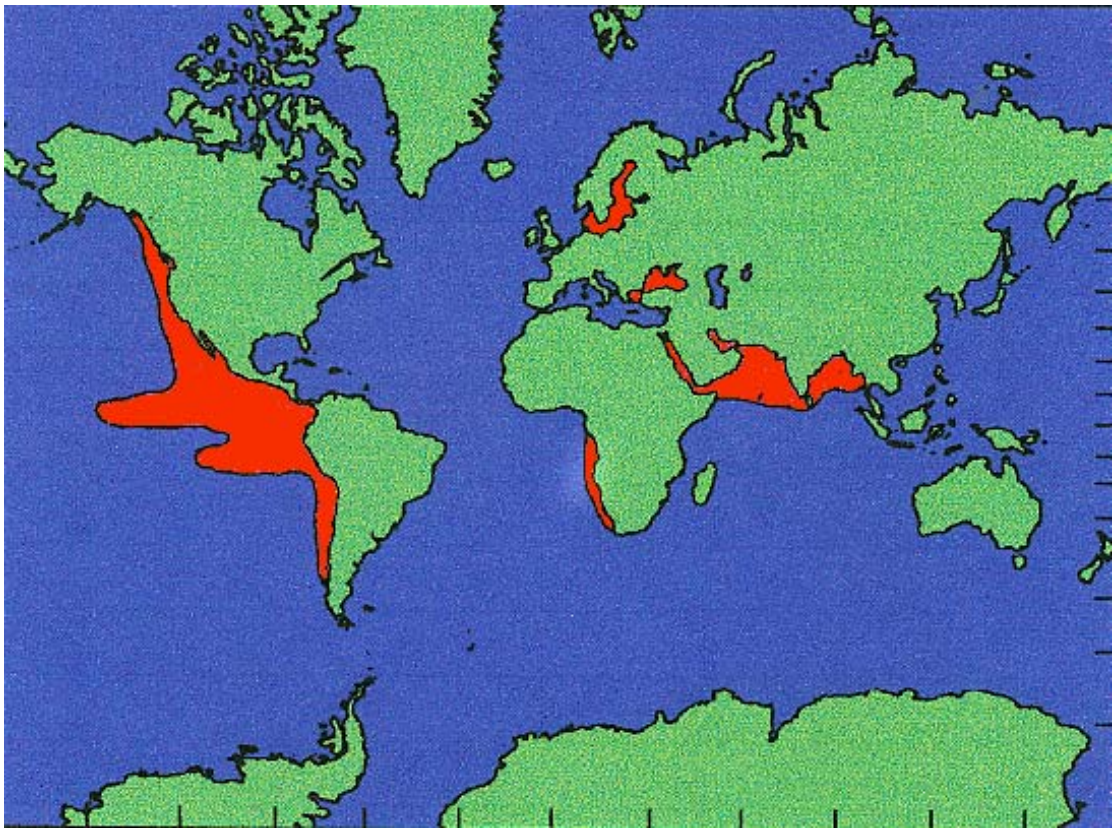
1.2. Modern marine hypoxic environments

Marine hypoxia (implying stressful conditions) occurs across the globe: in the Baltic Sea, Black Sea, Gulf of Aden, Arabian Sea, Bay of Bengal, Philippine region, northwest Pacific margin, eastern Pacific, Norwegian fjords and southwest African region (Figure 1.1) (Kamykowski and Zentara 1990; Helly and Levin 2004). Hypoxia within offshore waters at higher latitudes in both hemispheres is most pronounced during the summer season (Kamykowski and Zentara 1990). More generally, low oxygen environments (whether stressful or not) occur in areas with very high productivity, areas such as silled basins and fjords where natural circulation is restricted (Alve 2000), and environments such as marshes, methane "cold" seeps and oxygen minimum zones (Bernhard 1996). Recently, there seems to be an increase in the occurrence of

anthropogenically organic-enriched, polluted areas where there are major sewage outlets, particularly near large cities (Bernhard 1996; Coccioni 2000; Van der Zwaan 2000; Diaz and Rosenberg 2001).

OMZs are the focus of this thesis. These are midwater zones of oxygen depletion, caused by high levels of oxygen consumption that impinges on the seafloor and create strong oxygen gradients that strongly affect benthic faunas. The high levels of oxygen consumption are linked to enhanced surface primary productivity, often associated with upwelling. Seafloor OMZs typically occur on the outer shelf and upper slope and where seamounts intercept midwater OMZs in open ocean areas (Wishner et al. 1990). They occur throughout the world, namely off the west coast of North and South America between the latitudes of 50ºN and 30ºS, on oceanic seamounts in the Pacific Ocean, the southwest coast of Africa, the Arabian Sea and the Bay of Bengal (Helly and Levin 2004).

Figure 1.1 Map of the world showing locations where hypoxia occurs. Adapted from (Kamykowski and Zentara 1990).



1.3. The Arabian Sea OMZ

Oceanographically, the Indian Ocean is an area of great significance and interest. While the southern part is relatively stable, the northern part (the Arabian Sea) is characterised by highly

seasonal, monsoon-related upwelling, which is intensely developed off Oman and, to a lesser extent, off Somalia. In the Arabian Sea, the upwelling gives rise to high surface primary production, most of which escapes consumption by zooplankton and is exported to the bathyal seafloor. This high organic matter loading leads to the development of an intense OMZ. Where the OMZ intercepts the seafloor, between 400 m and 1000 m depth off Oman, it creates a strong oxygen gradient that profoundly affects the abundance, diversity and taxonomic composition of the benthic fauna (Gage et al. 2000). Dissolved oxygen concentrations are generally low in subsurface waters in the Arabian Sea. The surface waters are re-oxygenated directly from the atmosphere, but beneath, mixing is limited due to the intense tropical thermocline. There are two sources of midwater entering the Arabian Sea; Red Sea water enters through the Strait of Bab-el-Mandeb and the oxygen-depleted Persian Gulf water through the Strait of Hermuz (Swallow 1984). The sediment depositional rates vary between 2.45 and 13.21 cm/kyr (Hermelin and Shimmield 1995).

The isolation and stagnation of North Indian Intermediate Water and the lack of horizontal advection together with the high productivity of the northern Indian Ocean cause the development of a layer of extremely low oxygen concentration, extending from 200 to more than 1200 m depth with oxygen values less than 1 ml/l everywhere north of 3°N. A deep oxygen minimum directly corresponds to this huge layer of very low oxygen content. The lowest oxygen concentration in the Indian Ocean OMZ is found in the two northern bays, the Arabian Sea and the Bay of Bengal. The advection of water of moderate oxygen concentration from the Pacific Ocean through the Indonesian waters may explain enhanced oxygen depletion. Morphologically, the Indian Ocean is landlocked in the north and extends only to one region of cold climatic region, the Antarctic. It has therefore an asymmetrical hydrographic structure and circulation, which is reflected in the development of extremely low oxygen concentrations in the Arabian Sea and Bay of Bengal. The landmass of Asia also affects the ocean by causing a six-month change in monsoonally-forced circulation leading to seasonal upwelling. In addition, high salinity water derived from the sea surface, intensified by the Red Sea and Persian Gulf high salinity waters, creates an intermediate layer of extremely high salinity that prevents further mixing of deep-water masses (Wyrtki 1973).

Seasonal monsoonal winds are also important for understanding the development of the Arabian Sea OMZ. The word ‘monsoon’ is derived from the Arab word meaning ‘winds that change seasonally’. The North-East Monsoon occurs during the northern winter, when the air over southern Asia is cooler and denser than the air over the ocean and therefore the surface atmospheric pressure is greater over the continent than over the ocean. This leads to a low-level northerly or north-easterly flow of air from the Asian landmass to south of the equator. After crossing the equator, the flow of air is turned to the left by the Coriolis force and converges with

the south-east Trades at about 10-20°S. As the year progresses, the Asian land mass heats up and the high pressure over southern Asia weakens. The South-West Monsoon starts in May/June, when a low has developed; suddenly the wind direction changes, and a southerly or south-westerly wind blows across the region until September (Open University 1989).

The surface circulation of the northern Indian Ocean changes seasonally in response to the monsoons. In the northern winter, during the North-East monsoon, there is a North and a South Equatorial current, as well as an Equatorial Counter-Current. In the northern summer, during the South-West monsoon, the flow in the North Equatorial Current reverses and combines with a weakened Equatorial Counter-Current. The South Equatorial Current is still present. Current flows are weaker during the South-West monsoon than during the north-east monsoon. There is also the reversal of the Somali Current. During the North-East Monsoon, the Somali Current flows to the south-west, but for the rest of the year it flows to the North-East. During the South-West Monsoon it becomes a major western boundary current. A particularly interesting aspect of the South-West Monsoon is the appearance over the western side of the ocean of an intense, southerly low-level atmospheric jet that plays an important role in the generation of the intense upwelling that occurs off Somalia during the South-West Monsoon. At the same time, upwelling occurs off Arabia, both along the coast where the north-easterly current diverges from it, and offshore in response to local cyclonic winds (Open University 1989). This monsoon-driven upwelling loads the area with high organic matter that stimulates phytoplankton growth. The resulting high rates of respiration in the upper column reduces oxygen concentrations resulting in the development of the OMZ.

The Arabian Sea OMZ was first discovered during the John Murray expedition in 1936 (Gage et al. 2000). It was the first known example of a deep-water oxygen minimum zone. Although found to be underlain by sediments that appeared azoic, the significance of this major oceanographic feature was not appreciated at the time and, furthermore, the detailed temperature, salinity and oxygen profiles obtained were never published (Rice 1986a; Rice 1986b).

1.4 Influence of hypoxia on marine benthic organisms

The first realization that an OMZ has a powerful effect on the deep-sea benthic community structure came in the 1960s, with the work of Sanders and his colleagues at the Woods Hole Oceanographic Institution (Sanders 1968; Sanders 1969). They studied benthic faunas of soft-bottom marine environments on the outer shelf and upper and lower slope in a number of different regions. Although the Bay of Bengal sites had high species diversity values, lowest

values were in the Arabian Sea, presumably reflecting the influence of the OMZ. Furthermore, a study of a transect off Walvis Bay, southwest Africa, an area of intense upwelling and consequent low bottom water oxygen, showed an inverse relationship between species diversity and oxygen saturation of the bottom water.

The majority of marine organisms require oxygen in order to survive. Within OMZs, hypoxia has an effect on many characteristics of the benthic fauna, notably the abundance, diversity and taxonomic composition. Although most bottom waters around the world contain fairly high levels of oxygen, there is a recent increase in areas of relatively low oxygen concentrations, which has consequences for the ecosystems in these locations. Some marine organisms, however, thrive in these conditions, particularly where there is high food availability, and others even live in areas close to anoxia, by using compounds other than oxygen as electron receptors (Diaz and Rosenberg 1995). For many benthic eukaryotes, the critical oxygen concentration, where it becomes limiting, is probably around 0.4 –0.5 ml/l (Levin et al. 2000). Below this value, the community structure changes, species diversity decreases, higher abundances lead to an increase in dominance, and the overall taxonomic composition changes.

The oxygen concentration separately has an effect on the different components of benthic community. Generally, megafauna is the most sensitive group, and the macrofauna is less tolerant than the meiofauna. Within each size group (meiofauna, macrofauna and megafauna) there are also differences between major taxa. In general, polychaetes are the most tolerant macrofaunal group, nematodes and foraminiferans the most tolerant meiofaunal groups. Metazoans with calcareous hard parts (e.g. crustaceans and echinoderms) are often less tolerant than those without such structures (Rhoads and Morse 1971).

The measurement of oxygen concentration is important. When comparing the tolerance of organisms to oxygen concentration, it is important to be clear about where oxygen concentrations were measured. Generally, oxygen concentration is measured in the bottom water. This is acceptable for organisms with direct contact to the bottom water but not for small infaunal organisms exposed to sediment pore waters, because oxygen concentration may vary within the sediment. Ideally, oxygen profiles within the sediment porewater should be determined using an oxygen electrode (Schönfeld 2001). Oxygen values decrease with depth in the sediment; however, there are a number of factors that may disturb this pattern. Bioturbation by motile organisms may stir the sediment and the existence of sulphur-oxidizing bacteria may allow oxygen to penetrate further within the sediment (Schmaljohann et al. 2001).

1.4.1 Bacteria

Thioploca is a genus of multicellular, colourless, sulphide-oxidizing, nitrate-reducing, gliding, filamentous benthic bacteria that inhabit freshwater and marine sediments (Gallardo et al. 1998; Jorgensen and Gallardo 1999). *Beggiatoa* is phylogenetically close to *Thioploca* and can only be distinguished morphologically by the absence of a sheath surrounding the bundle of filaments (Schmaljohann et al. 2001). These filamentous bacteria occur in areas of upwelling and high productivity where hypoxic waters at intermediate depths impinge on the shelf (Gallardo et al. 1998). In some cases, they possess a large liquid vacuole used to store nitrate, which acts as an electron receptor for sulphide oxidation. *Thioploca* sp. appears to have a lower tolerance towards oxygen and sulphide than *Beggiatoa* sp. Within low oxygen environments, the availability of nitrite seems to be an overriding ecological factor for *Thioploca*. *Thioploca* forms 1-2 cm thick mats that incorporate polychaete tubes and pelletized sediments to create a form of microhabitat of porous, spongy texture, which is permeable to current-driven advective porewater flow. This flow filaments allows other taxa less tolerant of low oxygen to exist. In the Arabian Sea, sheaths with 30-40 μm wide *Thioploca* were found to be abundant in sediments within the core of the OMZ (400 m depth) (Jorgensen and Gallardo 1999).

1.4.2 Foraminiferans

Foraminiferans are eukaryotic, unicellular, testate protists characterized by an extendable granuloreticulose pseudopodial net used in feeding, locomotion and other life processes (Travis and Bowser 1991). They are ubiquitous in marine environments and also occur in freshwater environments. Most, although not all species have a shell (test). One species has recently been described from terrestrial soils (Meisterfeld et al. 2001). This group of organisms seem to be particularly tolerant of low oxygen, with some species thriving in such environments and developing very high population densities (Phleger and Soutar 1973; Bernhard 1986; Gooday 1986; Cedhagen 1993; Gooday 2003).

There are three basic test types within the foraminiferans: organic tests, agglutinated tests and calcareous tests. These groups exhibit different degrees of tolerance to low oxygen concentrations. Calcareous foraminiferans seem to be more tolerant of low oxygen environments than either agglutinated or organic-walled foraminiferans (Moodley et al. 1997; Gooday et al. 2000).

Foraminiferans from low oxygen environments, and specifically from the deep-water, OMZs, will be described in section 1.5 below.

1.4.3 Meiofauna

Generally, meiofaunal metazoan are more tolerant of low oxygen concentrations than macrofaunal metazoan taxa. Within the meiofauna, nematodes are the most abundant, and sometimes virtually the only metazoan taxa in OMZs. A study by Cook et al. (2000) showed that the abundance of nematodes is not affected by bottom-water oxygen concentrations. It has been suggested by Levin et al. (1991) that food supply, or biological interactions between larger organisms and meiofaunal might override oxygen concentrations in determining nematode population densities. Very low oxygen concentrations generally have a positive effect on nematode density by reducing predator and competitor densities and therefore enhancing good availability and quality (Neira et al. 2001).

When present, taxa other than nematodes (such as harpacticoid copepods, nauplii, polychaetes, gastrotriches, kinorynchs, ostracods) may show different patterns of distribution. A study by Neira et al. (2001a) showed that nematode densities decreased, while other taxa densities actually increased, down slope along a transect, beneath the OMZ in the south-eastern Pacific.

1.4.4 Macrofauna

Unlike the meiofauna, macro and megafauna are often reduced both in individual and particularly in species numbers in OMZs. Eukaryote macrofaunal communities in low oxygen environments are usually dominated by annelids (mainly polychaetes and some oligochaetes) followed by molluscs (almost exclusively aplacophorans gastropods and bivalves) and crustaceans (almost exclusively amphipods) (Diaz and Rosenberg 1995; Gallardo et al. 1995; Levin and Edesa 1997; Levin and Gage 1998; Gutierrez et al. 2000; Levin et al. 2000; Oliver 2001). Filamentous bacteria, in particular *Thioploca* species, dominate the prokaryote macrofaunal community in low oxygen environments (Gallardo et al. 1995).

Generally, oxygen deficiency limits macrofaunal abundance, biomass and species richness (Gutierrez et al. 2000). Species richness, diversity and evenness are lower and dominance is higher within the OMZ (Levin et al. 2000). Density and biomass are both higher within the OMZ. There is an oxygen threshold (0.45 ml/l), above which oxygen effects on macrobenthic community diversity are minor relative to organic matter influence, but below which oxygen becomes a critical factor. Oxygen at low concentrations has more influence on species richness, while organic carbon regulates the distribution of individuals among species (community evenness) (Levin and Gage 1998).

In order for benthic invertebrates to tolerate permanent hypoxia, there is powerful evolutionary forcing for morphological adaptations aimed towards enhancing oxygen diffusion by increasing body area/mass ratio (Lamont and Gage 2000). Polychaetes exhibit morphological adaptations to low oxygen in the form of elongate, filamentous branchiae (Levin et al. 2000). A significant trend showing an increase in respiratory area relative to body size, resulting from an enlargement in size and branching of the branchiae relative to similar species living in normal levels of dissolved oxygen, was observed in two spionid species with decreasing depth and oxygen concentration within the Arabian Sea OMZ (Lamont and Gage 2000). These within-species differences in size and number of branchiae may be direct responses by the phenotype to the intensity of hypoxia. Alternatively, they may either reflect a pattern of differential post-settlement selection among a highly variable genotype, or represent early genetic differentiation among depth-isolated populations (Lamont and Gage 2000). These findings have implications for taxonomic studies of polychaetes since species descriptions normally utilise the number and morphology of branchiae (Lamont and Gage 2000). Studies have also shown an increase in the respiratory apparatus in crabs, often the largest organisms inhabiting low-oxygen environments. A study by Astall et al. (1997) also showed that two of the decapods species exposed to temporary hypoxia to possessed larger branchiae than the other four (Lamont and Gage 2000).

1.4.5 Megafauna

Megafauna are generally rare within the core of the OMZ. To a certain effect, this may reflect the fact that most megafauna taxa (echinoderms, molluscs and large crustaceans) have calcareous shells which are difficult to maintain under low oxygen conditions. There are some exceptions, however in particular, the gastropod *Tibia delicatula* Melvill, 1881 is reported to be common in the core of the Arabian Sea OMZ (Olabarria et al. 2003). Another gastropod, *Mitrella permodesta* (Dall 1890), occurs in the centre of the Santa Barbara Basin where bottom-water oxygen concentrations are less than 0.1 ml/l (Bernhard et al. 2003).

Nevertheless, the greatest concentration of megafaunal animals are found around the boundaries of OMZs where oxygen concentration start to rise. Here, some megafaunal species may be abundant, as in the Arabian Sea OMZ, at around 1000 m, where large ophiuroids are abundant (Levin et al. 2000). Generally, echinoderms, which have calcareous skeletons, are difficult to maintain under low-oxygen conditions. However, Thompson noted abundant calcareous taxa within the central California OMZ at oxygen levels equal or greater than 0.3 ml/l (Thompson et al. 1985). Bett (1995) also found very high abundances of the spider crab *Encephaloides armstrongi* Wood-Mason, 1891 around 1000 m in the Arabian Sea OMZ. The abundance of megafauna around the lower boundaries of OMZs may reflect an “edge effect” whereby a release from severe oxygen depletion combined with an abundance of food leads to the

development of large population densities. This edge effect was first reported by Mullins et al. (1985). Vertebrates are usually absent from OMZs; fish catches are negatively correlated with the occurrence of filamentous bacteria and positively correlated with macrobenthic biomass. Benthic and demersal fish biomass increase above and below hypoxia (Diaz and Rosenberg 1995).

Echinoderms occur in small numbers but as a group are most abundant along the upper edge of the OMZ. Biomass and density of polychaetes decrease where echinoderms are abundant. Asteroids are predominant where sediments are coarse and firm, with highest abundance along the upper edge. In contrast, echinoids are most abundant near the lower edge of the OMZ. Ophiuroids are most abundant along the lower edge of the OMZ, increasing with increasing oxygen concentrations and water depth. The core of the OMZ is devoid of echinoderms. There is a distinct depth zonation for asteroids, echinoids and ophiuroids, being influenced by grain size and oxygen concentrations (Thompson et al. 1985).

A strong megafaunal zonation occurs where seamounts penetrate a midwater OMZ. An excellent example is provided by Volcano 7 in the Eastern Pacific (Wishner et al. 1990). The uppermost summit which is situated within the core of the OMZ has the lowest densities, with gradual increases in a transition zone. Highest numbers occur between 780 and 1000 m, with a maximum at 800-810 m where oxygen concentrations start to increase. Below 1000 m, average megafaunal abundances never exceed 0.5 per m^2 (Wishner et al. 1990; Wishner et al. 1995).

1.5 Foraminiferans from low oxygen environments

Foraminiferans are an important component of modern benthic communities. There are 3,620 genera according to Loeblich and Tappan (1987) and their densities can reach $10^6/m^2$ (Culver 1993). These protists are often major components of meiofauna in terms of abundance and biomass on both the continental shelf and in the deep sea (Gooday 1986; Gooday et al. 1992), in some cases accounting for over 50 % of the eukaryotic biomass. They play an important role in ecosystem functioning and biogeochemical cycling, modifying the sediment structure, providing refuges and substrates for metazoans and other foraminiferans, influencing particle depositions on the seafloor, preventing larval settlement, and in some cases out-competing metazoans for scarce sources (Gooday 1994). They possess a test that is either organic, agglutinated or calcareous. Foraminiferans are also the most abundant benthic organisms and because they possess a test, they are preserved in the deep-sea fossil record and provide powerful tools for making paleoceanographic reconstructions.

Distributional studies based on counts of rose Bengal stained foraminiferans suggest that they are often very abundant in low oxygen environments (e.g. Bernhard and Sen Gupta 1999). However, there are problems involved in recognising "live" specimens. For example, studies by Bernhard (1988) on foraminiferans from low oxygen settings, revealed that specimens that had been dead for weeks, still stained when treated with rose Bengal. Furthermore, Corliss and Emerson (1990) also suggested that protoplasm can persist for months or even years after death, even in oxic settings. This implies that stained foraminiferans may not accurately represent the living community. To overcome this problem, Bernhard and colleagues (Bernhard and Reimers 1991; Bernhard 1992; Bernhard 1993; Bernhard and Alve 1996), conducted a series of studies using biochemical assays to determine adenosine triphosphate (ATP) concentrations, a method originally developed by DeLaca (1986). High levels of ATP, together with low oxygen concentrations measured using microelectrodes, have confirmed that foraminiferans do inhabit low oxygen environments. However, Bernhard (1992) found that foraminiferal numerical densities determined by the ATP method were significantly lower than those determined using rose Bengal, implying that density values will depend on the method employed. In Bernhard's study, an inverse correlation was observed between the density of foraminiferans determined using rose Bengal staining and bottom-water oxygen concentration, but there was no correlation with water depth or organic carbon content. On the other hand, densities based on the ATP method showed no correlation with bottom-water oxygen concentration, water depth or organic carbon content. Benthic foraminiferans are also found associated with *Beggiatoa* mats, suggesting that they can tolerate the presence of sulphides (Bernhard and Bowser 1996), which sometimes occur where oxygen levels are low and organic matter supply is high. These observations further confirm that foraminiferans do live in low oxygen settings.

When trying to assess the tolerance of foraminiferans to low oxygen environments, it is important to have an accurate *in situ* measure of oxygen concentration, as sediment surface oxygen concentration may not reflect oxygen concentrations within the sediment layers. Oxygen concentration generally decreases with sediment penetration, but where metazoans are abundant, the existence of burrows may allow deeper oxygen penetration. For example Langer et al. (1989) found that there are a number of microhabitats formed around macrofaunal burrows and tubes where higher concentrations of oxygen exist that may allow oxyphilic foraminiferans, intolerant of low oxygen, to survive in what appears to be a low oxygen environment. To overcome this problem, microelectrodes are the best available method to measure oxygen vertically within the sediment pore water in order to accurately determine oxygen concentrations within foraminiferal microhabitats (Revsbech and Jorgensen 1986).

Generally, dysoxic foraminiferal assemblages have high abundances of a few dominant species. This high dominance reflects the fact that few species are able to tolerate dysoxia. These

species, however, thrive because of high food availability. Moreover, macrofauna and megafauna generally are less abundant or absent from low oxygen environments, so foraminiferans have reduced predation and competition from other organisms. The most important factor shaping foraminiferal communities in low oxygen settings is an ongoing debate. The classical study by Phleger and Soutar (1973) on benthic foraminiferans from OMZs in the eastern Pacific debates which factor, either low oxygen or high food availability from high organic input, is responsible for the high foraminiferans standing stocks observed in low oxygen environments. They came to the conclusion that low oxygen concentrations eliminate macrofaunal predators and competitors of foraminiferans while the high concentration of organic matter (food) allows a few tolerant species to develop large populations. The resulting assemblages exhibit low species diversity, high abundance and dominance. The argument continues but food supply and dissolved bottom-water oxygen concentrations, two inversely related parameters, are now generally regarded as the main factors controlling the distribution pattern of modern benthic foraminiferans in dysoxic environments (Jorissen et al. 1995; Schmiedl et al. 1997; Gooday 2003).

There are general taxonomic trends among foraminiferans in relation to oxygen gradients. Calcareous foraminiferans, particularly rotaliids and buliminids, tend to survive better in low oxygen environments than soft-shelled species, and are often abundant (Jorissen 1999). This may be because the bilamellar test is composed of numerous crystals of elongate low-Mg calcite. But not all calcareous foraminiferans are abundant in these settings. In particular, miliolids are usually completely absent. These trends are illustrated by an experiment conducted by Moodley et al. (1997). In this microcosm study, sulphide was present after 53 days, and there was a drop in *Reophax* sp. (an agglutinated foraminiferan) numbers, suggesting intolerance to sulphide. These experiments also confirmed the higher tolerance to low oxygen of calcareous foraminiferans compared to agglutinated foraminiferans. However, some agglutinated taxa can withstand low oxygen and may even be abundant in such settings. For example, Bernhard et al. (1997) found abundant *Reophax gracilis* Kiär, *Saccammina longicoelis* (Wishner 1931), *Trochammina pacifica* Cushman, 1941, *Haplophragmoides columbiense* Cushman, 1925, *Spiroplectammina earlandi* (Parker 1952) and *Textularia schenki* Cushman and Valentine, 1930 (the last two found at lowest oxygen concentrations) in the Santa Barbara Basin. Kaminski et al. (1995) found *Bathysiphon filiformis* M. Sars, 1872, *Saccorhiza* sp. and *Marsipella* sp., agglutinated species, in the San Pedro and Santa Catalina Basins in the California Borderland where oxygen was 0.4 ml/l. Several agglutinated species were also reported by Gooday et al. (2000a) in the 10 top ranked species collected from the core of the Oman margin OMZ (O_2 ~ 0.13 ml/l). These included *Leptohalysis* sp., *Morulaeplecta* sp., *Trochammina* sp., *Bathysiphon* sp., *Textularia* and *Spiroplectammina* sp. Large agglutinated species are usually absent in low oxygen settings. However, *Pelosina arborescens* Pearcy, 1914, an erect tree-like species, is

common in anaerobic sediments from Kosterfjorden, Skagerrak (Cedhagen 1993) and is also abundant in the core region of the Pakistan margin OMZ (Gooday and Bowser 2005). Small organic-walled and agglutinated monothalamous foraminiferans are usually uncommon in OMZs, but some allogromiid and saccamminid species do occur (Gooday et al. 2000).

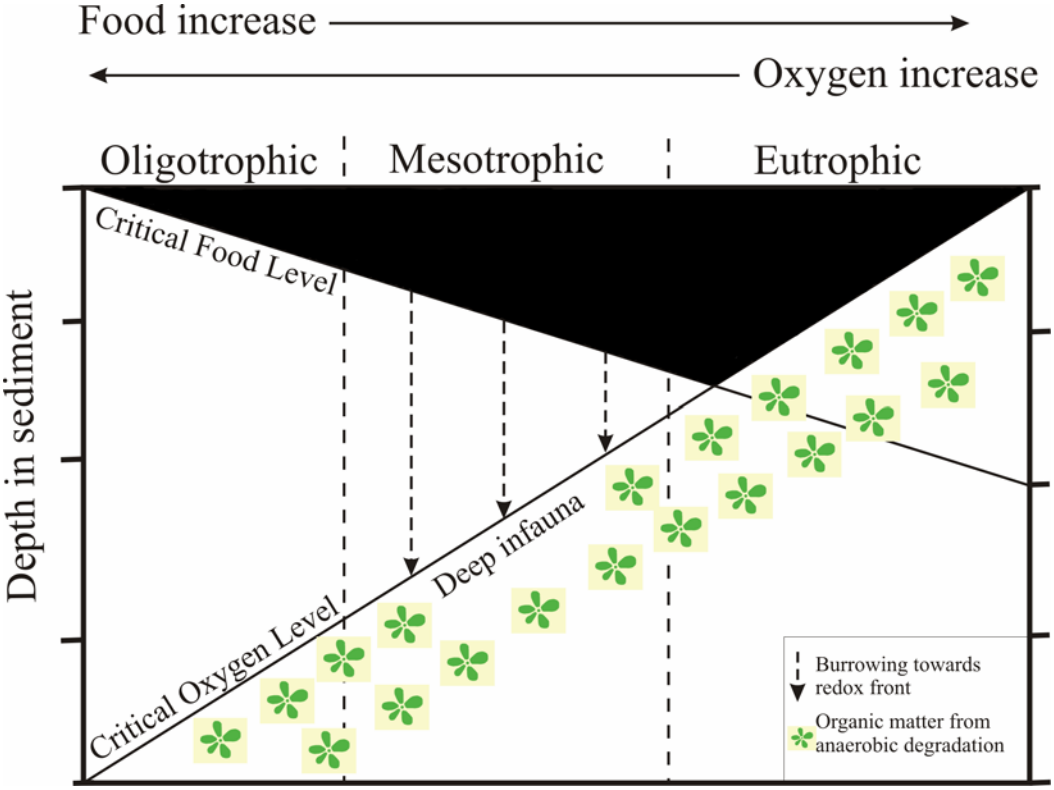
Typical low-oxygen taxa include the following genera: *Bolivina, Bulimina, Globobulimina, Uvigerina* and *Chilostomella* (Jorissen 1999). A study by Bernhard et al. (1997) looked at species distribution along an horizontal oxygen gradient and found the following progression of species with decreasing oxygen concentrations (from 0.02 to 0.5 ml/l): 1) *Uvigerina juncea* Cushman and Todd, 1941; 2) *Suggrunda eckisi* Natland, 1950; 3) *Bolivina argentea* Leutenegger and Hansen, 1979 and *Loxostomum pseudoberichi* Cushman; 4) *Trochammina pacifica*, *Buliminella tenuata* Leutenegger and Hansen, 1979 and *Bolivina seminuda* Cushman, 1919; 5) *Chilostomella ovoidea* Reuss, 1850 and *Spiroplectammina earlandi*; 6) *Nonionella stella* Cushman and Moyer, 1930, *B. seminuda*, *B. tenuata, S. eckisi* and a species resembling *S. earlandi*. Note that some species occur across the oxygen gradient at more than one station. *Uvigerina* is a genus that is often abundant in relatively low oxygen environments. For example, Hermelin and Shimmield (1990) found that *Uvigerina peregrina* Cushman, 1923 is related to areas of high organic matter fluxes and low oxygen content in the Northwest Arabian Sea. However, Schmiedl et al. (1997) reported that it avoids areas of extreme oxygen depletion in the North Atlantic Ocean, suggesting that the distribution of *Uvigerina peregrina* is not controlled by the dissolved oxygen content of the bottom water mass. Furthermore, Bernhard et al. (1997) found *Uvigerina* to be associated with high organic loading, but not to tolerate severe dysoxia. Paleoceanography studies reviewed by Corliss et al. (1986) also suggested that the dominance of *Uvigerina* species during glacial intervals reflected increased amounts of organic carbon at the sea floor compared to modern values.

Oxygen concentrations not only vary horizontal across OMZs but also vertically within the sediment. As a consequence, variations in foraminiferal assemblages with oxygen concentration of bottom water may be mirrored by variation in foraminiferal assemblages vertically in the sediment with reducing pore-water oxygen concentrations. Besides oxygen concentration, food availability, which is inversely proportional to oxygen, is an important factor to consider. The TROX model from Jorissen et al. (1995) demonstrates the three dimensional characteristics of foraminiferal assemblages in low-oxygen, organic-enriched environments (Figure 1.2).

In oxic environments, foraminiferans can live down to 10-15 cm depth within the sediment, with the vertical stratification of taxa reflecting species-specific microhabitat preferences (Corliss and Emerson 1990). Pore-water oxygen concentrations, sulphide levels and food availability are the factors known to determine how deep foraminiferans can live in the sediment

(Gooday 2003). Oxygen levels decrease with sediment depth and so does fresh organic matter, resulting in a decrease in the diversity and abundance of foraminiferans. Assemblages dominated by a few species are typical of high-organic flux and low oxygen environments. Low oxygen concentrations at the sediment surface generally means that oxygen disappears just below the sediment surface. As a result, deep infaunal species move upwards in the sediment and become epifaunal in low oxygen environments (Mackensen and Douglas 1989; Gooday 2003). For example, the genus *Globobulimina* includes deep infaunal species that consume low quality organic material that has already been processed by sediment interface organisms. This seems to suggest that they are not dependent on fresh organic material as a food source and thus are non-opportunistic k-selection species, with constant densities throughout the year. However, recent tracer experiments by Nomaki et al. (2005) suggests that *Globobulimina* will consume fresh phytodetritus when it has the opportunity to do so, although not as quickly as shallow-infaunal taxa such as *Uvigerina*.

Figure 1.2 TROX-model: a conceptual model explaining benthic foraminiferans living depth (black area) in terms of food availability and oxygen concentration. From Jorissen et al. (1995).



Foraminiferans show morphological adaptations to living in low oxygen environments in the form of different test shapes. Studies by Bernhard (1986) on foraminiferans from presumed dysoxic paleoenvironments of Jurassic to Holocene, looked at test size and morphology. Also in the mid 1980's, Corliss (1985) and Corliss and Chen (1988) showed that, generally, test morphology is a good indicator of the depth that foraminiferans live within the sediment and

therefore their tolerance to oxygen depletion. Although Bernhard and colleagues examined foraminiferal distribution across a large horizontal scale and Corliss and colleagues looked at foraminiferal distribution at a smaller vertical sediment scale, they were both addressing the same basic issue, the relationship between test characteristics and oxygen. Bernhard suggested that foraminiferal assemblages from dysoxic environments consists of mainly flattened, unornamented morphotypes, often with highly perforated and thin-walled tests. There was a strong correlation between test morphology and inferred oxygen content. However, there was also a strong correlation with the total organic carbon, suggesting that these inversely related parameters cannot be considered separately. Bernhard (1986) also showed that locations with periodic anoxia (Bernhard refers to anoxia, although the term dyxoxia would be more appropriate, as there is no evidence of 0 ml/l oxygen concentrations) yield assemblages of mixed sizes. Larger test sizes may become more abundant during periodic oxygenation of bottom water. Species with larger tests die, while small specimens survive, once waters become oxygen depleted. The observations of Corliss (1985) and Corliss and Chen (1988) on the relationship between foraminiferal microhabitats and test morphologies tend to mirror these trends. Infaunal species tend to be planispiral, globular or flattened while epifaunal species are planoconvex or biconvex in shape. Moreover, infaunal species which are tolerant of dysoxia have higher test surface area volume ratios than epifaunal species.

Adaptations that allow foraminiferans to inhabit oxygen depleted environments were reviewed by Bernhard (1996) and later by Bernhard and Sen Gupta (1999). These reviews dealt mainly with experimental and ultrastucture evidence suggesting that certain benthic foraminiferans are microaerophiles, requiring only trace amounts of oxygen. One important type of adaptation is the possession of endosymbionts (e.g. methanogens and sulphate-reducing bacteria similar to those seen in certain ciliates). Four species from the Santa Barbara Basin seem to have bacterial endosymbionts (Bernhard 2000). Ultrastructure images of *Buliminella tenuata* show numerous intact rod-shaped bacteria within its cytoplasm (Bernhard 1996). Bernhard (2000) indicated that an unidentified allogromiid and *Fursenkoina rotundata* (Parr 1950) also harbour bacterial endosymbionts. Bernhard and Reimers (1991) reported bacteria inside the test, but not within the cytoplasm, of *Nonionella stella*. Finally, a single specimen of the infaunal species *Globocassidulina* cf. *G. biora* (Crespin 1960) collected from shallow Antarctic sediments containing anoxic pore waters showed numerous rod-shaped bacteria within the confines of the organic lining. These bacteria which were associated with pore plugs could have been endosymbionts. *Globocassidulina cf. G. biora* has intracellular bacteria (Bernhard 1993). Bernhard and Sen Gupta (1999) suggested that symbiotic bacteria benefit foraminiferans by oxydifying sulphide and consequently detoxifying the pore-water.

Sequestration of chloroplasts is another ultrastructure feature of some foraminiferans from low oxygen environments (Leutenegger 1984; Cedhagen 1991; Bernhard 1996; Bernhard and Bowser 1999; Bernhard 2000) including *Stainforthia fusiformis*, *Nonionella stella*, *Nonionellina labradorica* (Dawson 1860). Chloroplast symbiosis or retention is a phenomenon in which the host ingests algae and isolates the algal chloroplasts which remain as viable organelles within the foraminiferal cytoplasm. Ultrastructural investigations by Cedhagen (1991) showed free chloroplasts in the cytoplasm of *Nonionellina labradorica* from depths well below the photic zone in the Gullmarfjord, Kosterfjord, Skagerrak and Kattegatt, Sweden. This symbiosis is facultative as the species is able to survive without chloroplast sequestration. The retention of viable chloroplasts by a deep-water foraminiferan is also reported by Bernhard et al. (2000) and Bernhard (2003).

Physiological adaptations include alternative metabolic pathways and metabolic suppression through dormancy or the ability to encyst (Bernhard 1993; Bernhard and Alve 1996; Bernhard and Bowser 1999) that allow foraminiferans to survive microxia or dysoxia. A study by Bernhard and Alve (1996) observed the physiological responses of foraminiferans from dysoxic sediments collected in Drammensfjord, Norway, to nitrogen incubation over a period of 3.5 weeks. In the four species studied, three different physiological responses to nitrogen incubation were observed: 1) both survival and ATP were significantly decreased (e.g., *Bulimina marginata* d'Orbigny, 1826), 2) survival was not affected but ATP was significantly depleted (e.g., *Stainforthia fusiformis* and *Adercotyma glomeratum* Brady, 1878), and 3) no significant decrease in either survival or ATP (e.g., *Psammosphaera bowmanni* Heron-Allen and Earland, 1912). They concluded that benthic foraminiferans are facultative anaerobes because all four species survived anoxia for at least 3.5 weeks (Bernhard and Alve 1996). Ultrastructure images of *Stainforthia fusiformis* showed numerous peroxisome-ER complexes. Peroxisomes are organelles where oxidative reactions produce hydrogen peroxide, which is then metabolized by catalase to water and oxygen. Another possible adaptation presented in this study was dormancy suggested by the presence of tubulin paracrystals indicating that specimens were not actively feeding.

A number of species from low oxygen environments have a higher density of mitochondria concentrated near pore openings within the cell while higher oxygen environment species have mitochondria more evenly distributed throughout the cell (Leutenegger and Hansen 1979; Corliss 1985). Pores are important for gas exchange in foraminiferans, illustrated by the osmiophilic organic lining of *Globobulimina pacifica* Leutenegger and Hansen, 1979 that does not cover the pore entrance, allowing a faster rate of molecular transport at low oxygen concentrations (Corliss 1985). However, in anoxic conditions, foraminiferal mitochondria are

most abundant in the cytoplasm nearest the aperture and also in the periphery of chambers, but they are not necessarily associated with test pores (Bernhard and Alve 1996).

One last physiological adaptation that foraminiferans have to survive temporary microxia was proposed by Bernhard and Reimers (1991). They suggested that *Nonionella stella* may be able to reduce NO_3^- through anaerobic respiration or with glycogen stores during periods of lack of oxygen. So the species may use both mitochondrial respirations and glycolysis. Cedhagen (1993) also found *Pelosina arborescens* to move actively (but slowly) and store glycogen under anoxia.

1.6 Gromiids

Gromiids are large testate, single chambered amoebae with organic tests that are best known in intertidal and sublittoral habitats (Arnold 1972). Characteristic features of the group are a layer of multiple "honeycomb membranes" on the inner wall surface (Hedley and Bertaud 1962) and filose pseudopodia. Gromiids belong to the Phylum Cercozoa, Class Filosia, Order Gromida. The Cercozoa is a morphologically heterogenous group of protists that is defined purely on the basis of molecular characteristics (Bhattacharya et al. 1995; Cavalier-Smith and Chao 1997). *Gromia oviformis* Dujardin, 1835, the best known representative of this group, is a cosmopolitan species that inhabits coastal waters. It is found on the weed of coralline pools, on *Cladophora*, on the walls of rock crevices , undersurface of stones, holdfasts of kelp surface layer of sandy and muddy sediments (Jepps 1926; Hedley and Bertaud 1962). Pawlowski and colleagues' studies on phylogeny based on partial small-subunit ribosomal DNA sequences, show that gromiids, based on *Gromia oviformis* sequences, are most closely related to the foraminiferans (Berney and Pawlowski 2003; Longet et al. 2003; Nikolaev et al. 2003; Longet et al. 2004). According to this interpretation, gromiids are the immediate outgroup of the foraminiferans, and therefore their possible Pre-cambrian ancestors. The taxonomic placement of gromiids is currently in a state of flux. Recent molecular studies suggest that they either branch within the Cercozoa or within the Rhizaria, a supergroup that includes the Cercozoa (Burki et al. 2002; Cavalier-Smith and Chao 2003; Longet et al. 2004). Whatever their affinities, they differ from foraminiferans in having filose, rather than reticulated pseudopodia. Gooday et al. (2000b) described the first deep-sea gromiid from bathyal depths on the Oman margin. This species was identified as a gromiid on the basis of its wall structure and described as *Gromia sphaerica* Gooday, Bowser, Bett and Smith, 2000.

1.7 Aims and objectives

This thesis has two main topics that are related to one another but are distinct. The first part focuses on foraminiferan and metazoan picked from samples collected during 1994 from the Oman margin. Several questions were addressed in this part of the thesis:

- Are benthic foraminiferal trends (abundance, diversity and taxonomic composition) related to dominant environmental variables, such as bottom-water oxygen concentrations and organic carbon concentrations?
- Are taxonomic trends observed across the OMZ mirrored by changes in sediment penetration?
- Are foraminiferal macrofaunal trends comparable to those of macrofaunal metazoans (data from published sources) across the OMZ?

The second part of the thesis focuses on *Gromia*, which, as mentioned above, is a relatively unknown group of organisms. This was the most ground-breaking part of this project and sought to establish the importance of this group in the deep Arabian Sea. Several questions were addressed:

- Are there similarities between the lifestyle of gromiids (large organic-walled protists, genus *Gromia*) in the deep Arabian Sea and shallow water settings?
- Are there differences between *Gromia* populations from the Oman and the Pakistan margins of the Arabian Sea?
- What is the phylogenetic relation between *Gromia* and other Protista?
- What does molecular analysis reveal about diversity within *Gromia*?

1.8 Null hypotheses

- Total foraminiferal abundances are not influenced by bottom-water oxygen concentrations.
- Species diversity and dominance are not affected by bottom-water oxygen concentrations.
- Calcareous foraminiferans are not important in dysoxic (relative to soft-shelled foraminiferans) when compared to oxygenated areas.
- The position of benthic foraminiferans within the sediment is not affected by bottom-water oxygen concentrations.
- Foraminiferans and metazoans do not respond in the same way to bottom-water oxygen gradients across the OMZ.
- There is no difference between Oman and Pakistan *Gromia*
- There is only one species of deep-sea *Gromia*

CHAPTER 2

Foraminiferal community attributes in relation to the Oman margin oxygen minimum zone: a comparison with the metazoan macrofauna

2.1 Introduction

Foraminifera from low oxygen environments have been described in the previous chapter, and therefore a brief account of foraminifera from OMZs and more specifically the Oman margin OMZ is given here. Other previous studies of modern foraminifera from the Oman margin are those of Stubbings (1939), Hermelin and Shimmield (1990), Naidu and Malmgren (1995) and Gooday et al. (2000). Foraminifera from the eastern side of the Arabian Sea have been studied by Zobel (1973) and Zobel (1988) while Thies and Kuhnt (1995) and Maas (2000) reported on foraminifera collected along the northern margin. Kurbjeweit et al. (2000) analysed foraminiferal assemblages in deeper water (>1900 m) in the central region of the Arabian Sea. Stubbings (1939) first reported *Rhabdammina parabyssorum* Stchedrina, 1952 (as *Rhabdammina abyssorum* Sars, 1869) from NW Arabian Sea and specimens from this region were later described in detail by Gooday and Smart (2000). Hermelin and Shimmield (1990) gave a first full description of foraminifera, retained in a 125 μm sieve, living across the Oman margin OMZ. Later they also reported fossil foraminiferal from the same cores (Hermelin 1992). They found a strong correlation between foraminiferal assemblages and sediment biogeochemistry. The upper part of the OMZ (440-530 m; O_2 ~ 0.2 ml/l) was organically-enriched and *Bolivina pygmaea* (Brady 1881), *Bulimina* sp.1 and *Lenticulina iota* (Cushman 1923) were characteristic of this depth interval. The lower part of the OMZ (770-955 m; O_2 ~ 0.2 ml/l) had a high carbonate content and was dominated by *Ehrenbergina trigona* Goës, 1896, *Hyalinea balthica* (Schroeter 1783) and *Uvigerina peregrina*. Just below the OMZ (1540-1570 m; O_2 ~ 0.5-1 ml/l) the fauna was dominated by *Bulimina aculeata* d'Orbigny, 1839 and *Uvigerina hispida* Schwager, 1866. *Reophax bilocularis* Flint, 1899 and *Reophax dentaliniformis* Brady, 1881 were dominant at the base of the continental slope (2780-3395 m; O_2 ~ 2-3 ml/l), which was characterized by high contents of hydrogenous metals in clay. The depositional area furthest from land (2495-4040 m; O_2 ~ 2-3 ml/l) was dominated by *Bulimina aculeata*, *Oridorsalis umbonatus* (Phleger and Parker 1951) and *Uvigerina spinicostata* Cushman and Jarvis, 1929. The station at the base of the continental slope in the gulf of Oman

(3240 m; O_2 ~ 2-3 ml/l) had terrigenous sediments and was characterized by *Cribrostomoides wiesneri* (Parr 1950) and *Reophax bilocularis*.

The study by Gooday et al. (2000) compared surface (0-1 cm) foraminiferal meio- (63-300 μm fraction) and macro- (> 300 μm fraction) fauna from two stations, one in the core of the Oman OMZ (412 m; O_2 = 0.13 ml/l) and one well below the OMZ (3400 m; O_2 ~ 3 ml/l, oxygen and food availability were considered to shape the foraminiferal assemblages. In the core of the OMZ, assemblages were species poor and a few dominant species were highly abundant. Most of the abundant species belonged to hyaline calcareous taxa, and some trochamminaceans, spiroplectamminaceans and small *Bathysiphon* species were also common. On the other hand, soft-shelled monothalamous species (allogromiids and saccamminids) were uncommon. Conversely, the deep, well-oxygenated station was dominated by hormosinaceans, and soft shelled monothalamous species and calcareous taxa were uncommon. Gooday et al. (2000) also showed that foraminifera and metazoan respond in similar ways to organic enrichment and oxygen depletion.

The present study examined macrofaunal (> 300 μm) foraminifera from the 0-5 cm layer at sites across the Oman margin OMZ, one situated above, one below and four within the OMZ. The main aim is to analyse foraminiferal community structure within the sediment profile across this strong oxygen gradient. An additional aim is to compare foraminiferal faunal trends with those of metazoans.

2.2 Materials and Methods

2.2.1 Study site and sampling

Multicorer samples were collected from the Oman margin of the Arabian Sea during Cruise 211 of the R.R.S *Discovery* (9 October to 11 November 1994) (Figure 2.1). Samples were collected along a bathymetric transect that crosses the OMZ at depths ranging from 100 m to 3400 m, between 19° and 20° N latitude and 58° and 59° E longitude (Figure 2.2). The OMZ occurs between 300 and 1000 m water depth, with bottom-water oxygen values of 0.46 ml/l at 100 m, decreasing to 0.13 ml/l in the core of the OMZ at 400 m, then slowly increasing to 0.16 ml/l at 700 m, 0.20 ml/l at 850 m, 0.52 ml/l at 1250 m and 2.99 ml/l at 3400 m. (Table 2.1). The temperature was 13.3°C at 400 m, decreasing steadily with water depth to 10.8°C at 700 m, 9.6°C at 850 m and 6.7°C at 1250 m, followed by a steep decrease to 1.7°C at 3400 m (Table 2.1). Measures of potential food availability, such as % total organic carbon (TOC), surface pigment and the hydrogen index, all exhibited higher values within the core of the OMZ at 400 and 700 m water depths, suggesting higher food availability where oxygen concentrations are

lower (Table 2.1). Sediments were fine, soupy mud in the core of the OMZ (400 and 700 m) with firmer mud at 850 m, coarser *Globigerina* sands at 1250 m and with a phytodetrital layer overlying fine mud at the deep 3400-m site (Table 2.1).

Samples were obtained using the multicorer (Figure 2.3) equipped with 57 mm internal diameter core tubes (Barnett et al. 1984). This device obtains samples in which the sediment-water interface is virtually undisturbed and organisms are maintained in their life positions (Figure 2.4). As soon as possible after recovery, samples were taken to the shipboard temperature-controlled laboratory adjusted to bottom-water temperature. Initially, a small amount of the topmost sediments (<1 ml) was taken using a plastic pipette in order to sample organisms living at the sediment-water interface. Cores were then sliced into 1 cm thick layers and each layer was fixed in 10% sodium-borate-buffered formalin and stored for further analysis. Table 2.2 shows the samples available for analysis.

Table 2.2 Station information. Samples were taken between 9 October and 11 November, 1994 during *Discovery* cruise 211. Two samples were analysed for foraminifera by Gooday et al. (2000).

Site	Station sample no.	Water depth (m)	Latitude °N	Longitude °E	
100-m	12708#3	106	19°22.28	58°11.43	
	12708#5	119	19°22.18	58°11.44	
400-m	12695#5	402	19°22.02	58°15.55	
	12692#4	412	19°22.07	58°15.43	Gooday et al. (2000)
700-m	12685#2	680	19°18.91	58°15.44	
	12682#5	685	19°18.66	58°15.55	
850-m	12713#3	827	19°15.13	58°22.87	
	12711#3	833	19°14.10	58°22.86	
1250-m	12723#5	1252	19°14.38	58°31.46	
	12723#3	1268	19°14.33	58°31.56	
3400-m	12687#3	3348	18°58.96	59°00.45	
	12687#8	3350	18°59.33	58°59.09	Gooday et al. (2000)

Figure 2.1 Location of area sampled during RRS *Discovery* cruise 211 on the Oman margin of the Arabian Sea. From Levin et al. (2000).

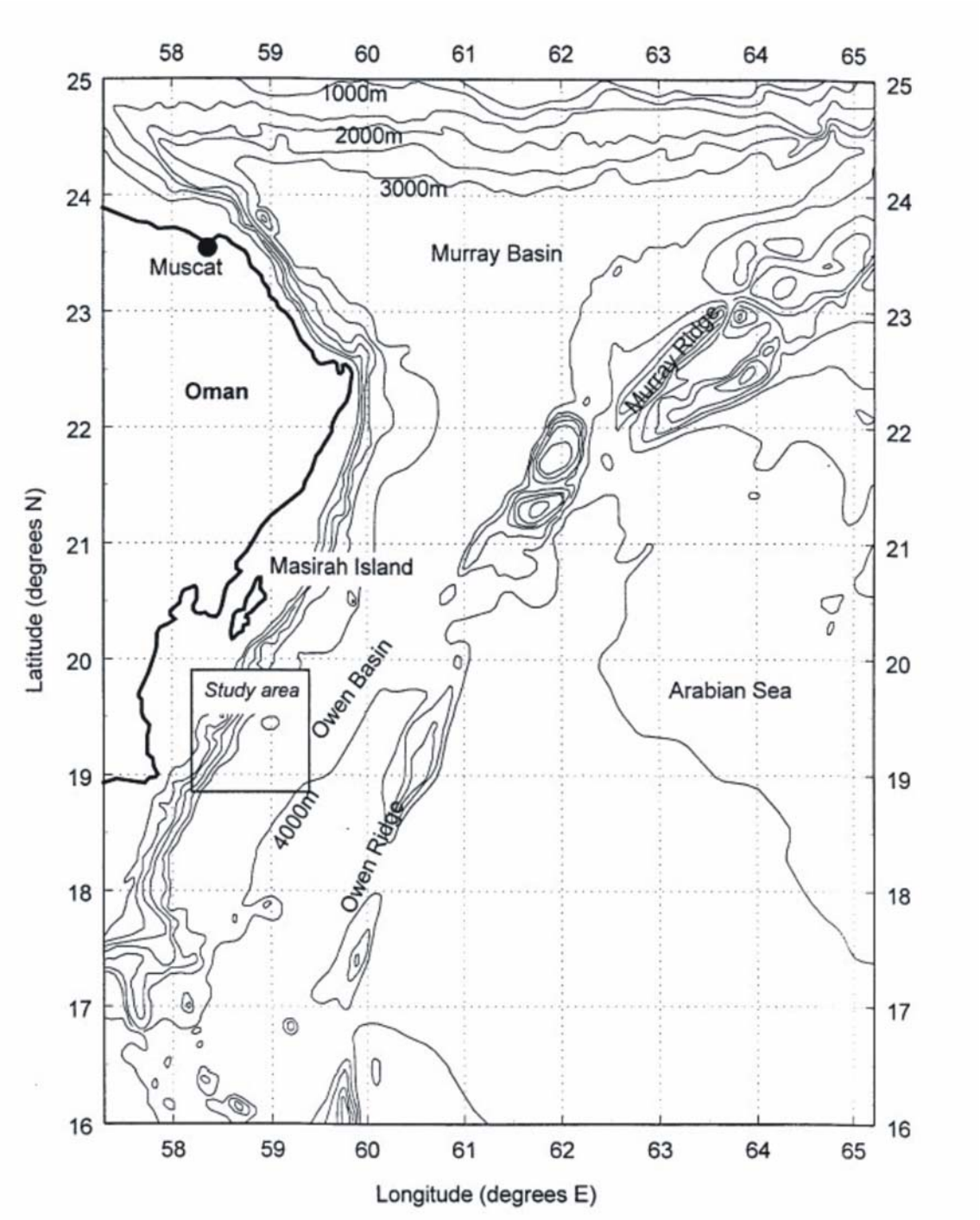


Figure 2.2 Sample locations in relation to bathymetry on the Oman continental margin. From Cook (2001).

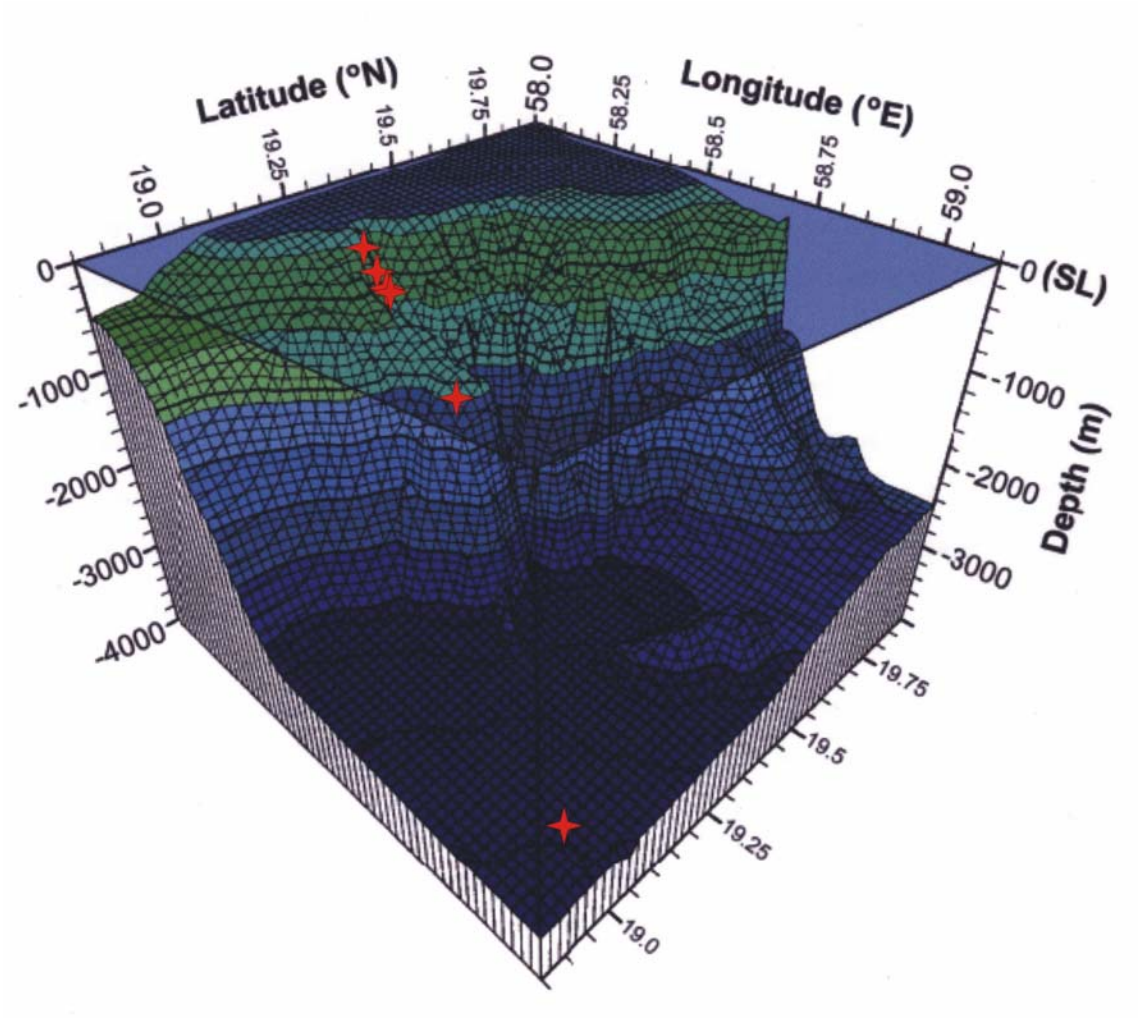


Table 2.1 Physical and chemical characteristics of stations sampled on the Oman margin during October-November, 1994. S.E (Standard error), N/D (no data). Compiled from Levin et al. (1995 and 2000) and Meadows et al. (1995).

Site	**100-m**	**400-m**	**700-m**	**850-m**	**1250-m**	**3400-m**
Bottom-water temp. (°C)	n/d	13.3	10.8	9.6	6.7	1.7
Bottom-water oxygen (ml/l)	0.46	0.13	0.16	0.20	0.52	2.99
% TOC (0-0.5 cm)	n/d	4.99	4.03	4.01	2.67	2.72
(S.E.) n = 3		(0.44)	(0.34)	(0.16)	(0.07)	(0.12)
C:N (0-0.5 cm)	n/d	8.52	9.04	8.8	7.82	9.42
(S.E.) n = 3		(0.44)	(0.34)	9(0.16)	(0.07)	(0.12)
Surf. Pig. 0-0.5 cm (µg/g)	n/d	770	242	167	68	185
(S.E.)		(49)	(39)	(26)	(101)	(49)
n		1	3	3	3	3
Hydrogen index (0-0.5 cm) (mg Hydrocarbon/g TOC)	n/d	490	517	441	423	366
(S.E.)		(12.5)	(55.2)	(0)	(11.7)	(5.5)
n		2	3	2	3	2
% Sand (0-1 cm) (n = 1)	n/d	22.3	24.5	37.6	56.8	21.3
Mean grain size (um) (n = 1)	n/d	42.2	46.4	66.6	79.0	42.8
Median grain size (µm) (n=1)	n/d	28.7	34.3	47.1	42.1	26.5
% $CaCO_3$ (0-0.5 cm)	n/d	55.10	56.70	60.50	66.10	34.48
(S.E) n = 3		(2.5)	(0.4)	(1.7)	(1.0)	(3.29)
Redox Eh	n/d	310	320	330	420	410
Redox mV		330	330	400	430	430
Shear strength kN	n/d	0.12	0.02	0.10	0.15	0.10
M2		0.68	0.50	0.30	0.30	0.25
Range of bioturbation number of burrows per m^2:						
sediment surface	n/d	390-1170	520-4550	2800-5590	390-2470	260-1300
10 cm		260-650	0-130	520-1300	0	0-130
20cm		0-910	0	0	0	0
Bioturbation	Occasional burrows well visible. Homogenous downcore with laminations at > 4 cm depth, some crosscutting structures and minor diffuse mottling	Clay aggregates, little structure, mottling to 12 cm, boundary at 2 cm	Horizontal and vertical tube and burrows < 5 cm consolidated clay	Mudballs to 1.5 cm, extensive small scale bioturbation > 12 cm	Moderate mix vertical tubes, burrows to 8 cm, more extensive vertical burrows to 4 cm	Moderate mottling to 10 cm, horizontal and vertical structures throughout
Substrate	Shelly sand	Fine, soupy mud	Fine, soupy mud	Firmer mud	Globigerina sand	Phytodetrital layer over fine mud

Figure 2.3. Multiple corer equipped with 57 mm diameter tubes, seen here loaded onto the coring head. Picture from Alan Hughes.

Figure 2.4. Undisturbed multicore.

2.2.2 Laboratory processing and data analysis

In the laboratory, the sediment was sieved on a 300 μm screen, stained overnight using rose Bengal, and sorted in water under a binocular microscope for stained organisms. The foraminifera picked were identified to species level when possible. Specimens were sorted into 3 different categories: 1) stained ("live") tests, 2) dead (empty) tests and 3) tests with "brown" contents, the nature of which was uncertain. The criterion used to distinguish "live" specimens was the presence of bright red material filling at least one chamber (Walton 1952). The metazoans were identified to major groups (e.g. copepods, nematodes). Samples from 100 m depth with unmanageable numbers of organisms were split into fractions of $1/8^{th}$ using a wet sample splitter constructed according to the design of Jensen (1982). The volume of each split was measured in order to determine the accuracy of this process. Two splits were processed per sample, i.e. a quarter of the sample, in order to obtain a representative sub-sample.

One sample from each of 6 different water depths (100, 400, 700, 850, 1250 and 3400 m) was analysed down to 5 cm depth in the sediment. A replicate of the 0-1 cm layer was also analysed from each site, with the exception of those at 400 m and 3400 m where I used the published data of Gooday et al. (2000). Faunal data were plotted against physical data from published sources (Table 2.1). Diversity indices for foraminifera were calculated using Biodiversity Pro ®.

2.2.3 Specimen documentation and preservation

Specimens were identified, counted, described and photographed using a film camera attached to a Wild Photomicroscope M400 and the results recorded on Ilford Delta black and white film. Negatives were scanned into a computer. In some cases, specimens were air dried, coated with gold (in a Hummer VI-A sputter coater) and examined in a LEO 1450VP Scanning Electron Microscope (SEM).

Calcareous and hard-shelled agglutinated species were mounted on dry micro-palaeontology slides, while organic-walled allogromiids and other soft-shelled taxa were preserved in glycerol in cavity slides. Large organisms such as gromiids were preserved in vials with formalin. Species were identified by reference to the taxonomic literature. The most important papers were Flint (1899), Höglund (1947), Nyholm (1952), Nyholm (1953), Loeblich and Tappan (1987), Hermelin and Shimmield (1990), Jones (1994), Thies and Kuhnt (1995), Jannink et al. (1998), Gooday et al. (2000), Maas (2000) and Zheng and Fu (2001).

2.2.4 Analysis of vertical distribution

In order to compare the vertical distribution of live foraminifera at each site and, specifically, of each individual species, the Average Living Depth (ALD_x; Jorissen 1995) was calculated according to the following formula:

$$ALD_x = \sum_{i=1,x} (n_i D_i) / N) \text{ , where}$$

x = lower boundary of the deepest sample

n_i = number of specimens in interval i

D_i = midpoint of sample interval

N = total number of individuals for all levels

As the lower limit of the deepest sample (x), in this study is 5 cm, we calculated ALD_5. The term Average Depth Dead Tests (ADDT) is used for the equivalent parameter for dead tests.

2.3 Results

2.3.1 Foraminiferal macrofauna live assemblage

2.3.1.1 Abundance

Abundance is expressed as actual counts (per 25.5 cm^2), but in order to facilitate comparison with other studies, abundance per 10 cm^2 is given in Table 2.3. Complete (unfragmented) stained benthic foraminiferan tests (>300 μm) from the 0-5 cm sediment layer varied in abundance across the OMZ (Figure 2.5, Table 2.3, Appendix A). Considering sites above and below the core of the OMZ (100-m, 1250-m and 3400-m; 0.46, 0.52 and 2.99 ml/l O_2 respectively), abundances were two orders of magnitude higher at the shallowest (100-m) site (2858 per 25.5 cm^2) than the two deeper sites (1250-m and 3400-m) (129 per 25.5 cm^2 and 72 per 25.5 cm^2 respectively). Among the sites in the core of the OMZ (O_2 < 0.5 ml/l), abundance was highest at the 850-m site (263 per 25.5 cm^2), followed by the 400-m site (183 per 25.5 cm^2) where oxygen levels were lowest (O_2 = 0.13 ml/l), and the 700-m site (64 per 25.5 cm^2).

When only the top 0-1 cm layer was considered, the shallowest site (100-m) still yielded the largest number of foraminifera (1734 per 25.5 cm^2) (Table 2.3). When considering only sites between 400 m and 3400 m depth, the pattern of abundance in the 0-1 cm sediment layer was different from that in the 0-5 cm layer (Figure 2.8). The highest abundance (160 per 25.5 cm^2) was found at the 400-m site, where oxygen levels were lowest, and the lowest abundance (25 per 25.5 cm^2) at the deepest (3400-m site), where oxygen was highest. Furthermore, when the

two replicate cores (0-1 cm layer) were considered, mean densities became more similar across the transect (Table 2.3, Figure 2.6). Between 400 m and 3400 m, average abundance was highest at the 400-m site (188 per 25.5 cm^2) followed by the 700-m site (103 per 25.5 cm^2).

Stained fragments from the 0-5 cm sediment layer were found mainly at the deepest (3400 m) station where densities were 50407 per 25.5 cm^2 (Figure 2.7, Table 2.3). The 1250-m site also yielded many fragmented species with densities of 645 fragments per 25.5 cm^2. There were far fewer fragments within the core of the OMZ at 400 m depth (57 per 25.5 cm^2) and none or almost none at other depths.

Table 2.3 Abundance of complete (C) live foraminifera and stained fragments (F) from the >300 µm fraction of the 0-5 cm and 0-1 cm sediment layers of multicorer samples (*1 - 25.5 cm^2 surface area, *2 - 10 cm^2 surface area). ND = no data.

Site	Station	0-1 cm C *1	0-1 cm C *2	0-5 cm C *1	0-5 cm C *2	0-5 cm F *1	0-5 cm F *2
100-m	12708#5	1734	680	2858	1152	0	0
	12708#3	1297	509	ND	ND	ND	ND
400-m	12695#5	160	63	183	72	57	22
	12692#4	217	85	ND	ND	ND	ND
700-m	12682#5	62	24	64	25	6	2
	12685#2	144	56	ND	ND	ND	ND
850-m	12713#3	87	34	263	103	0	0
	12711#3	65	25	ND	ND	ND	ND
1250-m	12723#3	77	30	129	51	645	253
	12723#5	87	40	ND	ND	ND	ND
3400-m	12687#3	25	10	72	28	50407	19767
	12687#8	149	58	ND	ND	ND	ND

Figure 2.5 Abundance of complete (unfragmented), stained foraminifera (>300 μm) from the 0-5 cm sediment layer of multicore samples (25.5 cm^2 surface area).

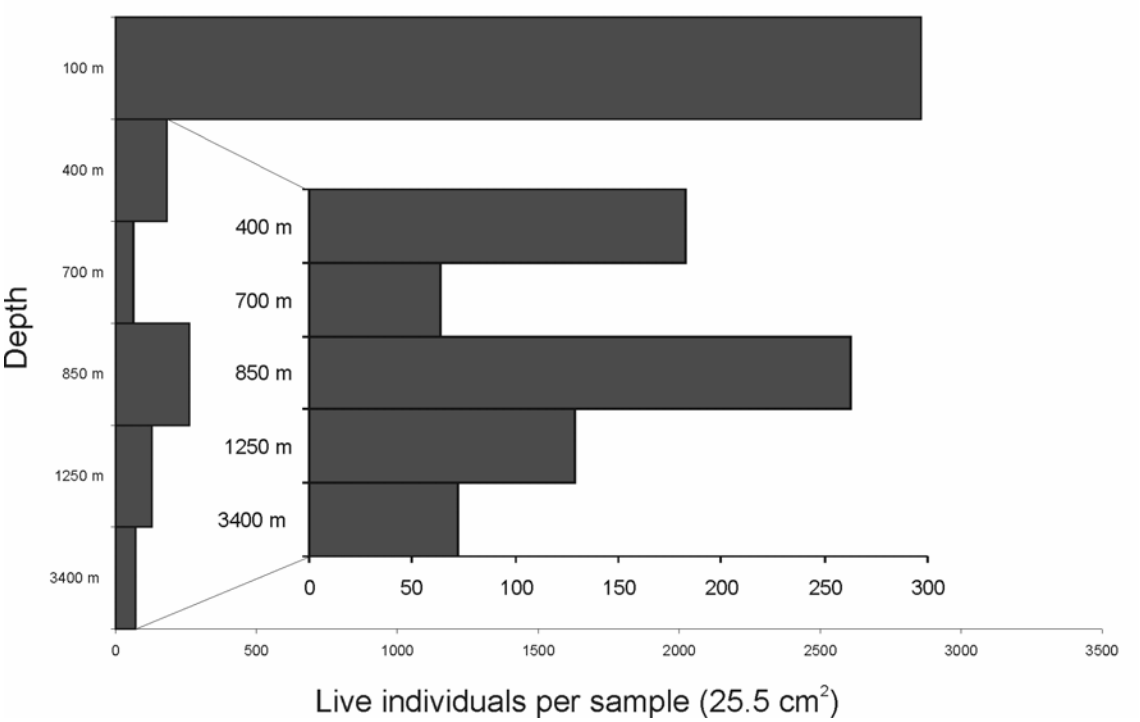


Figure 2.6 Average abundance of complete (unfragmented) stained foraminifera (>300 μm) from two replicates from the 0-1 cm sediment layer of multicore samples (25.5 cm^2 surface area).

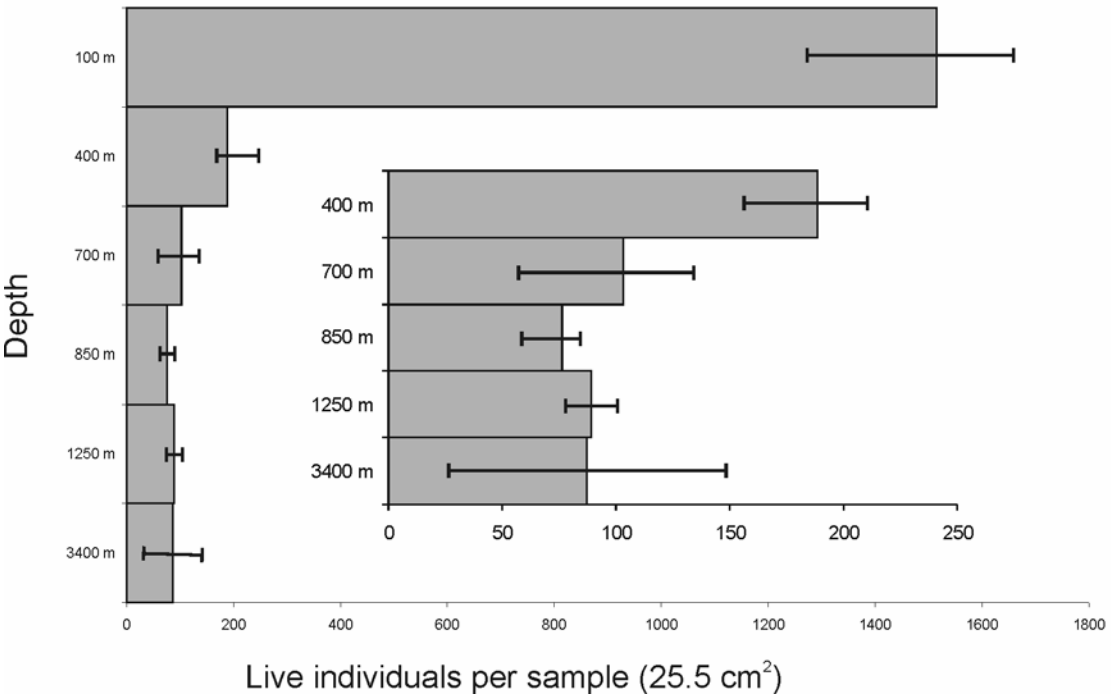
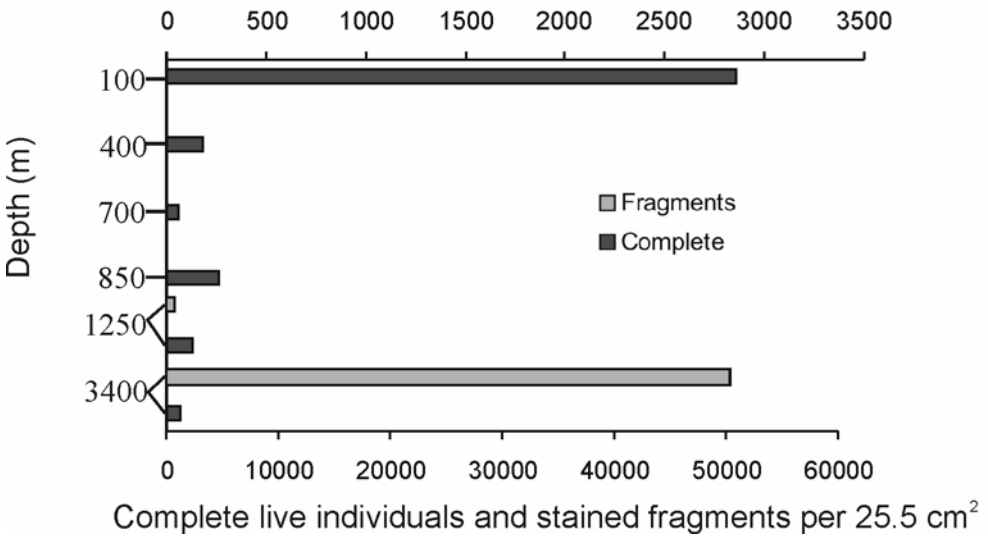


Figure 2.7 Abundance of stained complete foraminifera and stained fragments (>300 μm) from the 0-5 cm and 0-1 cm sediment layers of 25.5 cm^2 samples.

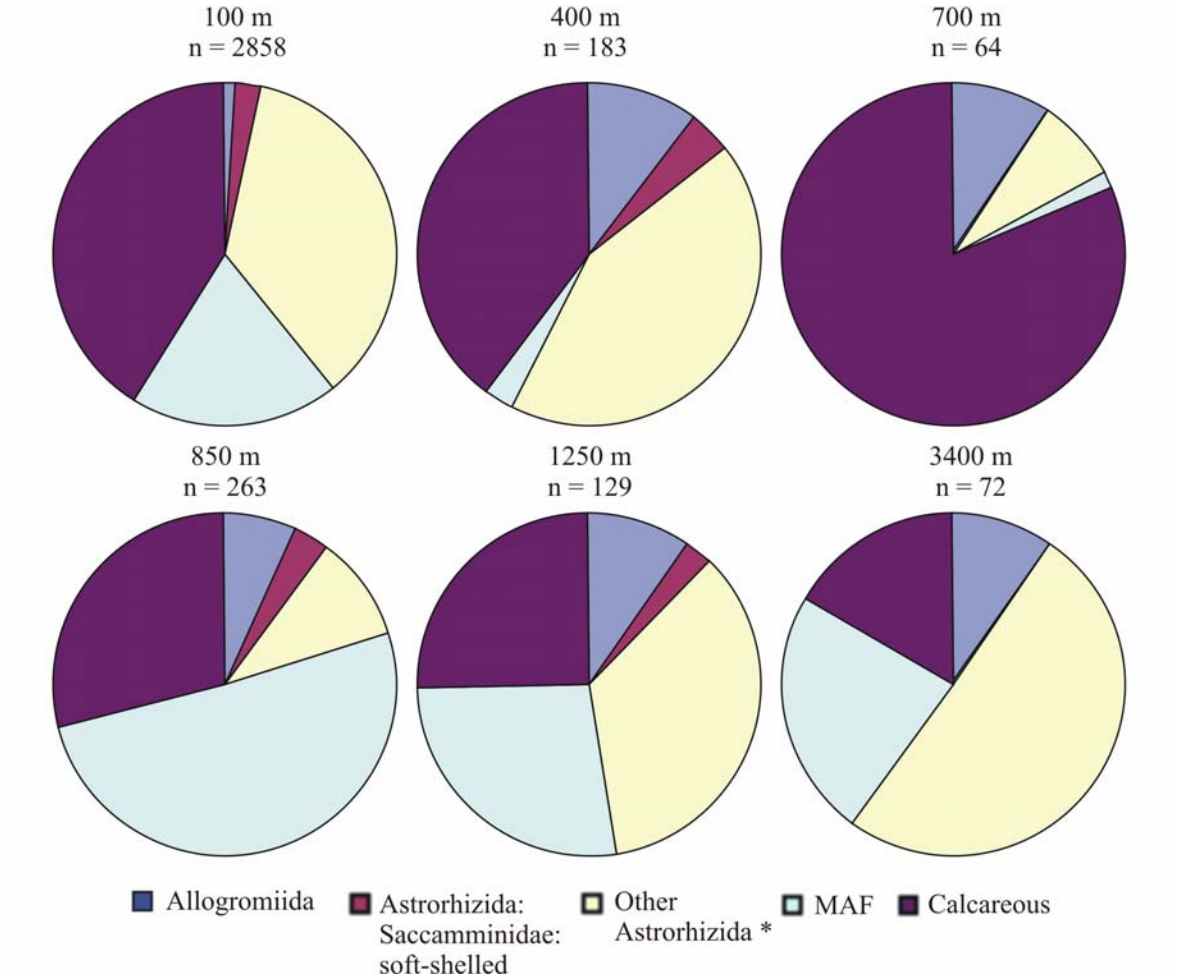


2.3.1.2 Taxonomic composition

2.3.1.2.1 *The 0-5 cm sediment layer*

The foraminiferal assemblages at the shallower sites (100-m and 400-m) consisted of a mixture of agglutinated and calcareous taxa, mainly buluminids, with agglutinated specimens slightly predominating (Table 2.4, Appendix 2.1). At the 100-m site, agglutinated taxa included both monothalamous species which accounted for 70.7% of the live assemblage and multilocular species which accounted for 19.4% of the live assemblage. Monothalamous species were represented mostly by *Psammosphaera* spp. (29.2% of the live assemblage) while hormosinaceans (14% of the live assemblage) represented most multilocular species. The very sparse fauna at the 700-m site was dominated by calcareous species which accounted for 81.2% of the 64 live foraminifera (Figure 2.8). The deepest sites, on the other hand, were dominated by agglutinated foraminifera. At 850 m, multilocular agglutinated foraminifera accounted for 50.6% of the live assemblage; again, most of them were hormosinaceans (44.5% of the live assemblage). Agglutinated foraminifera, many of them unilocular, represented 73.6% of the 74 complete specimens recovered at the 3400-m site (Table 2.4). Monothalamous soft-shelled taxa occurred at most stations. Organic-walled allogromiids were most abundant at 400 m, in the core of the OMZ, where they accounted for 10.4% of all live foraminifera.

Figure 2.8 Percentage abundance of major foraminiferal groups (live assemblage; >300 μm fraction) in the 0-5 cm layer of multicore samples (25.5 cm^2 surface area).



The ten top-ranked species at each site are listed in Table 2.5 (Appendix 2.2). The majority are either agglutinated or calcareous. A calcareous species, *Uvigerina* ex gr. *U. semiornata* d'Orbigny, 1846, and an agglutinated species, *Psammosphaera* sp. 5, were dominant at the 100-m site; these accounted for 30.4% and 29.3% of the live assemblage respectively (Table 2.5). At the 400 m site, the most abundant species was *Bathysiphion* sp.2, a monothalamous agglutinated form that accounted for 21.4% of all live foraminifera. The dominant species at the 700 m site was the robertinid *Hoeglundina elegans* (d'Orbigny 1826), which represented 35.9% of the sparse live assemblage. The 850-m site was dominated by the hormosinacean *Reophax* sp.1, which accounted for 36.1% of the live assemblage. No single species was dominant at the 1250-m site where two agglutinated species, *Lagenammina* sp.3 and *Reophax scorpiurus* Monfort, 1808, and the calcareous species *Bulimina aculeata*, each represented 7.0% of all live foraminifera. The sparse fauna at 3400 m was dominated by two agglutinated foraminifera, *Crithionina* sp.3 and *Reophax* sp.13. These accounted for 14.5% and 10.1% of the live assemblage respectively.

2.3.1.2.2 *The 0-1 cm sediment layer*

The assemblage in the 0-1 cm layer looked rather different from the 0-5 cm assemblage (Figure 2.9, Tables 2.6 and 2.7). For example, the proportion of calcareous taxa was much higher at the 100 m station, 64.0% of the live assemblage compared to 41.5% in the 0-5 cm layer, and also higher at the 850 m station where this group made up 50.6% of the live assemblage compared to 29.3% in the 0-5 cm layer.

Differences are evident in the taxonomic composition of assemblages from replicates of the 0-1 cm sediment layer (Figure 2.9, Table 2.6). For example, at the 100-m site, two separate cores from the same deployment showed different percentage abundance of major taxa. The station 12708#5 sample was dominated by calcareous species (64.0%), followed by multilocular agglutinated foraminifera (18.7%), other astrorhiizids (11.6%), soft-shelled saccamminids (4.3%) and allogromiids (1.4%). In the station 12708#3 sample, calcareous species were relatively more abundant (82.8%), wheareas other astrorhiizids (9.1%), multilocular agglutinated foraminifera (7.7%), allogromiids (0.3%) and soft-shelled saccamminids (0.1%) were relatively less abundant. A replicate sample from the 1250-m site (12723#5) yielded a substantially higher proportion of multilocular agglutinated foraminifera (69.3% of the live assemblage) compared to 12723#3 where multilocular agglutinated foraminifera represented 33.8% of the live assemblage. Note that specimen numbers at 1250 m were more than an order of magnitude lower than at 100 m.

Table 2.4 Percentage abundance of major foraminiferal groups (live assemblage; > 300µm fraction) from the 0-5 cm layer of 25.5 cm^2 samples. F – fragments, MAF – Multilocular Agglutinated Foraminifera

Site	**100-m**	**400-m**		**700-m**		**850-m**	**1250-m**		**3400-m**	
Station	**12708#5**	**12695#5**		**12682#5**		**12713#3**	**12723#3**		**12687#3**	
Species	**live**	**live**	**F**	**live**	**F**	**live**	**live**	**F**	**live**	**F**
Allogromiida	**1.0**	**10.4**	**0.0**	**9.4**	**0.0**	**6.8**	**10.1**	**0.6**	**9.7**	**0.0**
Astrorhizida: Saccamminidae: soft-shelled	**2.6**	**4.4**	**0.0**	**0.0**	**0.0**	**3.4**	**2.3**	**0.0**	**0.0**	**0.0**
Other Astrorhizida:										
Astrorhizida: Saccamminidae: *Lagenammina*	4.5	8.2	0.0	0.0	0.0	9.9	8.5	0.0	0.0	0.0
Astrorhizida: Psammosphaeridae: spheres and domes	29.2	0.0	0.0	0.0	0.0	0.0	17.0	0.0	4.2	0.0
Astrorhizida: Bathysiphonidae	1.7	34.1	0.0	7.8	0.0	0.0	2.3	0.0	4.2	0.0
Astrorhizida: *Hyperammina*	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Astrorhizida: Komokiacean-like	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.3
Various	0.0	0.0	0.0	0.0	0.0	0.0	6.2	0.0	41.7	0.0
Other tubes	0.0	0.0	100.0	0.0	100.0	0.0	0.0	97.8	0.0	99.7
Total	**35.4**	**42.3**	**100.0**	**7.8**	**100.0**	**9.9**	**34.9**	**99.4**	**50.0**	**100.0**
MAF:										
Lituolida: Ammodiscacea: Ammodiscidae	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
Lituolida: Hormosinacea	14.2	1.6	0.0	0.0	0.0	44.5	22.5	0.0	15.3	0.0
Trochamminida: Trochamminacea	0.4	0.0	0.0	0.0	0.0	3.4	0.8	0.0	4.2	0.0
Textulariida: Textulariacea	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0
Other MAF	0.0	1.1	0.0	1.6	0.0	0.0	3.9	0.0	1.4	0.0
Total	**19.4**	**2.7**	**0.0**	**1.6**	**0.0**	**50.6**	**27.1**	**0.0**	**23.6**	**0.0**
Calcareous:										
Miliolida	1.4	0.0	0.0	0.0	0.0	0.0	0.8	0.0	4.2	0.0
Lagenida	3.6	6.0	0.0	12.5	0.0	3.8	0.0	0.0	1.4	0.0
Buliminida	31.4	23.1	0.0	29.7	0.0	15.2	12.4	0.0	11.1	0.0
Rotaliida	5.0	11.0	0.0	3.1	0.0	9.9	12.4	0.0	0.0	0.0
Robertiniida	0.0	0.0	0.0	35.9	0.0	0.4	0.0	0.0	0.0	0.0
Total	**41.5**	**40.1**	**0.0**	**81.2**	**0.0**	**29.3**	**25.6**	**0.0**	**16.7**	**0.0**
Total specimens	**2858**	**182**	**57**	**64**	**6**	**263**	**129**	**645**	**72**	**50410**

Table 2.5. Top 10 ranked species in samples from the 0-5 cm sediment layer across the Oman OMZ (>300 μm). The percentage of each species is given in parentheses after the species names. The total numbers of live specimens in each sample are given at the bottom of each column.

100-m 12708#5 O_2 0.46 ml/l	**400-m 12695#5 O_2 0.13 ml/l**	**700-m 12682#5 O_2 0.16 ml/l**	**850-m 12713#3 O_2 0.20 ml/l**	**1250-m 12723#3 O_2 0.52 ml/l**	**3400-m 12687#3 O_2 2.99 ml/l**
Uvigerina ex gr. *semiornata* (30.2%)	*Bathysiphon* sp.2 (21.4%)	*Hoeglundina elegans* (35.9%)	*Reophax* sp.1 (36.1%)	*Lagenammina* sp.3 (7.0%)	*Crithionina* sp.3 (13.9%)
Psammosph. sp.5 (29.2%)	*Bathysiphon* sp.3 (12.6%)	*Globobulimina affinis* (14.1%)	*Cancris auriculus* (8.4%)	*Reophax scorpiurus* (7.0%)	"*Crithionina*" sp.2 (9.7%)
Reophax aff. *advenus* (7.1%)	*Globobulimina* aff. *turgida* (11.5%)	*Lenticulina* aff. *iota* (12.5%)	*Lagenammina* sp.1 (6.1%)	*Bulimina aculeata* (7%)	*Reophax* sp.13 (6.9%)
Reophax sp.9 (6.7%)	*Cancris auriculus* (10.4%)	Allogromiid sp.21 (7.8%)	*Reophax* sp.3 (6.1%)	*Psammosphaera fusca* (5.4%)	*Crithionina* sp.4 (5.6%)
Textularia pseudogramen (4.8%)	*Lagenammina* sp.6 (8.2%)	*Globobulimina turgida* (7.8%)	*Uvigerina* sp.1 (4.6%)	*Allogromiid* sp.13 (3.9%)	*Globo.* aff. *turgida* (5.6%)
Psammosph. sp.3 (4.3%)	*Globobulimina affinis* (5.5%)	*Bathysiphon* sp.2 (6.2%)	*Uvigerina peregrina* (4.2%)	*Reophax spiculifer* (3.9%)	*Globo* sp.3 (5.6%)
Cancris auriculus (2.8%)	*Uvigerina peregrina* (4.9%)	*Globobulimina* aff. *turgida* (4.7%)	*Lagenammina* sp.2 (3.8%)	*Reophax* sp.3 (3.9%)	*Bathysiphon* sp.4 (4.2%)
Lenticulina aff. *iota* (2.7%)	*Micrometula* sp.1 (4.4%)	*Cancris auriculus* (3.1%)	*Lenticulina* aff. *iota* (3.8%)	*Chilostomella oolina* (3.9%)	*Reophax* sp.14 (4.2%)
Saccamminid sp.9 (2.6%)	Saccamminid sp.9 (4.4%)	Allogromiid sp.22 (1.6%)	*Globobulimina* aff. *turgida* (3.0%)	*Hyalinea balthica* (3.1%)	Allogromiid sp.37 (2.8%)
Ammonia sp.1 (1.4%)	*Lenticulina* aff. *iota* (3.3%)	*Bathysiphon* sp.3 (1.6%)	*Ammodiscus cretaceous* (2.7%)	Allogromiid sp.14 (2.3%)	Indeterminate sp.14 (2.8%)
Triloculina tricarinata (1.3%)	*Saracenaria* sp.1 (2.2%)	*Cribrostomoides wiesneri* (1.6%)	*Nemogullmia longevariabilis* (2.3%)	*Bathysiphon* sp.1 (2.3%)	*Reophax horridus* (2.8%)
2858	**183**	**64**	**263**	**129**	**72**

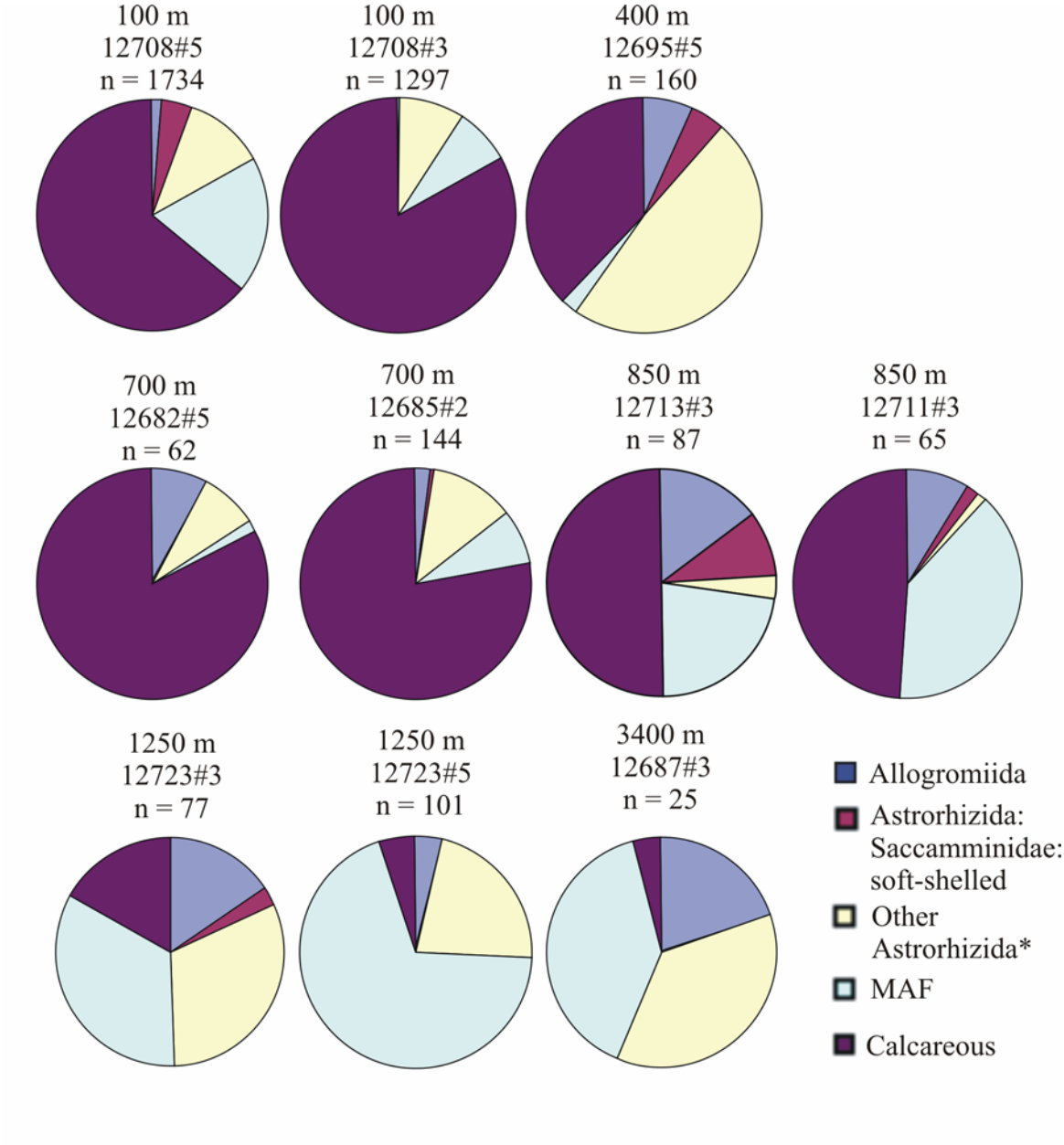
Table 2.6 Percentage abundance of major foraminiferal groups (live assemblage; > 300μm fraction) from the 0-1 cm layer of 25.5 cm^2 samples. F – fragments, MAF – Multilocular Agglutinated Foraminifera.

Site	**100-m**		**400-m**	**700-m**		**850-m**		**1250-m**		**3400-m**
Station	**12708#5**	**12708#3**	**12695#5**	**12682#5**	**12685#2**	**12713#3**	**12711#3**	**12723#3**	**12723#5**	**12687#3**
Allogromiida	**1.4**	**0.3**	**6.9**	**8.1**	**2.1**	**14.9**	**9.2**	**15.6**	**4.0**	**20.0**
Astrorhizida: Saccamminidae: soft-shelled	**4.3**	**0.1**	**5.0**	**0.0**	**0.7**	**9.2**	**1.5**	**2.6**	**0.0**	**0.0**
Other Astrorhizida:										
Astrorhizida: Saccamminidae: *Lagenammina*	2.0	5.9	9.4	0.0	0.0	3.4	1.5	7.8	14.8	0.0
Astrorhizida: Psammosphaeridae: spheres and domes	26.9	0.0	0.0	0.0	0.0	0.0	0.0	7.8	0.0	0.0
Astrorhizida: Bathysiphonidae	2.8	3.2	38.1	8.1	11.8	0.0	0.0	3.9	0.0	12.0
Astrorhizida: *Hyperammina*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0
Various	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.4	6.9	24.0
Total	**11.6**	**9.1**	**47.5**	**8.1**	**11.8**	**3.4**	**1.5**	**31.2**	**21.8**	**36.0**
MAF: total										
Lituolida: Ammodiscacea: Ammodiscidae	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	3.0	0.0
Lituolida: Hormosinacea	11.9	7.7	1.2	0.0	2.8	11.5	36.9	28.6	61.4	36.0
Trochamminida: Trochamminacea	0.7	0.0	0.0	0.0	0.0	8.0	0.0	1.3	2.0	0.0
Textulariida: Textulariacea	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
Other MAF	0.0	0.0	1.2	1.6	4.9	0.0	1.5	3.9	3.0	0.0
Total	**18.7**	**7.7**	**2.5**	**1.6**	**7.6**	**21.8**	**38.5**	**33.8**	**69.3**	**40.0**
Calcareous: total										
Miliolida	2.4	4.5	0.0	0.0	0.0	0.0	0.0	1.3	0.0	4.0
Lagenida	5.3	6.4	6.9	12.9	16.0	11.5	12.3	0.0	0.0	0.0
Buliminida	48.7	64.8	19.4	29.0	31.25	18.4	15.4	3.9	2.0	0.0
Rotaliida	7.6	7.1	11.9	3.2	0.7	19.5	16.9	11.7	3.0	0.0
Robertiniida	0.0	0.0	0.0	37.1	29.9	1.1	4.6	0.0	0.0	0.0
Total	**64.0**	**82.8**	**38.1**	**82.3**	**77.8**	**50.6**	**49.2**	**16.9**	**4.9**	**4.0**
Total specimens	**1734**	**1297**	**160**	**62**	**144**	**87**	**65**	77	**101**	**25**

Table 2.7 Top 10 ranked species in samples from the 0-1 cm sediment layer across the Oman OMZ (>300 µm). The percentage of each species is given in parentheses after the species names. The total number of live specimens in each sample are given at the bottom of each column.

100-m O_2 0.46 ml/l		400-m O_2 0.13 ml/l	700-m O_2 0.16 ml/l		850-m O_2 0.20 ml/l		1250-m O_2 0.52 ml/l		3400-m O_2 2.99 ml/l
12708#5	12708#3	12695#5	12682#5	12685#2	12713#3	12711#3	12723#3	12723#5	12687#3
Uvigerina ex gr. *semiornata* sp (46.8%)	*Uvigerina* ex gr. *semiornata* sp (61.9%)	*Bathysiphon* sp.2 (23.7%)	*Hoeglundina elegans* (37.1%)	*Hoeglundina elegans* (29.9%)	*Cancris auriculus* (19.5%)	*Reophax* sp.1 (26.1%)	*Reophax scorpiurus* (11.7%)	*Reophax scorpiurus* (40.6%)	*Reophax* sp.13 (20%)
Psammosphaera sp.5 (6.8%)	*Psammosphaera* sp.5 (5.9%)	*Bathysiphon* sp.3 (14.4%)	*Globobulimina affinis* (14.5%)	*Globobulimina* aff. *turgida* (20.8%)	*Uvigerina* sp.1 (12.6%)	*Cancris auriculus* (16.9%)	*Lagenammina* sp.3 (7.8%)	*Reophax* sp.1 (14.8%)	*Bathysiphon* sp.4 (12%)
Reophax sp.9 (6.5%)	*Lenticulina* aff. *iota* (5.8%)	*Cancris auriculus* (11.9%)	*Lenticulina* aff. *iota* (12.9%)	*Lenticulina* aff. *iota* (16.0%)	*Lenticulina* aff. *iota* (11.4%)	*Lenticulina* aff. *iota* (10.8%)	*Reophax spiculifer* (6.5%)	*Lagenammina* sp.4 (9.9%)	*Reophax* sp.14 (12%)
Textularia pseudogramen (6.0%)	*Cancris auriculus* (5.0%)	*Lagenammina* sp.6 (9.4%)	*Globobulimina turgida* (8.1%)	*Bathysiphon* sp.3 (7.6%)	*Reophax* sp.1 (11.4%)	*Uvigerina* sp.1 (93.2%)	Allogromiid sp.13 (5.2%)	*Crithionina* sp.4 (6.9%)	Allogromiid sp.37 (8.0%)
Reophax aff. *advenus* (5.4%)	*Reophax* sp.9 (3.7%)	*Globobulimina affinis* (6.2%)	*Allogromiid* sp.21 (6.4%)	*Globobulimina affinis* (6.9%)	*Nemogullmia longevariabilis* (6.9%)	*Reophax* sp.4 (7.7%)	*Hyalinea balthica* (5.2%)	*Lagenammina* sp.3 (4.9%)	Allogromiid sp.38 (4.0%)
Saccamminid sp.9 (4.2%)	*Bathysiphon* sp.3 (3.2%)	*Globobulimina* aff. *turgida* (6.2%)	*Bathysiphon* sp.2 (6.4%)	*Bathysiphon* sp.2 (4.2%)	Saccamminid sp.1 (6.9%)	*Hoeglundina elegans* (4.6%)	*Psammosphaera fusca* (5.2%)	*Ammodiscus* sp.1 (3.0%)	Allogromiid sp.39 (4.0%)
Lenticulina aff. *iota* (4.2%)	*Bolivina* sp.1 (2.8%)	*Uvigerina peregrina* (5.6%)	*Cancris auriculus* (3.2%)	*Cribrostomoides wiesneri* (3.5%)	Allogromiid sp.2 (3.4%)	*Bolivina inflata* (3.1%)	Allogromiid sp.14 (3.9%)	Allogromiid sp.50 (2.0%)	Allogromiid sp.40 (4.0%)
Cancris auriculus (3.9%)	*Reophax* aff. *advenus* (2.8%)	*Micrometula* sp.1 (5.0%)	*Globobulimina* aff. *turgida* (3.2%)	*Leptohalysis* sp.1 (2.1%)	*Lagenammina* sp.1 (3.4%)	Allogromiid sp.51 (1.5%)	*Bathysiphon* sp.1 (3.9%)	*Martinotiella* sp.1 (2.0%)	*Crithionina hispida* (4.0 %)
Ammonia sp.1 (2.4%)	Miliolid sp.4 (2.5%)	Saccamminid sp.9 (5.0%)	Allogromiid sp.22 (1.6%)	Allogromiid sp.47 (1.4%)	Allogromiid sp.1 (2.3%)	Allogromiid sp.52 (1.5%)	*Hippocrepinella hirudinea (3.9%)*	*Reophax* sp.17 (2.0%)	*Crithionina* sp.1 (4.0%)
Triloculina tricarinata (2.1%)	*Hanzawaia concentrica (1.3%)*	*Lenticulina* aff. *iota* (3.7%)	*Bathysiphon* sp.3 (1.6%)	*Globobulimina turgida* (1.4%)	*Ammodiscus cretaceous* (2.3%)	Allogromiid sp.53 (1.2%)	*Reophax* sp.6 (3.9%)	*Velevoninoides scitulus (2.0%)*	*Crithionina* sp.2 (4.0%)
1734	**1297**	**160**	**62**	**144**	**87**	**64**	**77**	**101**	**72**

Figure 2.9 Percentage abundance of major foraminiferal groups (live assemblage; >300 μm fraction) in the 0-1 cm layer of multicore samples (25.5 cm^2 surface area).



2.3.1.3 Diversity and dominance

The total number of species in the live assemblage including replicates was 199, of which 162 (82%) were found in the samples sorted down to the 0-5 cm (Appendix A). The four replicates for the 100-m, 700-m, 850-m and 1250-m sites (0-1 cm layer only) added a total of 36 species (18%) to the total live assemblage.

2.3.1.3.1 *0-5 cm*

A total of 162 species was recognised in the six samples analysed down to 5 cm depth in the sediment (Appendix A). The 1250-m site had the highest number of species with 45 complete and 5 fragment species (Table 2.8). In contrast, the 700 m station, where faunal densities were much lower, yielded only 13 complete species and 1 fragment species. Diversity, measured by the Shannon Index H' (log_{10}), was highest at the 1250-m site and lowest at the 700-m site. Live assemblages showed a more even distribution (J' = 0.91) at the two deep-water sites (1250 m and 3400 m) than at the shallow 100-m site (J' = 0.63). Dominance, the converse of evenness, was highest at 850 m, where the top ranked species accounted for 36.1% of the live assemblage and lowest at the 1250-m site where the top ranked species represented only 7.0% of the live assemblage.

2.3.1.3.2 *0-1 cm*

A total of 156 species was recognised in the ten 0-1 cm samples analysed (Appendix A); in other words, only six species were not represented in the 0-1 cm layer. There were differences in species compositions between replicates from the same site (Table 2.9). At the 100-m site, replicates shared 42.1% of species, at the 700-m site 43.5%, at the 850-m site 16.7% and at the 1250-m site only 13.5%. Diversity, measured by the Shannon Index H' (log_{10}), and Evenness (J'), showed a pattern across the OMZ that was similar to that derived from the 0-5 cm sediment layer (Table 2.8). Diversity was highest at the 1250-m site (12723#3) and lowest at the 100-m site (12708#3). The trend in dominance for the 0-1 cm sediment layer was different from the trend based on the 0-5 cm sediment layer and behaved inversely to diversity. It was highest at the shallow (100-m) site, where the top-ranked species accounted for 61.9% (12708#3) of the live assemblage and lowest again at the 1250-m site where the top-ranked species represented only 11.7% (12723#3) of the live assemblage.

Table 2.9 Differences in total species numbers for replicate cores for 100-m, 700-m, 850-m and 1250-m sites, 0-1 cm layer.

Site	**100-m**	**700-m**	**850-m**	**1250-m**
Species in core 1	27	14	20	37
Species in core 2	27	19	29	22
Shared species	16	10	7	7
Unshared species	22	13	35	45
Total species	38	23	42	52
% shared	**42.1**	**43.5**	**16.7**	**13.5**

Table 2.8 Summary statistics for stained foraminifera (>300 µm) from the Oman margin. Except for species numbers, diversity measures are based on complete specimens only. ND = no data.

Station	**12708#5**	**12708#3**	**12695#5**	**12692#4**	**12682#5**	**12685#2**	**12713#3**	**12711#3**	**12723#3**	**12723#5**	**12687#3**	**12687#8**
Water depth (m)	**119**	**106**	**402**	**412**	**685**	**680**	**827**	**833**	**1268**	**1252**	**3348**	**3350**
Bottom water oxygen (ml/l)	**0.46**		**0.13**		**0.16**		**0.20**		**0.52**		**2.99**	
Bottom water temperature (°C)			**13.3**		**10.8**		**9.6**		**6.7**		**1.7**	
0-5 cm												
No. per sample												
Complete	2858	ND	183	ND	64	ND	263	ND	129	ND	72	ND
Fragments	1	ND	57	ND	6	ND	0	ND	645	ND	50407	ND
No. per cm^3 (complete)	1152	ND	72	ND	25	ND	103	ND	51	ND	28	ND
% 0-1 cm	60.67	ND	87.43	ND	96.88	ND	33.08	ND	59.69	ND	34.72	ND
Species per sample:												
Complete	30	ND	29	ND	13	ND	32	ND	45	ND	34	ND
Total	30	ND	30	ND	14	ND	32	ND	50	ND	44	ND
H' ($\log_{10}$)	0.93	ND	1.13	ND	0.89	ND	1.11	ND	1.50	ND	1.39	ND
J'	0.63	ND	0.78	ND	0.80	ND	0.74	ND	0.91	ND	0.91	ND
R1D (%)	30.23	ND	21.43	ND	35.94	ND	36.12	ND	7.00	ND	13.89	ND
$E(S_{100})$	15.79	ND	21.13	ND	12.76	ND	22.77	ND	40.13	ND	33.71	ND
Fisher α	4.59	ND	9.24	ND	4.93	ND	9.55	ND	24.54	ND	25.16	ND
0-1 cm												
No. per sample												
Complete	1734	1297	160	217	62	144	87	65	77	101	25	149
Fragments	1	1	3	ND	5	29	0	17	46	0	50168	ND
No. per cm^3 (complete)	680	509	63		24	56	34	25	30	40	10	
Species per sample:												
Complete	27	26	19	ND	13	19	20	21	34	22	16	ND
Total	27	27	20	ND	14	19	20	29	37	22	21	ND
H' ($\log_{10}$)	0.93	0.71	1.05	ND	0.88	0.92	1.11	1.07	1.43	0.94	1.12	ND
J'	0.65	0.50	0.82	ND	0.79	0.72	0.85	0.81	0.93	0.70	0.93	ND
R1D (%)	46.8	61.91	23.7	ND	37.1	29.86	19.5	26.15	11.7	40.59	20.00	ND
$E(S_{100})$	17.27	13.66	16.50	ND	12.92	16.11	19.44	20.14	32.72	22.00	14.06	ND
Fisher α	4.54	4.61	5.62	ND	5.01	5.86	8.13	10.76	23.28	8.67	19.16	ND

2.3.1.4 Vertical distribution patterns within the sediment

Stained foraminiferal assemblages exhibited changes across the OMZ but their distribution within the sediment profile also varied at each site. For all sites, the 0-1 cm sediment layer had the highest abundance of live foraminifera with 60.7, 87.4, 96.9, 33.1, 59.7 and 34.7% in the 0-1 cm layer at 100, 400, 700, 850, 1250 and 3400-m sites respectively (Figure 2.10). At the shallow sites, and in particular the two sites with lowest oxygen levels (400-m and 700-m, O_2: 0.13 and 0.16 ml/l respectively), most of the live assemblage was concentrated in the top one centimetre of the sediment, with average living depths (ALD_5) of 0.73 and 0.54 respectively. Furthermore, no stained tests were found below 3 cm depth in the sediment at the 700-m site, although total abundances here were much lower. The 850-m and 1250-m sites again had the highest abundance of live foraminifera at the top 0-1 cm layer, but there was a second abundance peak at the 3-4 cm sediment depth. The deepest site (3400 m) showed a gradual decrease in live foraminiferal abundance with sediment depth, with a slight increase in the 4-5 cm layer (Figure 2.10).

At each site, different foraminiferal species exhibited different vertical distributions within the sediment profile. Figure 2.11 shows the abundance, at each site, of live specimens of the top 5 ranked species (presented in Table 2.5) in each sediment layer. At the shallowest site (100 m) where oxygen concentrations were 0.46 ml/l, the average living depth for the top-ranked calcareous species, *Uvigerina* ex gr. *semiornata*, was 0.58, while agglutinated species had deeper ALD_5 (*Psammosphaera* sp.5 = 1.67, *Reophax* aff. *advenus* Cushman, 1919 = 1.45, *Reophax* sp.9 = 0.91 and *Textularia pseudogramen* Chapman and Parr, 1937 = 0.74). The top-ranked species found in the core of the OMZ (400 m) were mostly concentrated within the top 0-1 cm sediment layer, with the exception of the calcareous species *Globobulimina* aff. *turgida* (Bailey 1951), which was found down to 5 cm in the sediment with an ALD_5 of 1.26. The 700-m site species were all concentrated in the upper 1 cm and the top-ranked species were all calcareous (*Hoeglundina elegans*, *Globobulimina affinis* (d'Orbigny 1826), *Lenticulina* aff. *iota* and *Globobulimina turgida)*. At the deeper stations, where oxygen concentrations were higher, increasing with water depth to normal values at the deepest site, species occurred down to 5 cm in the sediment. The 850-m site had the deepest ALD_5 of 2.15. Calcareous species, *Cancris auriculus* (Fichter and Moll 1798) and *Uvigerina* sp.1, lived in the top 0-1 cm (ALD_5 = 1.00 and 0.67 respectively), while agglutinated species, *Reophax* sp.1, *Lagenammina* sp.1 and *Reophax* sp.3, lived deeper in the sediment with 2.83, 2.56 and 2.81 ALD_5 values respectively. At the 1250-m site, the ALD_5 was 1.67. The 5 top-ranked species were mainly concentrated at 0-1 cm sediment layer, with the exception of the calcareous species *Bulimina aculeata* which was concentrated in the 3-4 cm sediment layer. The deepest site was dominated by agglutinated foraminifera. In contrast to all other sites, only one agglutinated species (*Reophax* sp.13) was

most abundant in the top 0-1 cm. The rest peaked in deeper layers: 1-2 cm (*Crithionina* sp.3), 3-4 cm ("*Crithionina"* sp.2) and 4-5 cm (*Crithionina* sp.4).

Six different species were found in at least half of the sites (Figure 2.12); two agglutinated species, *Bathysiphon* sp.2 and *Bathysiphon* sp.3, and, four calcareous species, *Lenticulina* aff. *iota*, *Globobulimina affinis*, *Globobulimina* aff. *turgida* (found in 5 of the 6 sites) and *Cancris auriculus*. Both agglutinated species were more or less confined to the top (0-1 cm) sediment layer at the shallower sites (100 – 700 m). *Lenticulina* aff. *iota* was also found mainly in the top 0-1 cm sediment layer. *Globobulimina* aff. *turgida* was more abundant in the top layers at the shallower sites, but lived deeper in the sediment at the deepest stations. Likewise, *Cancris auriculus* was found in the top layer at the shallowest stations, but down to 4 cm in the sediment at the 850-m site.

Total abundance of fragments was highest at the deepest sites (1250 m and 3400 m) (Figure 2.13). However, fragments were found much deeper at 1250 m site (ALD_5 = 3.88), than at 3400 m, where they were much more abundant in the top sediment layer (ALD_5 = 0.51) with only scattered specimens occurring in deeper layers. The fragments represented different species at each of these two sites. The 1250-m site was dominated by two agglutinated tubes, Indeterminate sp.3 and Indeterminate sp.5; while the 3400-m site was dominated by *Rhizimmina* sp.1 and 2 and the komokiacean *Reticulum* sp.1.

Figure 2.10 Vertical distribution within the sediment profile of live foraminifera (>300 μm) across the OMZ.

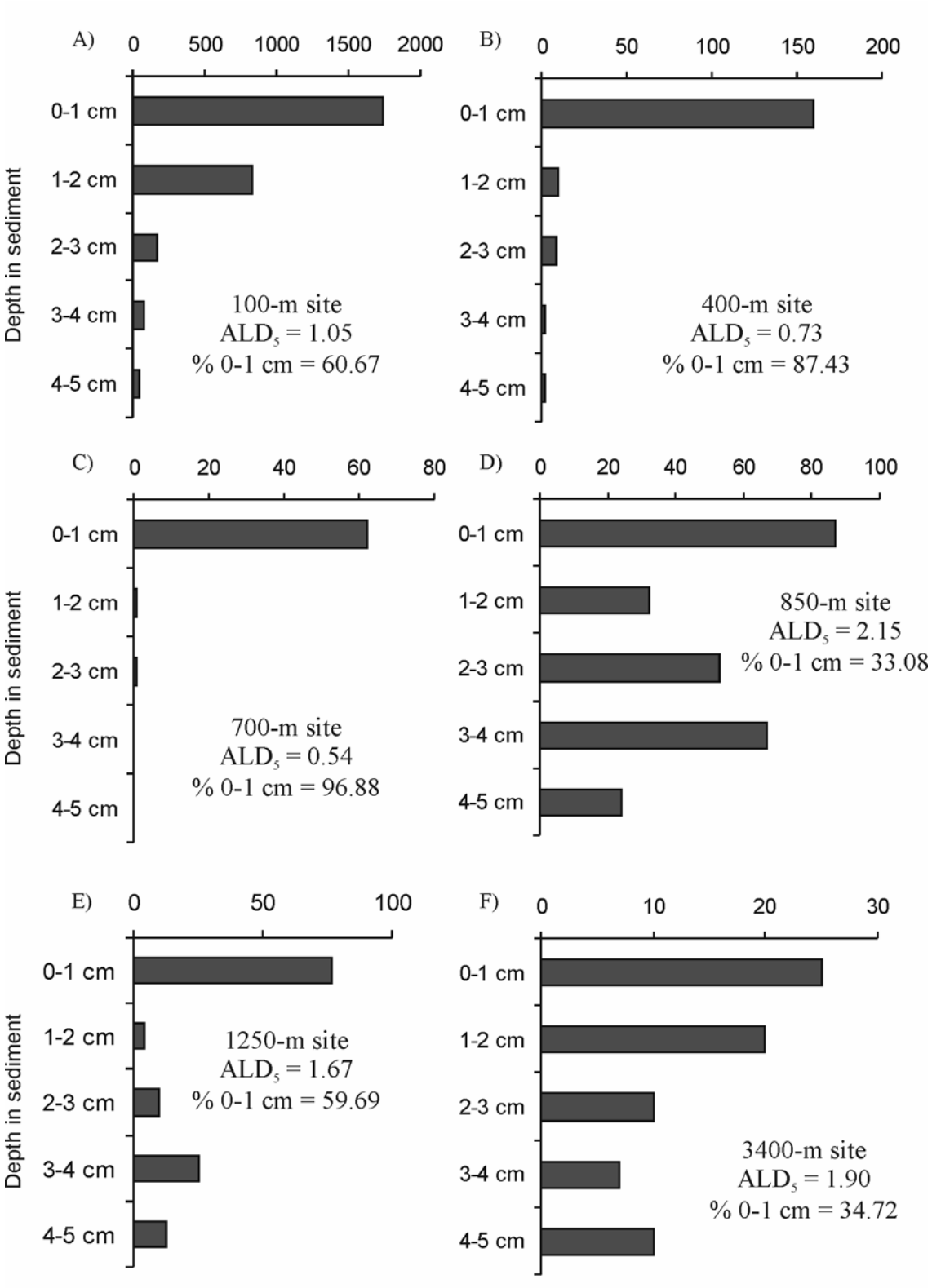
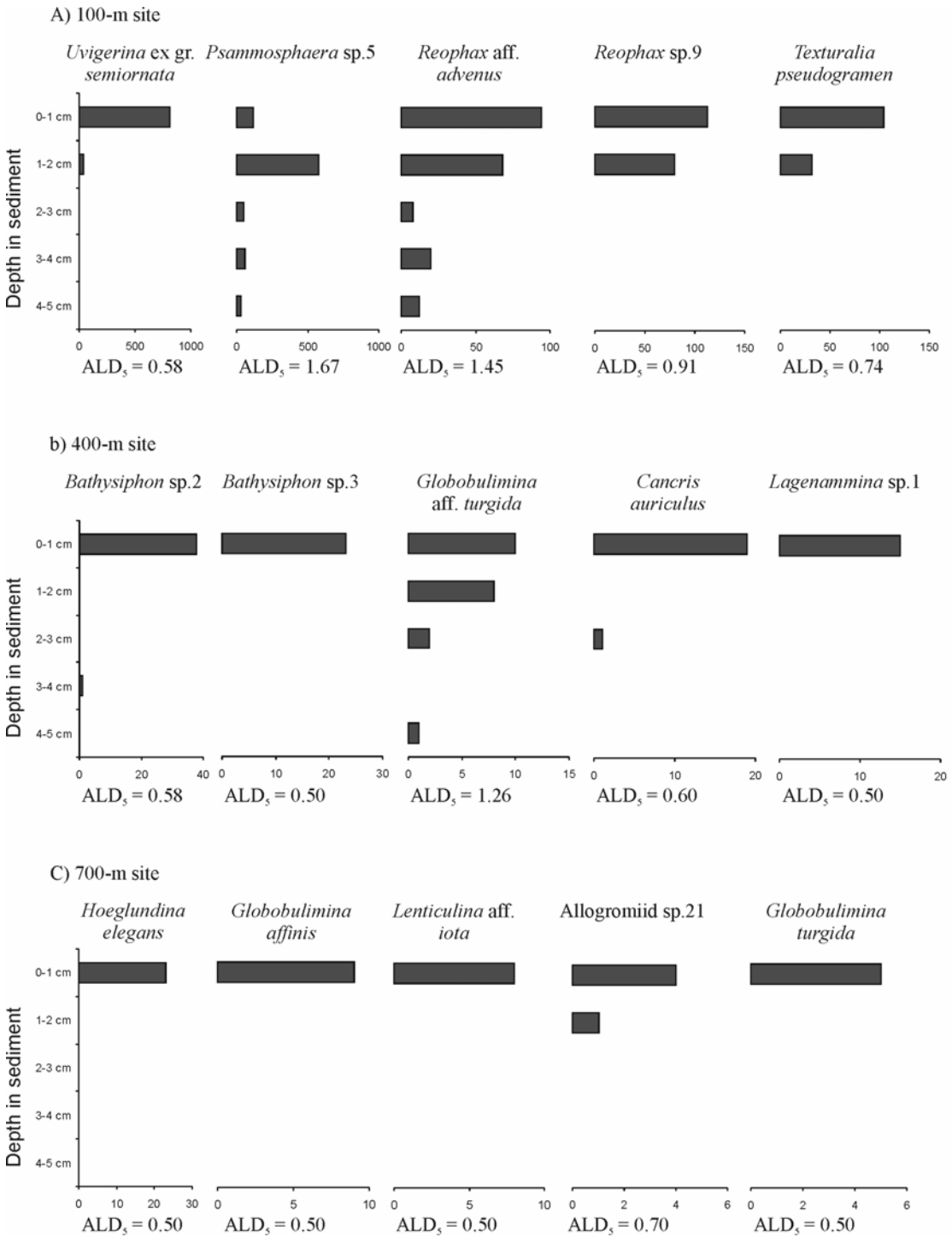


Figure 2.11 Vertical distribution within the sediment profile of live specimens (>300 μm) of the 5 top-ranked species at each site.



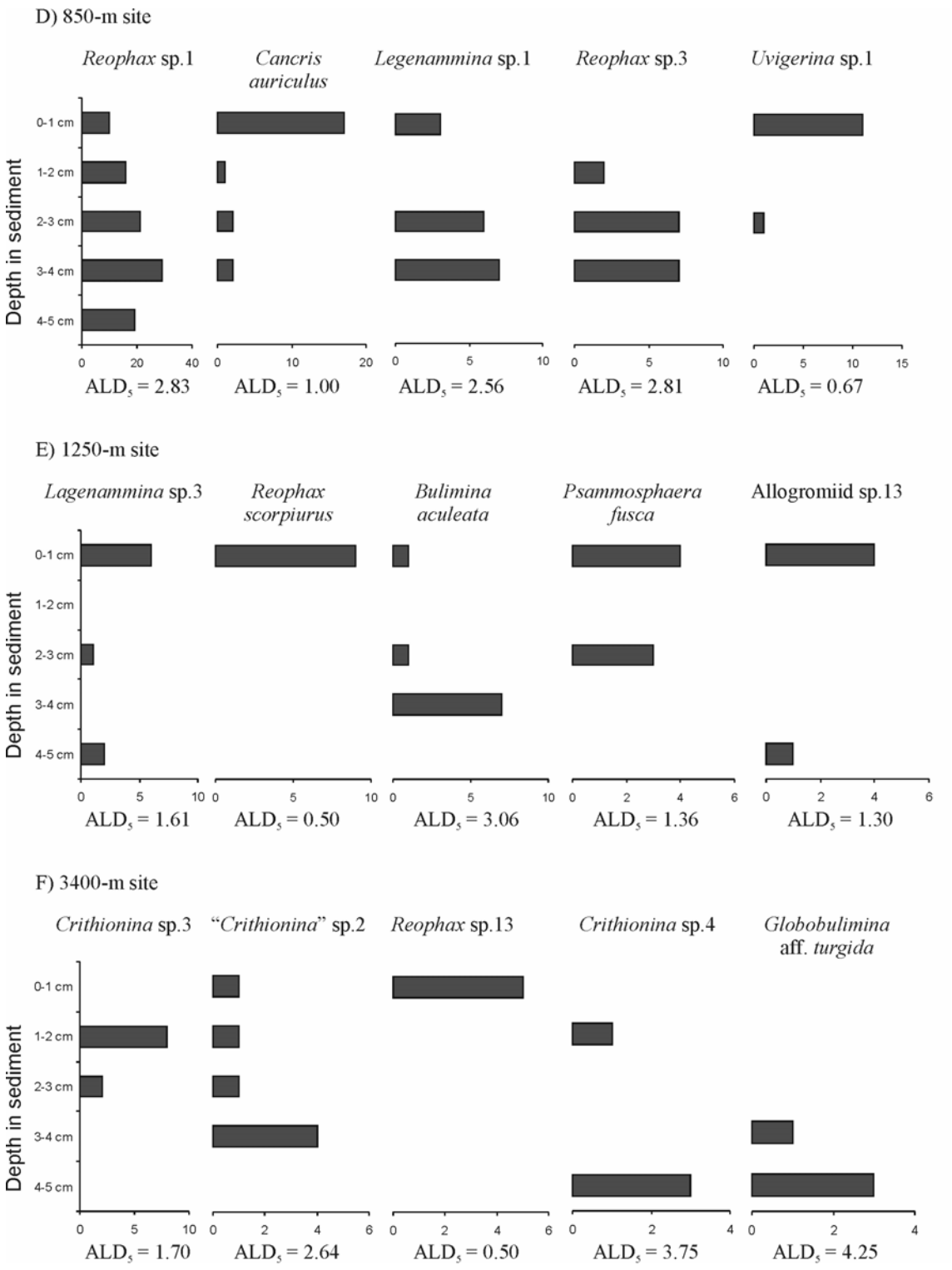
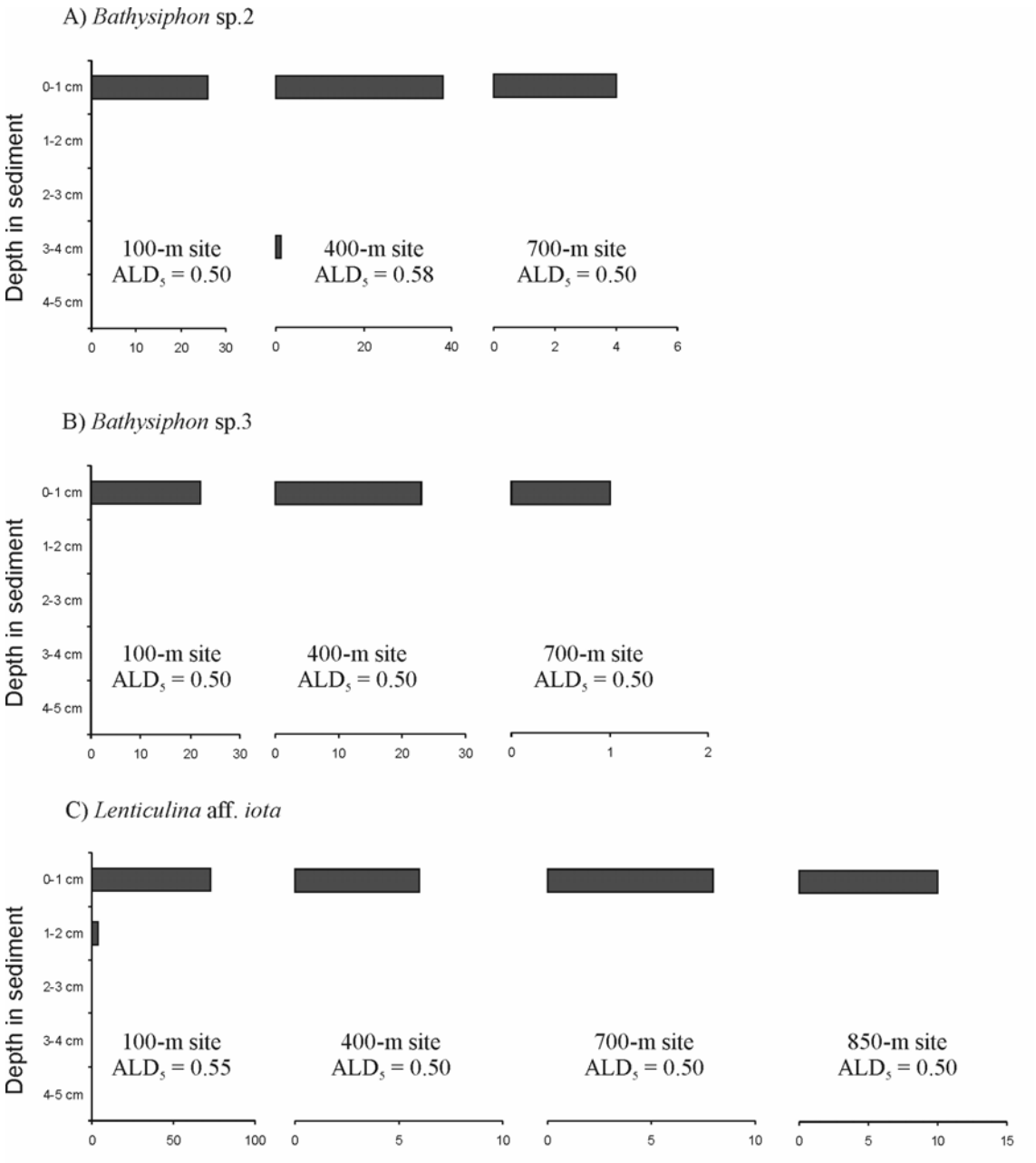
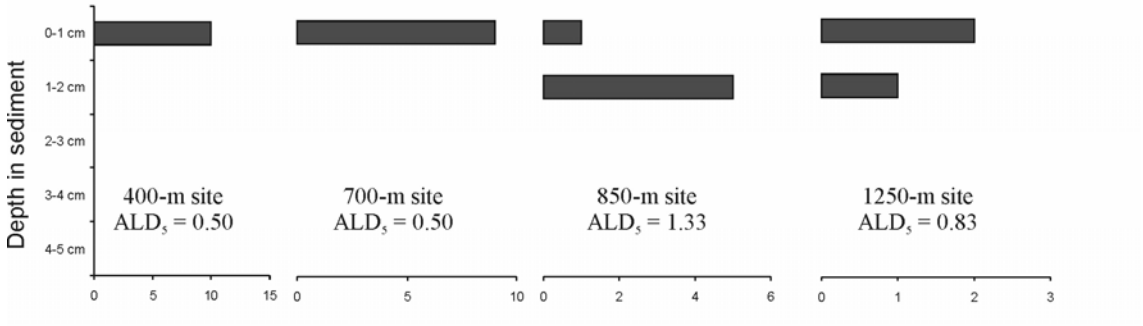

D) 850-m site
Reophax sp.1
Cancris auriculus
Legenammina sp.1
Reophax sp.3
Uvigerina sp.1
Depth in sediment
0-1 cm
1-2 cm
2-3 cm
3-4 cm
4-5 cm
ALD5 = 2.83
ALD5 = 1.00
ALD5 = 2.56
ALD5 = 2.81
ALD5 = 0.67
E) 1250-m site
Lagenammina sp.3
Reophax scorpiurus
Bulimina aculeata
Psammosphaera fusca
Allogromiid sp.13
ALD5 = 1.61
ALD5 = 0.50
ALD5 = 3.06
ALD5 = 1.36
ALD5 = 1.30
F) 3400-m site
Crithionina sp.3
"*Crithionina*" sp.2
Reophax sp.13
Crithionina sp.4
Globobulimina aff. *turgida*
ALD5 = 1.70
ALD5 = 2.64
ALD5 = 0.50
ALD5 = 3.75
ALD5 = 4.25

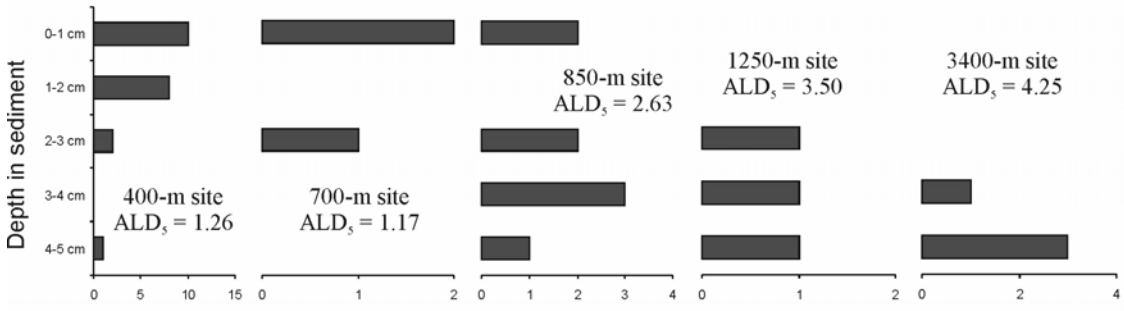
Figure 2.12 Vertical distribution within the sediment profile of live individuals (>300 μm) of species found in at least 50% of samples.



D) *Globobulimina affinis*



E) *Globobulimina* aff. *turgida*



F) *Cancris auriculus*

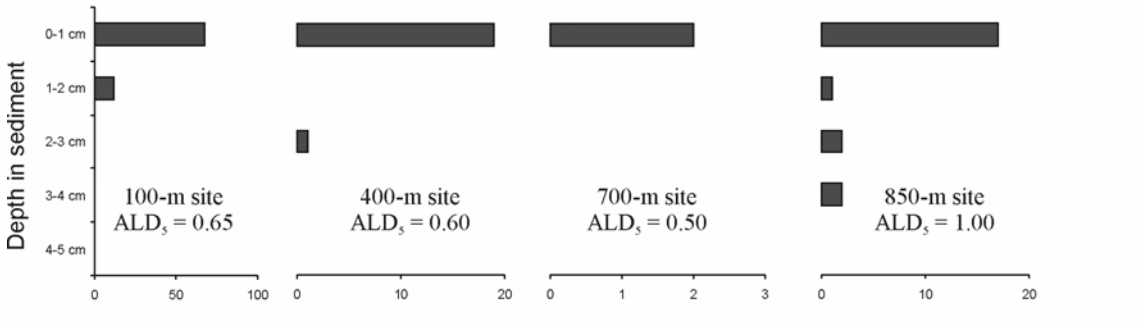
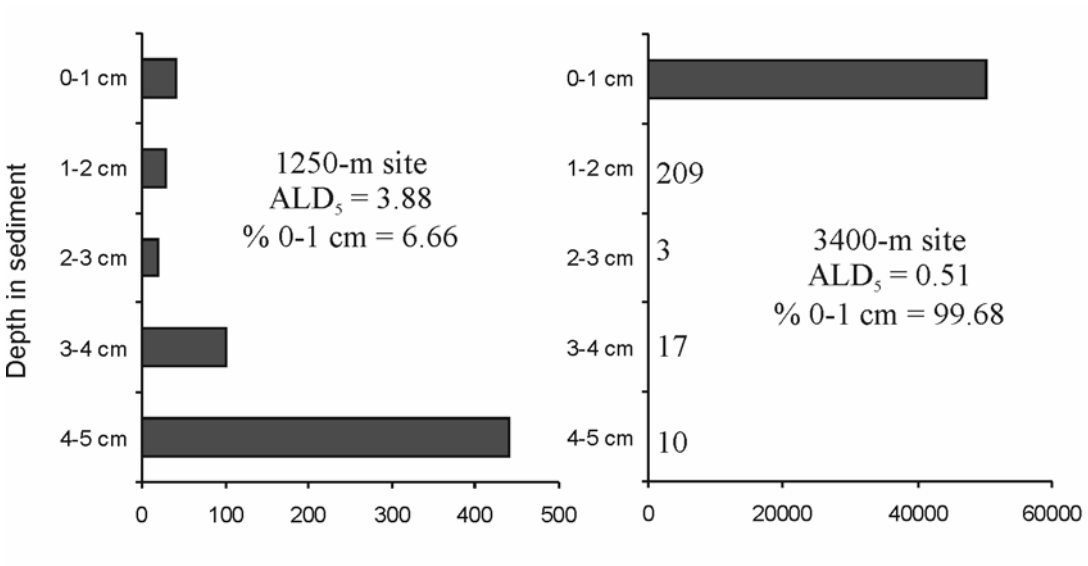


Figure 2.13 Total numbers of stained fragments at different sediment depths. Actual numbers are given for deeper layers in the core from 3400 m.



2.3.2 Metazoan macrofaunal assemblage

2.3.2.1 Abundance

Macrofaunal metazoans (>300 μm) from the 0-5 cm sediment layer were sparse but varied in abundance across the OMZ (Figure 2.14, Table 2.10). As in the case of foraminiferans, metazoans were most abundant at the shallowest 100-m site (295 individuals per 25.5 cm^2) and least abundant at the deepest 3400-m site (29 individuals per 25.5 cm^2). Interestingly, no consistent pattern was observed across the bathymetric transect and total abundance (0-1 cm) differed considerably between two cores taken at the same depth (Figure 2.15). For example, at the 100-m site, one core had a total abundance four times higher than the other core. When only the top 0-1 cm layer was considered, the shallowest site (100 m) still yielded the largest number of metazoans (195 per 25.5 cm^2) (Table 2.10). However, the abundance of metazoans was higher at the deeper sites, 1250 m (36 per 25.5 cm^2) and 3400 m (21 per 25.5 cm^2), where oxygen levels are higher than in the centre of the OMZ at 400 and 700 m.

Table 2.10 Abundance of metazoans in the >300 μm fraction of the 0-5 cm and 0-1 cm sediment layers of multicorer samples, including replicates (*1 - 25.5 cm^2 surface area, *2 - 10 cm^2 surface area). ND = No Data.

Site	Station	0-1 cm *1	0-1 cm *2	0-5 cm *1	0-5 cm *2
100-m	12708#5	195	76	295	116
	12708#3	44	ND	ND	ND
400-m	12695#5	8	3	81	32
700-m	12682#5	2	1	32	13
	12685#2	7	ND	ND	ND
850-m	12713#3	11	4	78	31
	12711#3	17	ND	ND	ND
1250-m	12723#3	36	14	45	18
	12723#5	12	ND	ND	ND
3400-m	12687#3	21	8	29	11

Figure 2.14 Abundance of metazoans (>300 μm) in the 0-5 cm layer of multicore samples (25.5 cm^2 surface area).

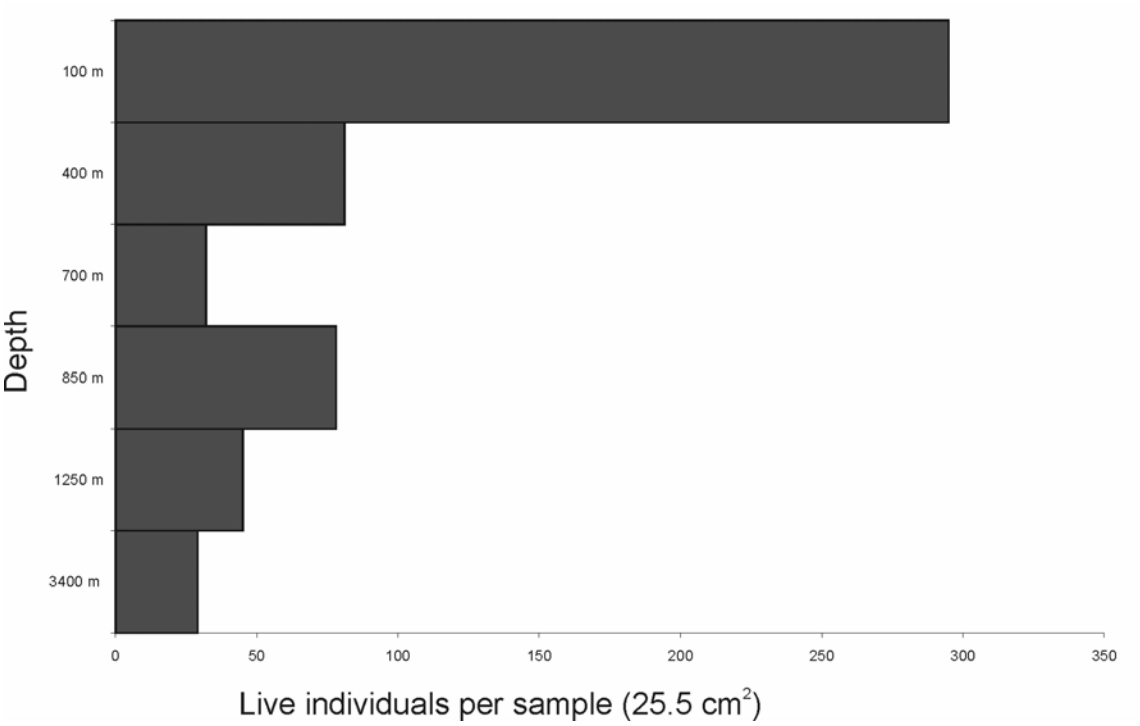
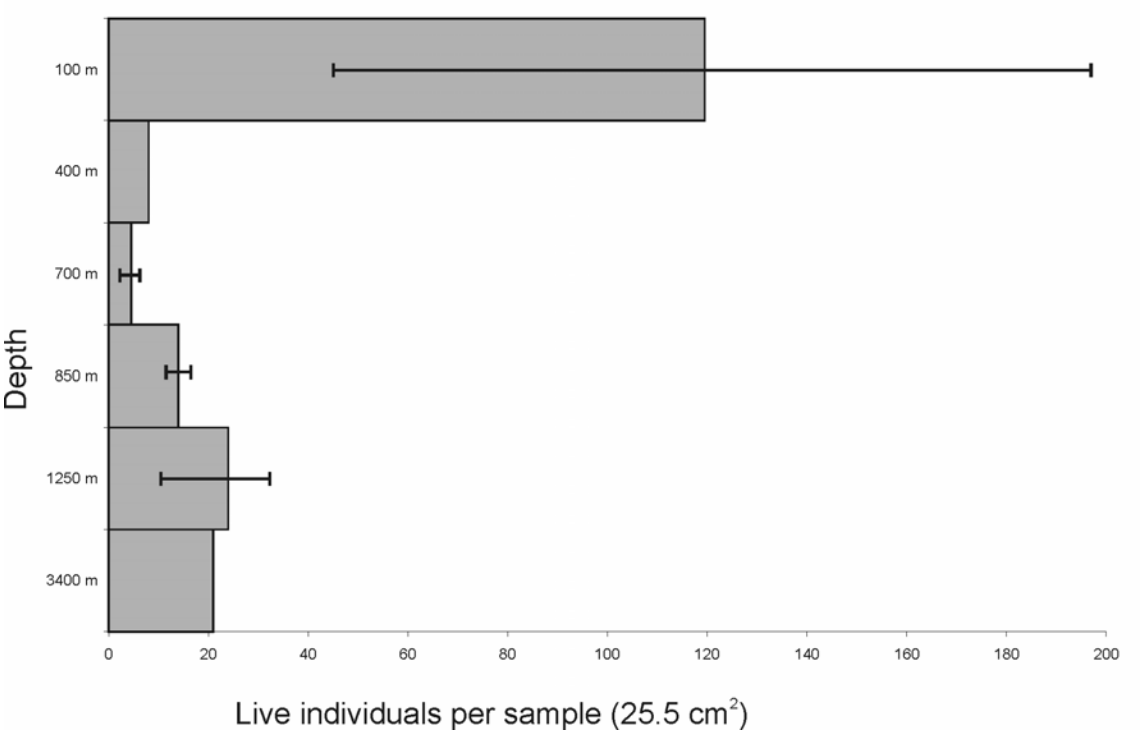


Figure 2.15 Average abundance of metazoans (>300 μm) from two replicates from the 0-1 cm sediment layer of multicore samples (25.5 cm^2 surface area). Note that there are no replicate data for the 400 m and 3400 m sites.



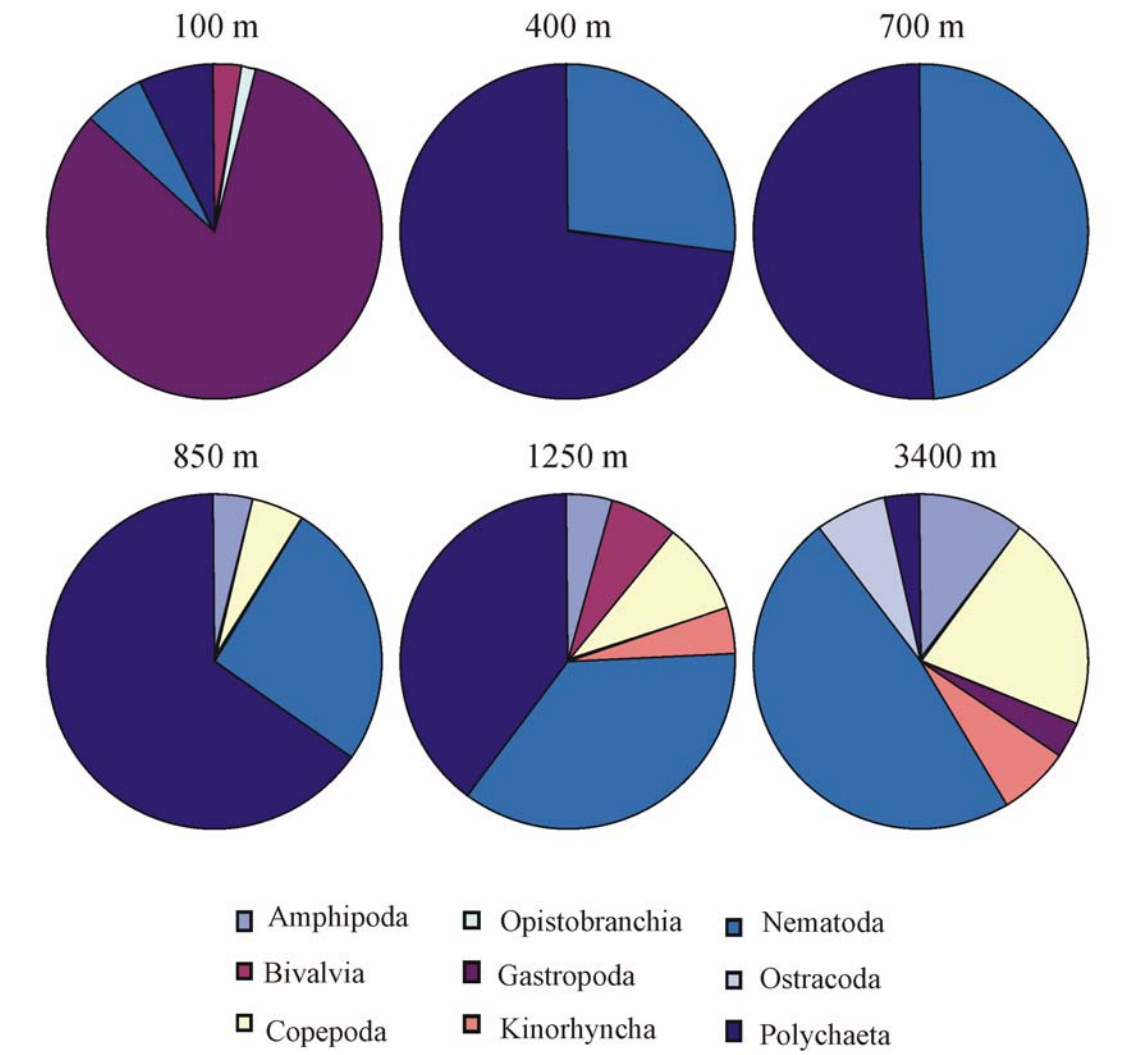
2.3.2.2 Taxonomic composition

Gastropods were the dominant metazoan group at the shallowest site (100 m), accounting for 82.7% of the total metazoan assemblage, followed by polychaetes (7.1%), nematodes (6.1%) and bivalves (2.7%) (Figure 2.16, Table 2.11). They were not found where oxygen levels were lower between 400 and 1250 m water depth, but appear again at the 3400 m site although, in much lower abundances, (3.4% of the assemblage). The 400 m and 700 m sites, in the core of the OMZ contained solely nematodes and polychaetes. Where the oxygen levels were lowest (0.13ml/l) at the 400-m site, polychaetes (72.8%) dominated over nematodes (27.1%), while at 700 m they were equally dominant, 51.5% and 48.5% respectively. The 850 m and 1250 m sites also were dominated by polychaetes (65.4% and 40% respectively) followed by nematodes (25.6% and 35.6% respectively) and two new groups, harpacticoid copepods (5.1% and 8.9% respectively) and amphipods (3.8% and 4.4% respectively). The deepest site contained most metazoan faunal groups found in this study with the exception of bivalves. Contrary to the rest of the sites, nematodes were the dominant group accounting for 48.3% of the total metazoan assemblage, followed by copepods (20.7%), amphipods (10.3%), two new groups, kinorhynchs and ostracods, each 6.9%, and polychaetes and gastropods (each 3.4%).

Table 2.11 Percentage abundance of metazoan groups (live assemblage; >300 μm fraction) from the 0-5 cm layer of 25.5 cm^2 samples.

Site	**100-m**	**400-m**	**700-m**	**850-m**	**1250-m**	**3400-m**
Station	**12708#5**	**12695#5**	**12682#5**	**12713#3**	**12723#3**	**12687#3**
Taxa	**0-5 cm**	**0-5 cm**	**0-5 cm**	**0-5 cm**	**0-5 cm**	**0-5 cm**
Amphipoda	0.0	0.0	0.0	3.8	4.4	10.3
Bivalvia	2.7	0.0	0.0	0.0	6.7	0.0
Copepoda	0.0	0.0	0.0	5.1	8.9	20.7
Opistobranchia	1.4	0.0	0.0	0.0	0.0	0.0
Gastropoda	82.7	0.0	0.0	0.0	0.0	3.4
Kinorhyncha	0.0	0.0	0.0	0.0	4.4	6.9
Nematoda	6.1	27.2	48.5	25.6	35.6	48.3
Ostracoda	0.0	0.0	0.0	0.0	0.0	6.9
Polychaeta	7.1	72.8	51.5	65.4	40.0	3.4
Total specimens	**295**	**81**	**32**	**78**	**45**	**29**

Figure 2.16 Percentage abundance of metazoan groups (live assemblage; >300 μm fraction) found in the 0-5 cm layer of multicore samples (25.5 cm^2 surface area).



2.3.2.3 Vertical distribution patterns within the sediment

As in the case of foraminifera, the metazoan assemblages changed across the OMZ but their distribution within the sediment also varied at each site. At the shallow 100-m and deeper 1250-m and 3400-m sites (sites above and below the OMZ), the metazoans were concentrated within the top 0-1 cm sediment layer (Figure 2.17). At the 100-m site, the 0-1 cm layer accounted for 66.1% of the total (0-5 cm) assemblage, resulting in an ALD_5 of 1.41. Gastropods, the most abundant group (Table 2.11) at this site were concentrated in the top 0-1 cm sediment layer (ALD_5 = 1.40) (Figure 2.18). Nematodes were also only found at the top 0-1 cm (ALD_5 = 0.50). This observation explains the second peak seen in total metazoan abundance at this site for the deepest layer (Figure 2.17). Bivalves and polychaetes were found at the top one centimetre and then in the 2-3 cm sediment layer (ALD_5 = 1.50 and 1.64 respectively). The 0-1 cm layer at 1250 m site accounted for 80% of the total 0-5 cm assemblage (ALD_5 = 0.88) (Figure 2.17). The total abundance of metazoan then decreased with sediment depth. Amphipods, bivalves, copepods and kinorhynchs were restricted to the 0-1 cm sediment layer, all with an ALD_5 of 0.50 (Figure 2.18). Nematodes were most abundant at the top 0-1 cm layer, decreasing with sediment depth and disappearing below 3 cm. Polychaetes, the most abundant metazoan group at this site (Figure 2.16) were also most abundant within the top 0-1 cm layer, but were found in all sediment depths. The metazoans present in the 0-1 cm sediment layer of the deepest site at 3400 m water depth represented 72.4% of the total (0-5 cm) assemblage. The ALD_5 at this site was 1.02, and total abundances decreased with sediment depth (Figure 2.18). Gastropods, kinorhynchs, ostracods and polychaetes were found only at the top 0-1 cm sediment layer, all with an ALD_5 of 0.50.

The 400 m site within the core of the OMZ had an ALD_5 of 2.18, with highest total metazoan abundances found at the 2-3 cm sediment layer (Figure 2.17). From this layer there was a decrease in abundance with sediment depth. Interestingly, the 0-1 cm and 1-2 cm sediment layers yielded the lowest abundances, with 0-1 cm accounting for only 9.9% of the total assemblage. The 700 m and 850 m sites showed highest metazoan abundances in the 1-2 cm sediment layer, with ALD_5 values of 2.47 and 2.26 respectively (Figure 2.17). From this peak, there was a decrease in total metazoan abundances with sediment depth. At 700 m, lowest number of metazoans was found in the 0-1 cm sediment layer (6.1% of total); at the 850-m site, the equivalent proportion was 14.1%. It is interesting to note that nematodes were absent from the top 0-1 cm layer of the sediment at 850 m.

Figure 2.17 Vertical distribution within the sediment profile of metazoans (individuals from >300 µm) across the OMZ.

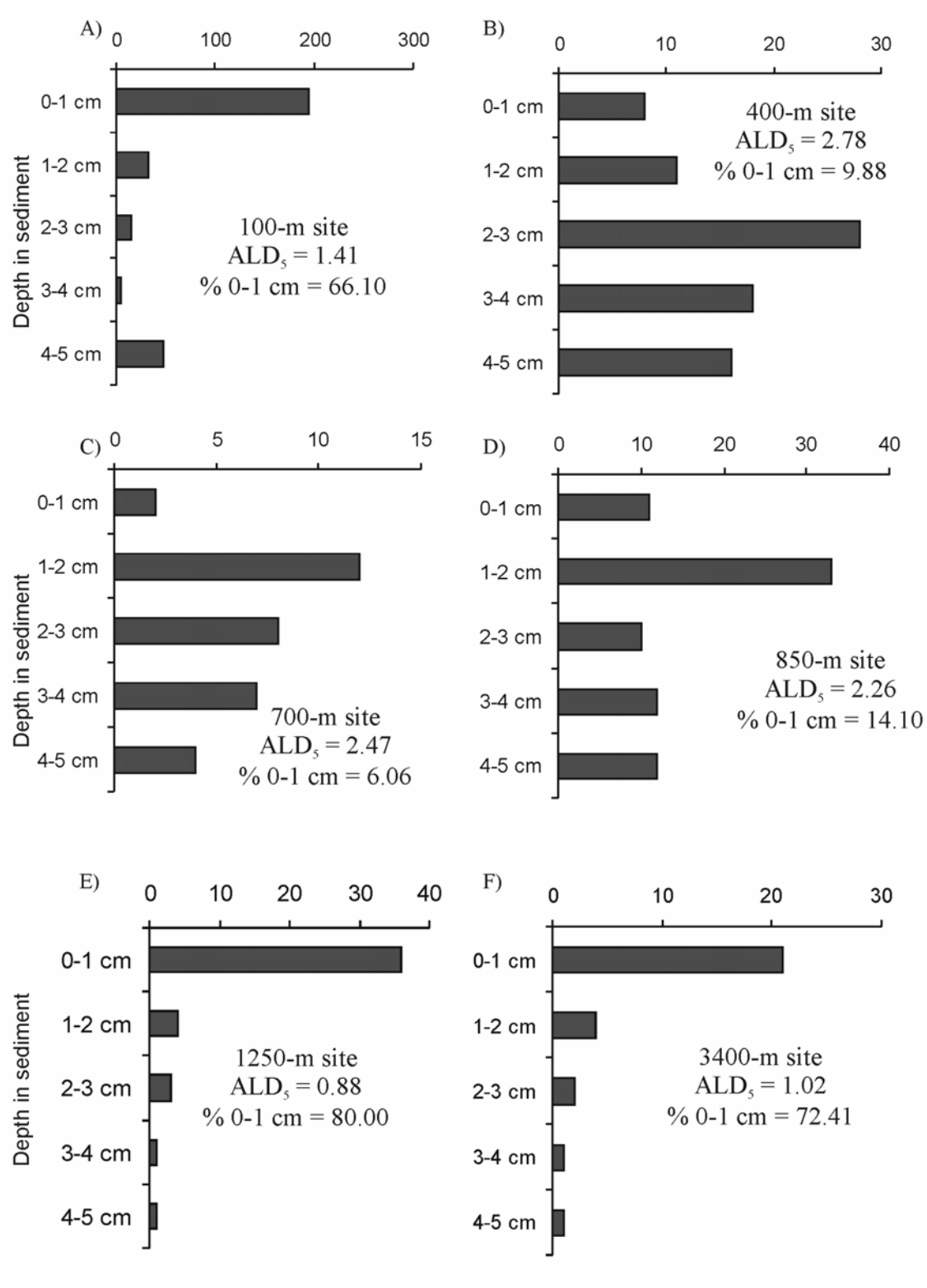
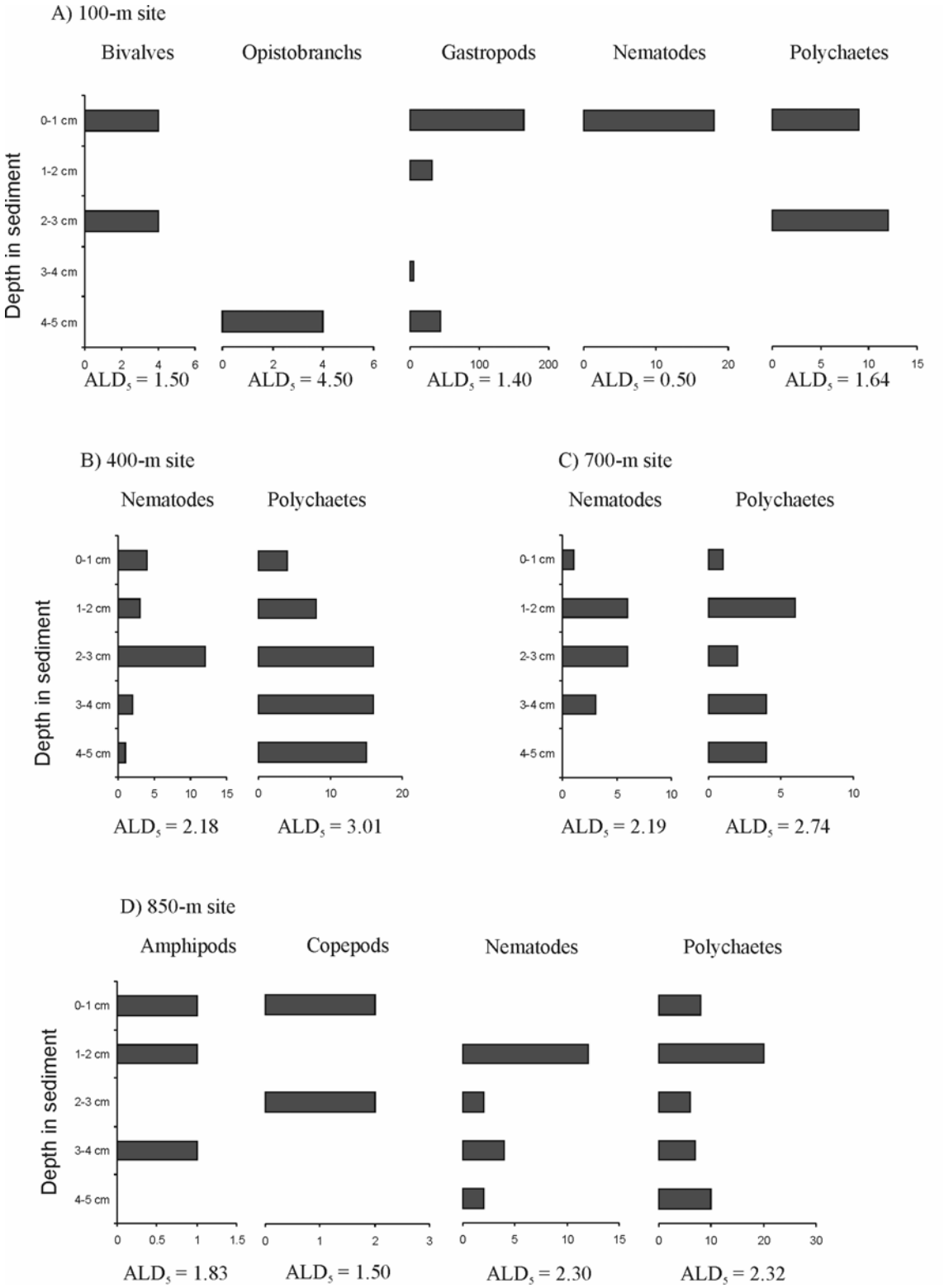
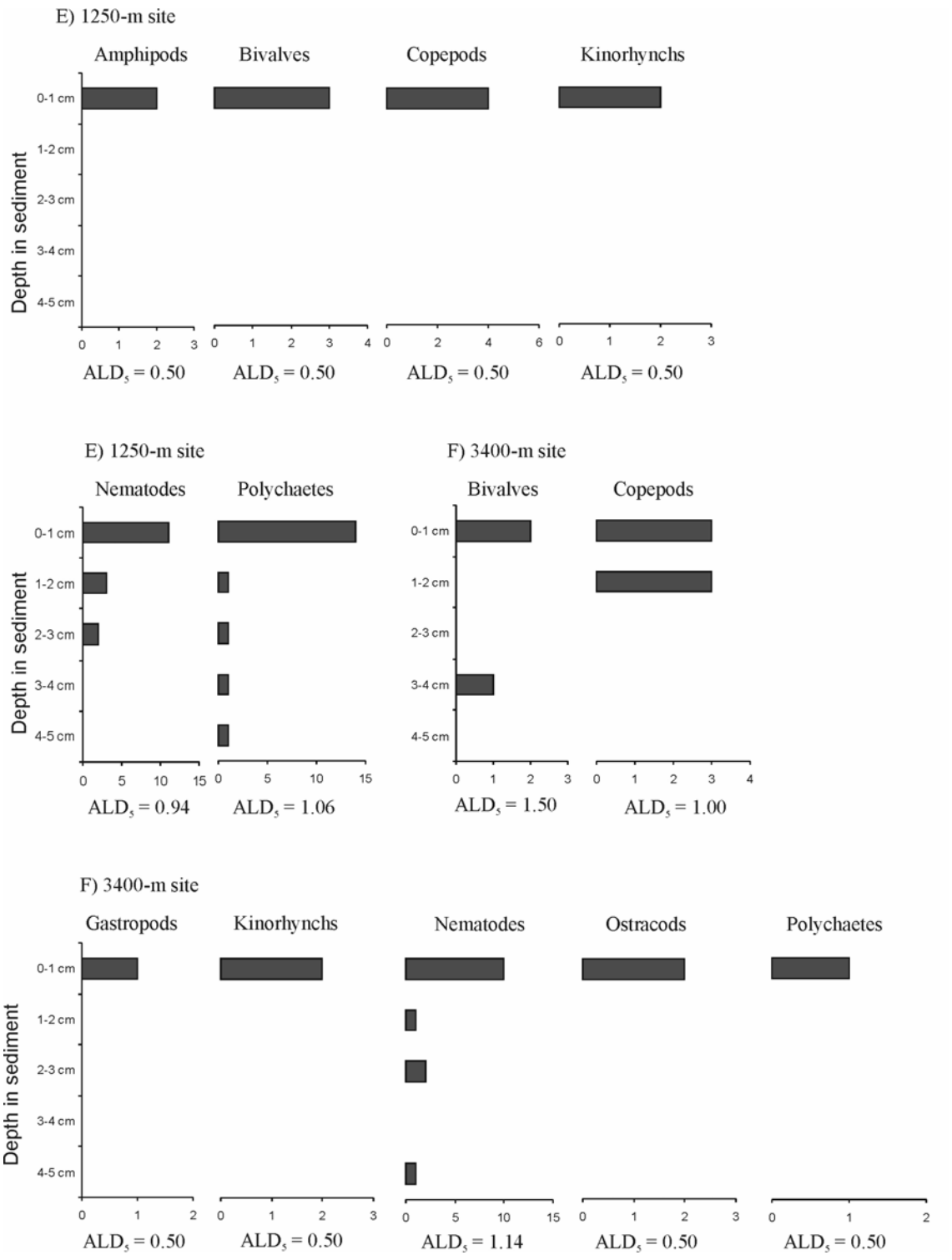


Figure 2.18 Vertical distribution within the sediment profile of each metazoan taxa (>300 µm).





It is difficult to draw any firm conclusions regarding the taxonomic composition of the metazoans or their vertical distribution because of the very small numbers of metazoan found in multicore samples in this study. The purpose of the results presented above is solely to give a brief idea of the metazoan found in the samples. For the purpose of discussion (see below), foraminiferal trends are compared to published metazoan results from Levin et al. (2000).

2.3.3 Foraminiferal dead assemblage

2.3.3.1 Abundance

Dead foraminiferans (including empty tests and tests with degraded brown contents) from the 0-5 cm sediment layer (>300 μm) varied in abundance across the OMZ (Figure 2.19, Table 2.12 and Appendix C). As in the case of the living community, the 100 m site had by far the highest abundance of dead tests. These comprised 8336 agglutinated tests, all of which were counted, and an estimated 50,000 tests of *Uvigerina* ex gr. *semiornata* giving a total density of around 58,000. This was substantially higher than the second highest density which was found at 700 m (2713 per 25.5 cm^2). Total abundance per 25.5 cm^2 at 400 m was 2190, followed by 1034 at 850 m and 554 at 1250 m. The lowest abundance (47 per 25.5 cm^2) was found at the deepest site (3400 m). The 0-1 cm sediment layer yielded relatively few dead tests. They were totally absent from the >300 μm fraction at the 400-m and 3400-m sites, although substantial numbers occurred in deeper layers. Interestingly, the 700-m site had the highest proportion (20.4%) of dead tests in the 0-1 cm layer.

Figure 2.19 Abundance of dead foraminifera tests (>300 μm) from the 0-5 cm and 0-1 cm sediment layers of multicore samples (25.5 cm^2 surface area).

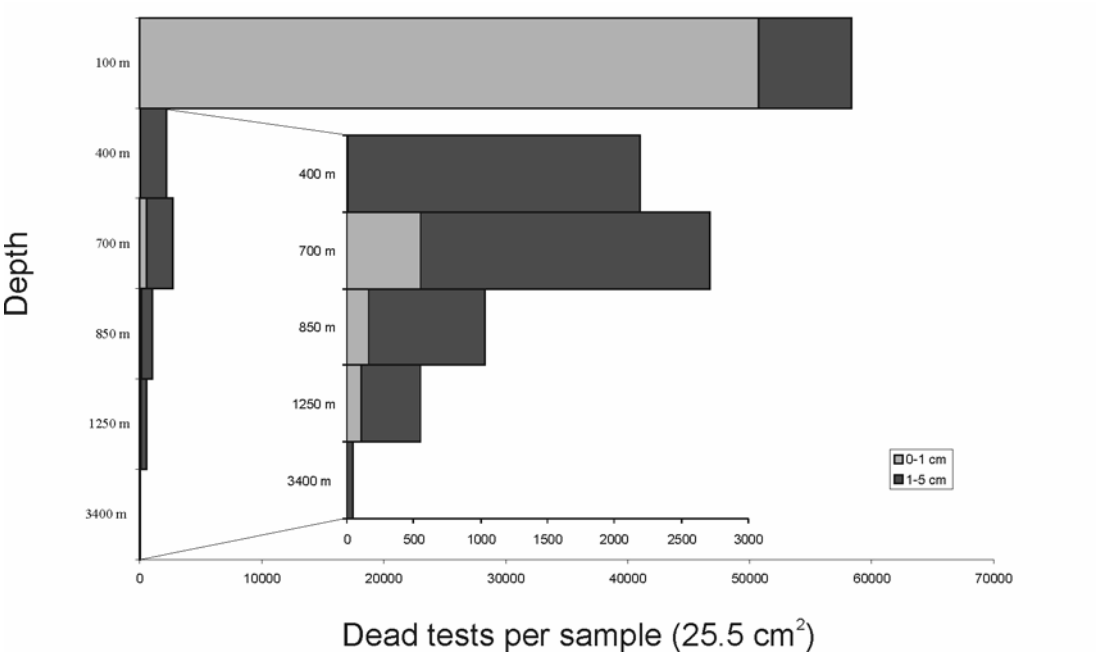


Table 2.12 Abundance of dead foraminiferal tests from the > 300 μm fraction of the 0-5 cm and 0-1 cm sediment layers of multicorer samples.

Site	Station	0-1 cm 25.5 cm^2	0-1 cm 10 cm^2	0-5 cm 25.5 cm^2	0-5 cm 10 cm^2
100-m	12708#5	~ 51,000	~ 20,000	~ 58,000	~ 23,000
400-m	12695#5	10	4	2190	855
700-m	12682#5	554	217	2713	1064
850-m	12713#3	162	64	1034	405
1250-m	12723#3	105	41	554	217
3400-m	12687#3	1	0	47	18

2.3.3.2 Taxonomic composition

Calcareous taxa dominated the >300 μm foraminiferal dead assemblage at all sites, representing 85.7%, 96.1%, 93.7%, 93.9%, 52.7% and 78.7% of all dead shells at 100 m, 400 m, 700 m, 850 m, 1250 m and 3400 m respectively (Table 2.13). At the shallowest site (100 m), the dead assemblage consisted of only three species. The abundance of *Uvigerina* ex gr. *semiornata* was estimated at about 50,000 (86% of dead fauna) while two agglutinated species, *Psammosphaera* sp.5 and *Reophax* aff. *advenus*, represented ~ 8% and ~ 6% of the dead assemblage respectively (Table 2.13, Table 2.14). At the 400-m and 3400-m sites, the Buliminida was the dominant calcareous taxon, accounting for 86.3% and 70.2% of all dead tests respectively. At the 1250-m site, buliminids represented 29.4% of the dead assemblage. In both cases, other calcareous taxa comprised a relative small proportion of the total (Table 2.13 and 2.14). Multilocular agglutinated foraminiferans (32.8%), most of them hormosinaceans (27.1%), constituted the second most abundant group. Dead tests of monothalamous, hard-shelled, agglutinated foraminiferans were found at the 400-m and 3400-m sites where they represented 2.8% and 4.3% of the dead assemblage respectively.

Globobulimina affinis and *Globobulimina* aff. *turgida* were the most abundant species at 400 m where they represented 45.5% and 38.7% of the dead assemblage respectively. The next most abundant species was *Lenticulina* aff. *iota* (7.6%). This last species was the most abundant (30.0%) at the 700-m site, ahead of *Uvigerina peregrina* (25.4%) and *Globobulimina turgida* (18.8%). It was also the top-ranked species (34.9%) at the 850-m site, followed by the robertinid *Hoeglundina elegans* (17.8%) and the buliminids *Globobulimina turgida* (12.1%), *G.* aff. *turgida* (9.6%) and *G. affinis* (6.9%). *Bulimina aculeata* was the dominant species at 1250 m, where it contributed 15.0% of the dead assemblage, followed by the hormosinaceans *Reophax scorpiurus* (9.6%) and *Reophax* sp.4 (9.0%). The very sparse dead assemblage at the deepest site (3400 m) consisted mainly of two species, *Uvigerina* sp.3 (44.7%) and *Globobulimina* aff. *turgida* (21.7%).

Table 2.13 Percentage abundance of major foraminiferal groups (dead assemblage; >300 μm fraction) from the 0-5 cm layer of 25.5 cm^2 samples. MAF – Multilocular Agglutinated Foraminifera.

Site	**100-m**	**400-m**	**700-m**	**850-m**	**1250-m**	**3400-m**
Station	**12708#5**	**12695#5**	**12682#5**	**12713#3**	**12723#3**	**12687#3**
Taxa						
Astrorhizida:						
Astrorhizida: Saccamminidae: hard-shelled *Saccammina*	0.0	2.8	0.0	0.0	0.0	4.3
Astrorhizida: Saccamminidae: *Lagenammina*	~ 8	0.2	0.0	3.1	3.25	0.0
Astrorhizida: Psammosphaeridae: spheres and domes	0.0	0.0	0.0	0.0	8.84	0.0
Astrorhizida: Bathysiphonidae	0.0	0.0	0.1	0.1	0.0	2.1
Various	0.0	0.0	0.0	0.0	2.35	4.3
Total	**~ 8**	**3.1**	**0.1**	**3.2**	**14.4**	**6.4**
MAF:						
Lituolida: Ammodiscacea: Ammodiscidae	0.0	0.0	0.0	0.1	0.4	0.0
Lituolida: Hormosinacea	~ 6	0.3	0.0	2.6	27.1	2.1
Textulariida: Textulariacea	0.0	0.0	100.0	0.1	2.2	4.3
Other MAF	0.0	0.6	5.3	0.1	3.2	4.3
Total	**~ 6**	**0.9**	**6.3**	**2.9**	**32.8**	**10.6**
Calcareous:						
Miliolida	0.0	0.0	0.0	0.0	5.4	0.0
Lagenida	0.0	9.0	30.1	35.0	0.5	6.4
Buliminida	~ 86	86.3	55.5	35.7	29.4	70.2
Rotaliida	0.0	0.8	0.1	5.3	16.8	2.1
Robertiniida	0.0	0.0	8.0	17.8	0.5	0.0
Total	**~ 86**	**96.1**	**93.7**	**93.9**	**52.7**	**78.7**
Total specimens	**~ 58000**	**2190**	**2714**	**1033**	**554**	**47**

Table 2.14 Top ranked dead species in samples from the 0-5 cm sediment layer across the Oman OMZ (>300 μm fraction). The percentage of each species is given in parentheses after the species names. The total numbers of dead specimens in each sample are given at the bottom of each column. * At 100 m, only dead specimens of the two agglutinated species were counted (n = 8336). Dead tests of *Uvigerina* ex gr. *semiornata* were too numerous to count. Instead, they were estimated to represent 90% of all dead tests, leading to a total estimate of 58,000 dead tests in this sample.

100-m 12708#5 O_2 0.46 ml/l	**400-m 12695#5 O_2 0.13 ml/l**	**700-m 12682#5 O_2 0.16 ml/l**	**850-m 12713#3 O_2 0.20 ml/l**	**1250-m 12723#3 O_2 0.52 ml/l**	**3400-m 12687#3 O_2 2.99 ml/l**
**Uvigerina* ex gr. *semiornata* (~ 86%)	*Globobulimina affinis* (45.5%)	*Lenticulina* aff. *iota* (30.0%)	*Lenticulina* aff. *iota* (34.9%)	*Bulimina aculeata* (15.0%)	*Uvigerina* sp.3 (44.7%)
**Psammosph.* sp.5 (~ 8%)	*Globobulimina* aff. *turgida* (38.7%)	*Uvigerina peregrina* (25.4%)	*Hoeglundina elegans* (17.8%)	*Reophax scorpiurus* (9.6%)	*Globo.* aff. *turgida* (21.3%)
**Reophax* aff. *advenus* (~ 6%)	*Lenticulina* aff. *iota* (7.6%)	*Globobulimina turgida* (18.8%)	*Globobulimina turgida* (12.1%)	*Reophax* sp.4 (9.0%)	*Saccammina* sp.15 (4.3%)
	Saccamminid sp.9 (2.8%)	*Hoeglundina elegans* (8.0%)	*Globobulimina* aff. *turgida* (9.6%)	*Psammosphaera fusca* (6.7%)	*Crithionina* sp.4 (4.3%)
	Uvigerina peregrina (1.7%)	*Globobulimina* aff. *turgida* (6.8%)	*Globobulimina affinis* (6.9%)	*Ehrenbergina* sp.1 (6.3%)	*Ammobacul. agglutinans* (4.3%)
	Saracenaria sp.1 (1.2%)	*Globobulimina affinis* (4.4%)	*Cancris auriculus* (5.2%)	*Globobulimina affinis* (5.4%)	*Globo.* sp.3 (4.3%)
	Cribrostomoides wiesneri (0.6%)	*Cribrostomoides wiesneri* (4.3%)	*Uvigerina* sp.1 (3.9%)	*Hyalinea balthica* (4.7%)	
	Chilostomella ovoidea (0.6%)	*Labrospira* sp.1 (0.9%)	*Uvigerina peregrina* (3.1%)	*Reophax* sp.6 (4.3%)	
	Uvigerina sp.1 (0.4%)	*Tritaxia* sp.1 (0.9%)	*Lagenammina* sp.2 (1.9%)	*Pyrgo depressa* (3.8%)	
	Reophax sp.11 (0.3%)		*Lagenammina* sp.1 (1.2%)	*Lagenammina* sp.3 (2.9%)	
***~ 58,000**	**2190**	**2714**	**1033**	**554**	**47**

2.3.3.3 Vertical distribution patterns within the sediment

The abundance of dead tests varied across the sampled transect but it also varied within the sediment profile. Unlike the live assemblage, dead tests were not necessarily most abundant in the top 0-1 cm sediment layer with the exception of the shallow site at 100 m. This layer yielded 52.7%, 0.46%, 20.4%, 15.7%, 18.9% and 2.1% of the dead assemblage at the 100-m, 400-m, 700-m, 850-m, 1250-m and 3400-m sites respectively (Figure 2.20). At 100 m, dead tests decreased in abundance with depth. The average depth of dead tests ($ADDT_5$) for the top-ranked calcareous species *Uvigerina* ex gr. *semiornata* was 1.18 (Figure 2.21), while agglutinated species had deeper $ADDT_5$ values (*Psammosphaera* sp.5 = 2.49 and *Reophax* aff. *advenus* = 2.98). The site at 400-m, where oxygen concentrations were lowest (O_2 0.13 ml/l), very few

tests (10) were present in the top 0-1 cm layer, there was a peak abundance at 3-4 cm and an $ADDT_5$ of 3.17. The 700-m, 850-m and 1250-m sites had $ADDT_5$ values of 2.13, 2.79 and 2.16 respectively with dead tests found throughout the vertical profile. At 700 m, dead tests were rather more abundant in the 1-2 cm sediment layer and the top-ranked species, all of which were calcareous (*Lenticulina* aff. *iota*, *Uvigerina peregrina*, *Globobulimina turgida, Hoeglundina elegans*, *Globobulimina* aff. *turgida* and *Globobulimina affinis*), exhibited a variety of patterns in the upper 5 cm of the sediment. The 850-m site was also dominated by dead calcareous tests (*Lenticulina* aff. *iota*, *Hoeglundina elegans*, *G. turgida*, *G.* aff. *turgida* and *G. affinis*) which tended to be more abundant in deeper sediment layers (3-4 and 4-5 cm). At 1250 m, dead tests of the calcareous species, *Bulimina aculeata*, were found mainly below 1 cm depth. Dead tests of two hormosinacean species (*Reophax scorpiurus* and *Reophax* sp.4) were found abundantly in the deep sediment layers at this site. The 3400-m site had very few specimens in the top 0-2 cm layers, with dead tests being confined largely to deeper layers, reflected by the $ADDT_5$ of 3.93. Dead tests of two calcareous species, *Uvigerina* sp.3 and *Globobulimina* aff. *turgida,* were most common.

Dead tests of three calcareous species, *Globobulimina affinis*, *Globobulimina* aff. *turgida* and *Lenticulina* aff. *iota*, were found in at least half the sites (Figure 2.21). *Globobulimina affinis* was more abundant in the deeper sediment layers at the 400 m site ($ADDT_5$ = 3.42), followed by 850-m and 1250-m site ($ADDT_5$ = 2.37 and 2.30 respectively). At 700 m, it was concentrated in the 1-2 cm layer with an $ADDT_5$ of 1.78. *Globobulimina* aff. *turgida* was mainly found deeper in the sediment at the 400-m and 3400-m sites ($ADDT_5$ = 2.99 and 3.90 respectively) and slightly shallower at 700 m and 850 m ($ADDT_5$ = 2.00 and 2.01 respectively). *Lenticulina* aff. *iota* was most common in the 3-4 cm sediment layer at the 400-m site. At the 700-m and 850-m sites dead tests of this species increased in numbers with sediment depth, a trend reflected by $ADDT_5$ values of 2.78 and 3.39 respectively.

Figure 2.20 Vertical distribution within the sediment profile of dead tests (>300 μm) across the OMZ.

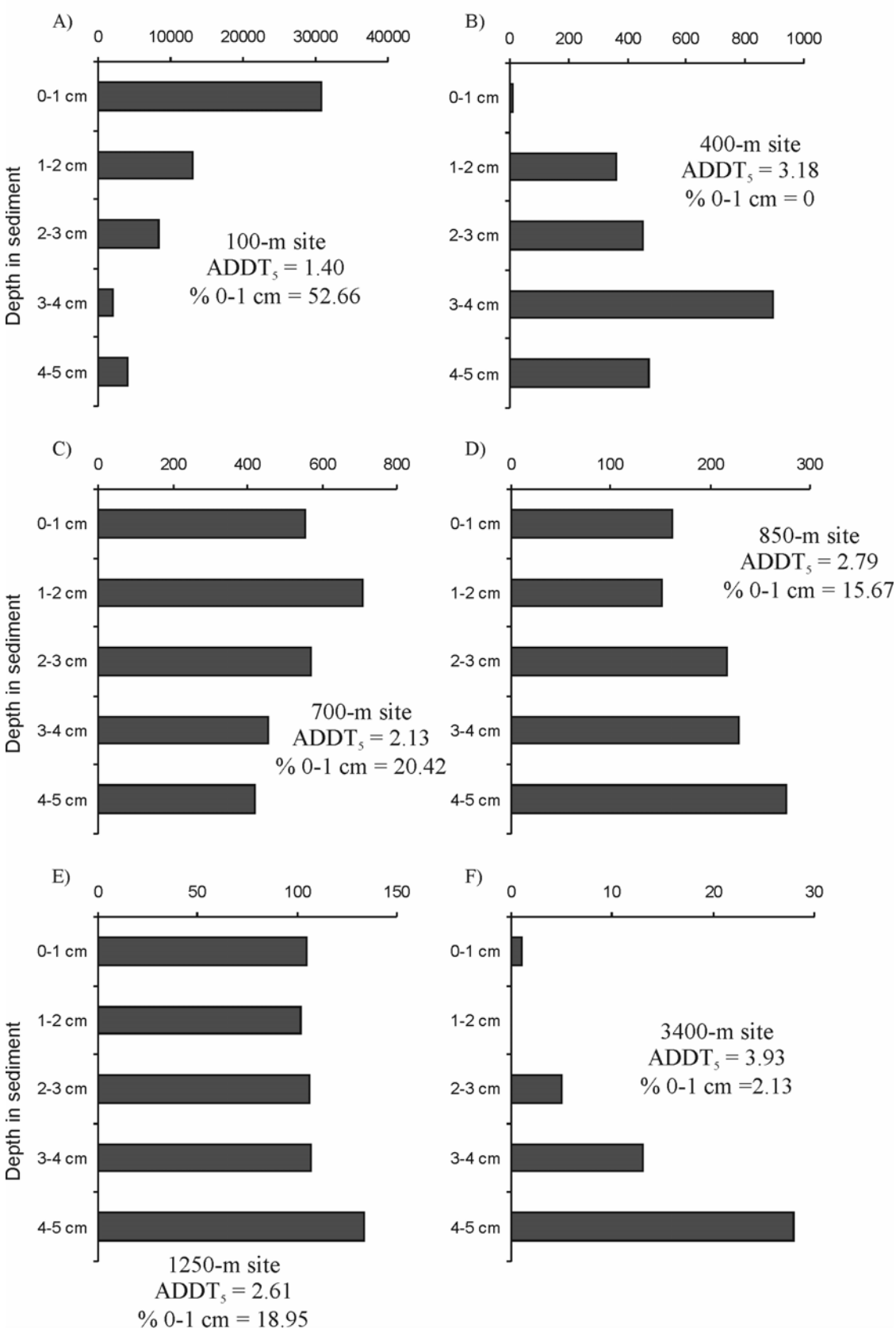
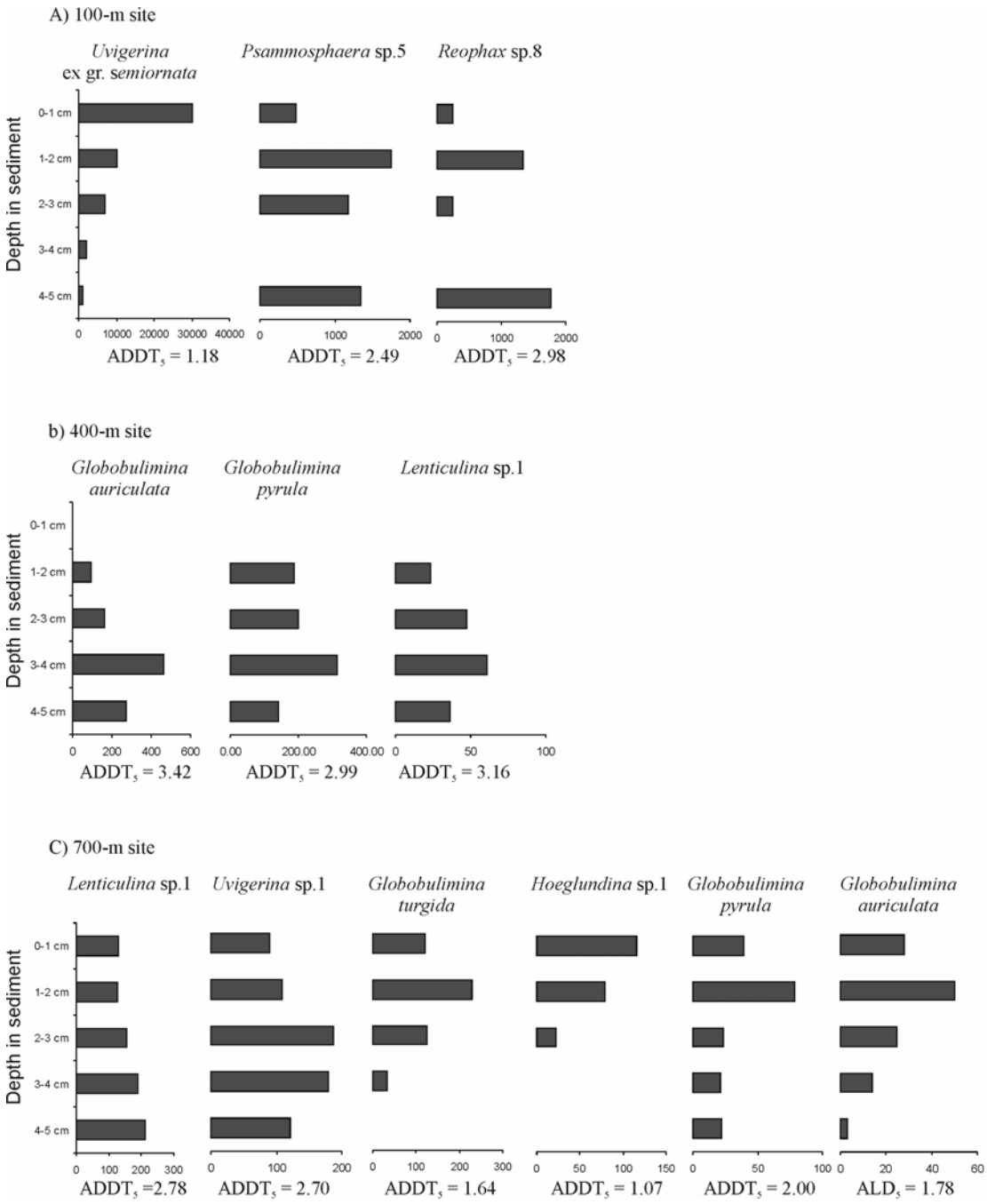
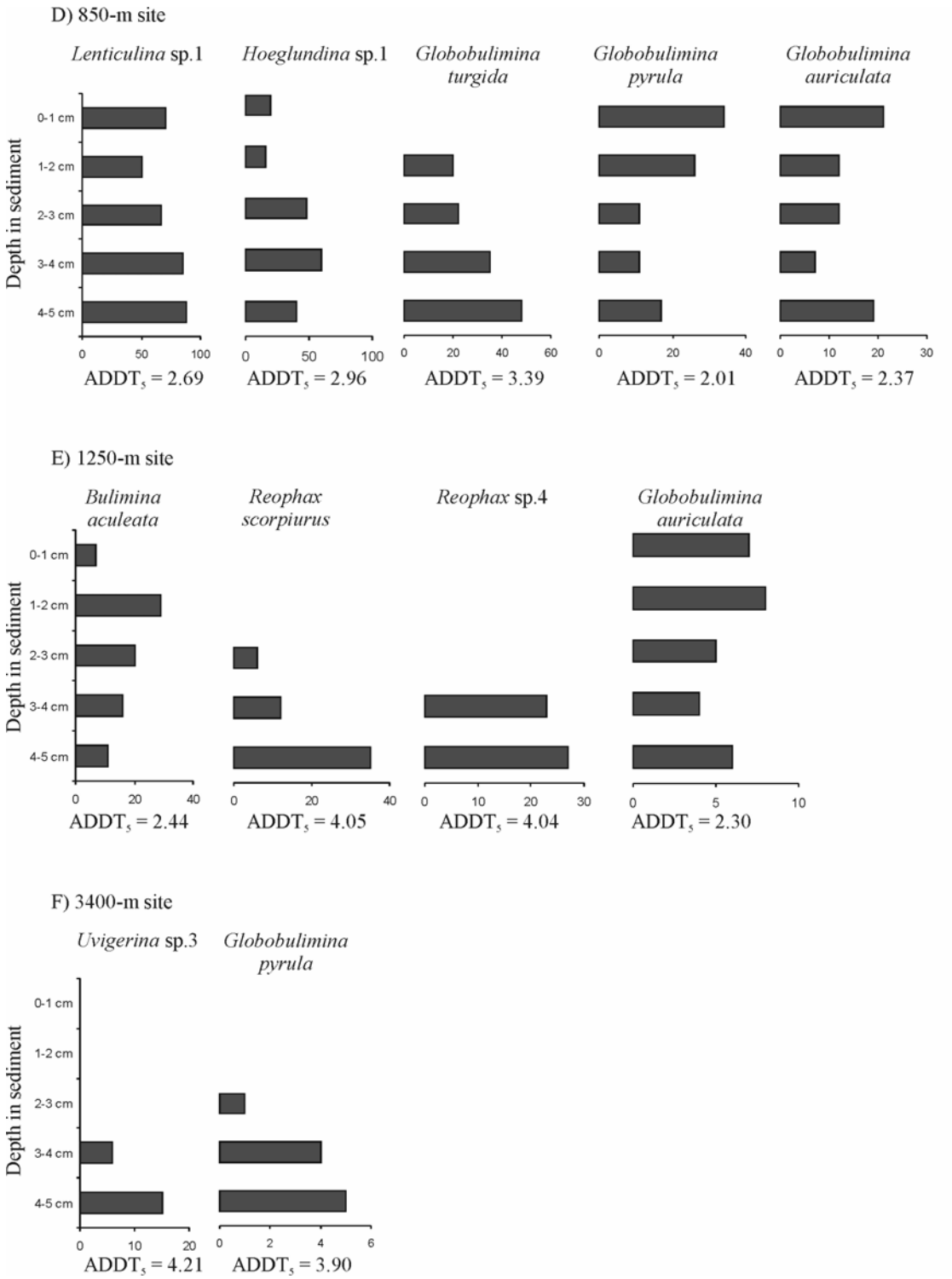


Figure 2.21 Vertical distribution within the sediment profile of dead tests (>300 μm) of the top-ranked species at each site.





2.3.3.4 Live:dead ratios

Although the abundance of dead tests was much greater than the abundance of live specimens, the number of species in the dead assemblage was much less. A total of 81 dead species, compared to 162 live species, were extracted from the cores sorted down to 0-5 cm in the sediment (Appendix C). The live:dead ratios were generally higher for the 0-1 cm than the 0-5

cm sediment layer reflecting the higher abundance of foraminifera living within the top 0-1 cm layer (Table 2.15). Live:dead ratios increased with water depth. For the 0-5 cm layer, the 700-m site was the only one that deviated from the trend with a lower live:dead ratios of 0.02.

Table 2.15 Ratios between the total abundances of live and dead foraminifera from the >300 μm fraction of the 0-5 cm and 0-1 cm sediment layers of multicorer samples.

Sediment layer Depth (m)	0-1 cm Live	0-1 cm Dead	0-5 cm Live	0-5 cm Dead	0-1 cm Live:dead ratio	0-5 cm Live:dead ratio
100	1734	~ 50,000	2858	~ 58,000	0.03	0.05
400	160	10	183	2190	16.0	0.08
700	62	554	64	2713	0.11	0.02
850	87	162	263	1034	0.54	0.25
1250	77	105	129	554	0.73	1.23
3400	25	1	72	47	25.0	1.53

Live:dead ratios of top-ranked species are presented in Table 2.16. At the 100-m site, despite the fact that live specimens of *Uvigerina* ex gr. *semiornata*, *Reophax* aff. *advenus* and *Psammosphaera* sp.5 were very abundant, the live:dead ratios were relatively low (0.02, 0.18, and 0.06 respectively). At the 400-m site, calcareous species had the highest live:dead ratios; in the case of *Cancris auriculus* there were no dead specimens. A hormosinacean, *Reophax* sp.11 had the second highest ratio of 0.3 followed by a hard-shelled saccamminid, Saccamminid sp.9, with a ratio of 0.14. At the 700-m site, astrorhiziids, represented by *Bathysiphon* sp.2, had the highest live:dead ratio,; note that only 6 specimens (live + dead) were counted in total. At 1250 m, another astrorhizid, *Lagenammina* sp.3, had the highest ratio (0.56), followed by another astrorhiziid, *Psammosphaera fusca* Schulze, 1875 (0.19). At 3400 m, *Globobulimina* sp.3 and *Crithionina* sp.4 both had a ratio of 2; note that 6 was the total number (live + dead) of tests for each of these species. Although unstained allogromiids and soft-shelled saccamminids were not found, empty test of Saccamminid sp.9 and *Saccammina* sp.15 were found at 400-m and 3400-m sites (Saccamminid sp.9 live:dead ratio = 0.13 at the 400-m site).

Table 2.16 Ratios between the abundance of live and dead top-ranked foraminiferal species from the >300 μm fraction of the 0-5 cm sediment layers of multicorer samples. * indicates that all specimens were live.

Site	100-m	400-m	700-m	850-m	1250-m	3400-m
Calcareous:						
Pyrgo depressa					0.05	
Lenticulina aff. *iota*		0.04	0.01	0.03		
Saracenaria sp.1		0.15				
Bulimina aculeata					0.11	
Globobulimina affinis		0.01	0.08	0.08	0.10	
Globobulimina aff. *turgida*		0.02	0.17	0.08		0.40
Globobulimina turgida			0.01			
Globobulimina sp.3						2.00
Hyalinea balthica					0.15	
Uvigerina sp.1		0.25		0.30		
Uvigerina ex gr. *semiornata*	0.02					
Uvigerina peregrina		0.24		0.34		
Cancris auriculus				* 0.41		
Chilostomella ovoidea		0.08				
Hoeglundina elegans			0.11	0.01		
MAF:						
Reophax scorpiurus					0.17	
Reophax sp.6					0.13	
Reophax aff. *advenus*	0.06					
Reophax sp.11		0.33				
Crithionina sp.4						2.00
Cribrostomoides wiesneri		0.08	0.02			
Astrorhizids:						
Saccamminid sp.9		0.14				
Lagenammina sp.1				1.33		
Lagenammina sp.2				0.50		
Lagenammina sp.3					0.56	
Psammosphaera sp.5	0.18					
Psammosphaera fusca					0.19	
Bathysiphon sp.2			2.00			

2.4 Discussion

2.4.1 Limitations of the study

This study involves a number of important limitations. The first is that the analysis focuses solely on the macrofaunal (>300 μm) fraction. Most foraminiferal studies are based either on the >150 μm, 125 μm or >63 μm fractions (Phleger and Soutar 1973; Mackensen and Douglas 1989; Bernhard et al. 1997; Jorissen et al. 1998; Gooday et al. 2000; Fontanier et al. 2002). The choice of the > 300 μm size fraction, which without a doubt underestimates the abundances and diversity of foraminifera, makes it difficult to compare our results with other studies. This is particularly so in the case of the site located in the core of the Oman margin OMZ (400 m), where Gooday et al. (2000) found the highest foraminiferal abundances ever recorded from any OMZ. Moreover, Gooday et al. (2000) showed that when the 63-300 μm was added to the >300

µm fraction, abundances increased by one order of magnitude. The main justifications for focussing on this size fraction were 1) it allowed direct comparison to be made with metazoan macrofauna and 2) it was less time consuming than sorting fine fractions, making it possible to analyse deeper layers and replicates for 0-1 cm. This made it possible to examine trends across the whole OMZ, not just at selected sites.

The second point to consider is the sample size. The multicorer is generally used for collecting meiofaunal organisms (>32 µm) (Barnett et al. 1984). Multicores are ideal for this purpose. Species numbers increase with size of the sample, up to a point when increasing the sample size will not add new species (Begon et al. 1990). The present study focus on macrofaunal foraminifera from multicores, so species numbers will certainly be under-estimated, even in this size fraction.

The third point concerns sediment penetration by foraminifera. According to Corliss and Emerson (1990), Jorissen et al. (1995), Van der Zwaan et al. (1999) and Geslin et al. (2004), to name a few authors, the depth at which foraminifera live in the sediments is controlled by two main factors food, availability and oxygen concentration, as illustrated by the TROX model of Jorissen et al. (1995). According to this model, where there is a high organic matter input and consequently low oxygen concentrations, foraminifera are concentrated in the surface sediment layers because of oxygen limitation. At the other extreme, i.e. low organic input and high bottom-water oxygen concentrations, foraminifera are concentrated near the sediment surface because of food limitation. In mesotrophic environments which lie between these extremes, foraminifera penetrate into deeper sediment layers because both food and oxygen availability are adequate within the sediment profile. This study looked at foraminifera from 0-5 cm sediment layer, which is sufficient for the stations within the OMZ, where foraminifera are expected to inhabit surface layers. However, at the mesotrophic 3400 m station, where oxygen levels are relatively high (2.99 ml/l) foraminifera may penetrate more deeply into the sediment and not be confined to the upper 5 cm.

2.4.2 Abundance

Published density data for stained foraminifera from low oxygen (O_2 ≤1.00 ml/l) and/or organically enriched localities are summarized in Table 2.17. Foraminifera have similar responses to oxygen depletion across the OMZ basins studied (Phleger and Soutar 1973; Mackensen and Douglas 1989; Bernhard et al. 1997; Jorissen et al. 1998; Gooday et al. 2000; Fontanier et al. 2002; Levin et al. 2002; Levin 2003). Where comparative data are available, surface densities (0-1 cm) of foraminifera are higher within the OMZ than above or below the OMZ. For example, densities are 32,603 (50 cm^3, > 150 µm) at 300 m off Peru, 16,107 (10 cm^2,

>63 μm) at 400 m off Oman and up to 9626 (ind. 10 cm^2, > 63 μm) at 550 m in the Santa Barbara Basin, compared to 855-1227 per 50 cm3, 586 per 10 cm2 and 133 per 10 cm2 respective outside the OMZ. However, this pattern is not seen in the current study.

Abundance of all live foraminifera (> 300 μm) was highest at the shallowest site at 100 m water depth (2858 per 25.5 cm^3, 0-5 cm; 1734 per 25.5 cm^3, 0-1 cm). This site is located closer to the coast where organic matter is higher because of land proximity, accentuated by greater river fluxes from the monsoons. Conversely, the 1250-m and 3400-m sites, which were deeper as well as more distant from land and therefore received much lower organic-matter input, exhibited lowest live foraminiferal abundances. The very high abundances at 100 m may be an upper boundary edge effect.

Among the sites within the OMZ (O_2 < 0.5 ml/l), abundance was highest at the 850-m site followed by the 400-m and 700-m sites. This was not expected, since abundances are generally highest where oxygen is lowest. On the other hand, according to Levin (2003), upper and lower boundaries of OMZs may exhibit maximum densities of organisms at specific oxygen concentrations which reflect a physiological threshold. In this case, the 850-m site sits within the lower boundary of the OMZ, where the oxygen concentration of bottom-water is 0.2 ml/l. The idea that this oxygen level represents a physiological threshold for macrofaunal foraminifera is not in accordance with what was found for the marcofaunal metazoan along the same transect. Levin et al. (2000) found the 700-850 m sites (O_2 = 0.15-0.02 ml/l) to be the lower boundary of the Oman margin OMZ for marcofaunal metazoan, indicating a slightly lower physiological limit for the metazoans.

The most likely explanation for the relatively low numbers of live foraminifera found in the core of the OMZ is that this study considers only foraminifera retained in a 300 μm mesh sieve, and therefore do not reflect the whole assemblage. For example, Gooday et al. (2000), found greater abundances at the same site, but their study considered the >63 μm fraction. Moreover, the large densities at this site were attributed mostly to a buliminid, *Bolivina seminuda,* which was <300 μm in size. Stressful conditions, such as oxygen depletion, favour small test sizes. Bernhard (1986) has suggested that assemblages subjected to periodic anoxia are of mixed sizes and that larger tests develop during periodic oxygenation, and then die during anoxic periods. This suggests that in areas of low oxygen concentration it is necessary to look at the smaller size fractions in order to fully understand the foraminiferal response to these stressful conditions. There is, however the exception of *Pelosina aroborescens* a species with a test reaching 70 mm length that can live in anoxic conditions (Cedhagen 1993).

The 3400-m site, well below the OMZ (O_2 = 2.99 ml/l) had very small abundances (72 per 25.5 cm^3, 0-5 cm; 25 per 25.5 cm^2, 0-1 cm). This could be because more oxygen is available, and some foraminifera therefore live below the 0-5 cm layer analysed in the study. However, a more important factor is probably the lower organic-matter flux to the seafloor at this deep site.

Very few other foraminiferal studies are based on the >300 µm fraction. Hence, the only densities with which the data obtained during this study can be compared directly are those reported of Gooday et al. (2000) (Oman margin) and Gooday et al. (2001) (North Carolina margin). The outstanding feature of the current dataset is the very high abundances in the >300 µm fraction at 100 m, which as mentioned above, may reflect an edge effect. Cursory examinations of the <300 µm fraction, which was small in volume did not reveal a superabundance of foraminifera, suggesting that this site is dominated by larger foraminifera. Abundances at 100 m are similar to those reported from the organic-enriched, well-oxygenated Bay of Biscay at a similar depth (1989 per 25.5 cm^3, 0-1 cm at 140 m) (Fontanier et al. 2002). Abundances at the 850 m sites off North Carolina, reported by Gooday et al. (2001), were all much higher (between 326 and 2400 individuals per 10 cm^2) than those found in this study (103 individuals per 10 cm^2). This can only be explained by the much larger sample size than that used in the current study.

Table 2.17 Density data for stained foraminiferal faunas from deep-sea low-oxygen environments, and organically enriched environments. Adapted from Gooday et al. (2000).

Locality and depth	**Bottom water O^2(ml/l)**	**Stained specimens**		**Reference; horizon and sieve fraction examined**
Florida slope:				Sen Gupta et al. (1981) and Sen Gupta and Strickert (1982)
185 m	~ 5.00	320-65,420		>63 µm, 0-3 cm, 10 cm^2
North Carolina:				Gooday et al. (2001)
850 m	~ 4-5	0-15:	0-2 cm:	Boxcorer
Site I		430	326	>300 µm
		868	678	10 cm^2
			392	
Site II		865	545	
Site III		2400	806	
		1565	653	
			445	
Santa Barbara Basin:				Bernhard et al. (1997)
339 m	0.51	133		>63 µm
431 m	0.35	1176		0-1 cm
522 m	0.08	1886		10 cm^2
537 m	0.04	1270		
578 m	0.03	3459		
591 m	0.06	3958		

Santa Barbara Basin:				Bernhard (2000)
486 m slope (Feb 1988)	~ 0.11		532	7.5 cm diameter
550 m slope (June 1998)	< 0.10		6901 4340	subcores of
550 m centre (Feb 1988)	< 0.10		9557 9626	boxcores
550 m centre (Jun 1988)	< 0.10		27	>63 µm
550 m centre (Oct 1988)	0.01			0-1 cm
550 m centre (Jul 1988)	Anoxic			10 cm^2
Santa Barbara Basin:				Phleger and Soutar (1973)
575 m	~ 0.10		1175	>63 µm, surface
590 m	~ 0.10		1050	10 cm^2
Soledad Basin:				Phleger and Soutar (1973)
530	0.10		2150	>63 µm, surface 10 cm^2
Santa Monica Basin:				Mackensen and Douglas (1989)
529	< 0.20		23	>125 µm, 0-1 cm, 1 cm^2
Santa Catalina Basin:				Mackensen and Douglas (1989)
893 m (slope)	0.20-0.50		52	>125 µm, 0-1 cm
897 m (slope)	0.20-0.50		45	1 cm^2
Bay of Biscay:		0-10 cm:	0-1 cm:	Fontanier et al. (2002)
140 m (Oct. 1997)	4.90	1989	1221	Multicorer
553 m (Oct.1997)	4.80	1345	1040	>150 µm
1012 m (Oct. 1997)	4.36	476	208	25.5 cm^2
1264 m (Feb. 1998)	4.70	122	76	
1993 m (Oct 1998)	5.85	179	125	
Cape Blanc:		0-10 cm:	0-1 cm:	Jorissen et al. (1998)
1200 m	3.67	1297	848	Multicorer
1525 m	4.29	369	223	>150 µm
2002 m	4.44	272	187	25.5 cm^2
2530 m	4.48	449	214	
3010 m	4.88	359	139	
Sagami Bay, Japan:		>63 µm:	>28 µm:	Ohga and Kitazato (1997)
1450 m (spring)	1.00	1500-	2000	0-15 cm
1450 m (summer)	1.00	200	500	10 cm^2
Off Peru:			50 cm^3:	Levin et al. (2002)
305 m	0.02		32,603	Multicorer
562 m	0.26		1227	> 150 µm
830 m	0.84		855	0-1 cm #
1210 m	1.78		921	
Oman margin:		<125 µm:	<63 µm:	Gooday et al. (2000)
412 m	0.13	2533	16,107	0-1 cm
3350 m	~ 3.00	342	586	10 cm^2
Oman margin:		0-5 cm:	0-1 cm:	This study:
100 m	0.46	1152	680	>300 µm
400 m	0.13	72	63	10 cm^2
700 m	0.16	25	24	
850 m	0.20	103	34	
1250 m	0.52	51	30	
3400 m	2.99	28	10	

2.4.3 Taxonomic composition

The 100-m site, above the OMZ, was dominated by *Uvigerina* ex gr. *semiornata*. The identity of this species is unclear. It resembles *Uvigerina mediterranea* Hofker 1932 and *Rectuvigerina cylindrica* Salvatorini 1967, but is not identical to either of these species. However, the closest illustration is that of *Uvigerina semiornata* d'Orbigny 1846 from Maas (2000) who reported it from 200 m on the Pakistan margin of the Arabian Sea. Molecular data may resolve this problem. A very commonly reported *Uvigerina* species, *Uvigerina peregrine*, is associated with fine-grained sediments in organically-enriched environments irrespective of bottom-water oxygen concentrations in the Indian Ocean, west African continental margin and north African margin (Corliss et al. 1986). The second and third most abundant species at this site were *Reophax* aff. *advenus* Cushman 1919 and *Psammosphaera* sp.5. These two species are very similar in wall composition; however, *Lagenammina* sp.5 only has one chamber, while *Reophax aff. advenus* has between two and three chambers. Species of *Reophax*, *Lagenammina* and *Psammosphaera* are widely distributed in continental shelf and deep-sea environments. Although they are rarely reported from low oxygen environments, Bernhard et al. (1997) found species of these genera in the dysoxic Santa Barbara Basin. Another *Reophax* species, *Reophax* sp.1, was the top-ranked species at 850 m.

The 400 to 1250 m stations yielded typical low-oxygen faunas. Sen Gupta and Machain-Castillo (1993) and Bernhard and Sen Gupta (1999), compiled information on foraminiferal species reported from oxygen-depleted environments and recognized as live by rose Bengal staining and it will now be compared with the results of the current study. *Globobulimina affinis*, *G.* aff. *turgida* and *G. turgida* were most common within the OMZ in the present dataset. This genus is commonly found in dysoxic environments (0.1-1 ml/l) across the world, as well as in deep infaunal microhabitats with undetectable oxygen concentrations (Fontanier et al. 2002). It therefore appears able to tolerate anoxic conditions, at least temporarily. *Chilostomella ovoidea* and *C. oolina* are common inhabitants of dysoxic environments. Recent experiments suggest that they are not closely linked to fresh organic matter (Nomaki et al. 2005). Interestingly, small undescribed *Bathysiphon* species were common at the Oman margin site with lowest oxygen concentrations (400 m, O_2 = 0.13 ml/l). Apart from the Oman margin OMZ (Gooday et al. 2000), small *Bathysiphon* species have been reported from the organic-rich muds in the Gullmar Fjord, Sweden (Höglund 1947). They may be more common and widely distributed than published records suggest.

An important point to note regards the relatively high abundance of organic-walled allogromiids at these low-oxygen stations. In particular, at the 400-m site, where oxygen was lowest, allogromiids represented 10.4% of the live assemblage. This finding contradicts experimental

work conducted by Moodley et al. (1998) which suggested that soft-shelled foraminifera were more sensitive to anoxia than hyaline or agglutinated species. Gooday et al. (2000) found allogromiids to be uncommon at the 412 m station, although his study included finer fractions. Miliolids are generally absent from low-oxygen settings (Bernhard and Sen Gupta 1999), possibly because they lack pores in the test wall, making oxygen exchange difficult. This is in accordance with our results, where miliolids were confined to the stations either above or below the OMZ. Cedhagen and Frimanson (2002) found that *Quinqueloculina seminulum* Linné, 1758 has faster pseudopodia than other species that could compensate the lack of pores, allowing them to inhabit low oxygen environments. However, another possible explanation for the lack of miliolids in low oxygen setting is the fact that the tests are more soluble and also the energetic cost in producing a calcareous test (Cedhagen pers. comm.).

The 3400 m represents a typical deep-sea assemblage. Agglutinated species predominate over calcareous species, and komokiaceans are particularly abundant. Tendal and Hessler (1977) reported that komokiaceans reach their highest relative abundances in abyssal oligotrophic areas and hadal trenches. Schröder et al. (1988 and 1989) and Bernhard et al. (1997) also found high abundances of komokiaceans in the North Pacific and Nares Abyssal Plain in the Atlantic, mainly living in the top 2 cm of the sediment. The current study site is located in a eutrophic setting, however, demonstrating that these organisms are also common in environments with higher organic inputs. The assemblage here was predominantly agglutinated. Bernestein et al. (1978) also showed that agglutinated species dominated foraminiferal assemblages in the central North Pacific and Saidova (1965) recognized an astrorhiziid dominated assemblage at abyssal depth in the Pacific Ocean. In these cases, the predominance of agglutinated foraminifera is largely due to the location of sites below the Carbonate Compensation Depth (CCD). The 3400-m site in the Arabian Sea lies above the CCD. According to Gupta (1994), the CCD occurs below 5000 m in this region. However, Stubbings (1939) found a transition zone from *Globigerina* ooze to *Globigerina* ooze-red clay at around 3700-3800 m, and Gooday et al. (2000) suggested that some carbonate dissolution may occur at the 3400 m.

Typical agglutinated deep-sea species found on the Oman margin include: *Reophax scorpiurus*, *Rhizammina* sp.1 and 2, *Cribrostomoides wiesneri*, Saccamminid sp.15. *Rhizammina*-like species and Saccamminid sp.15 were found at the deepest station (3400 m). *Reophax scorpiurus* and *Cribrostomoides wiesneri* were most abundant at the 1250 m station. Top-ranked species, based on complete individuals, at the 3400-m site is *Crithionina* sp.3 (Table 2.5). However, tubular fragments of a *Rhizammina*-like species were very abundant at this deep site (Appendix A). Kurbjeweit et. Al. (2000) found *Rhizammina algaeformis* Brady, 1879 communities between 2000 and 4500 m depth in the Arabian Sea, suggesting this large tubular species are major contributors to foraminiferal biomass in the deep Arabian Sea.

2.4.4 Diversity and Dominance

The diversity of foraminifera and other benthic organisms is generally low at low oxygen concentrations (Levin et al. 2001; Levin 2003). The main result of the present study is that diversity is depressed between 100 and 850 m, when compared to diversity at 1250 and 3400 m. The 100 m station lies at the upper boundary of the OMZ where numbers of *Uvigerina* ex gr. *semiornata* increase dominance and this may lead to lower diversity. At the 3400 m oxygen levels are reasonably high, allowing more species to occur. The enhanced abundance of foraminifera at the 850-m site, where oxygen concentrations are 0.2 ml/l, may be due to an edge effect, suggesting that this is a critical value for some foraminiferal species. Below this value, only species with particular adaptations are able to survive. Low oxygen environments are often associated with high organic availability and it is difficult to distinguish the separate effects on abundance and diversity of these two parametrs. The analysis of a large metazoan macrofaunal data set from the Indian and eastern Pacific Oceans suggests that organic matter availability has a greater impact on dominance and abundance, but oxygen has a greater effect on species richness (Levin and Gage 1998). While oxygen stress causes loss of species, it also creates habitat homogeneity that further reduces niche diversity. Where most larger organisms are excluded, the sediment lacks the heterogeneity that normaly results from the activities of macro- and megafaunal animals (Levin et al. 2001). The lack of burrows, tubes and surface traces mean that fewer niches are available for smaller benthic organisms such as foraminifera.

2.4.5 Vertical distribution

The present study looks at distribution of foraminifera with a 3D perspective; across a bathymetric transect that crosses an OMZ, but also down to 5 cm in the sediment at each water depth. Generally, oxygen concentrations decrease with sediment depth, and as a consequence, deeper sediment layers are similar to top-sediment layers from stations of low bottom-water oxygen concentrations. Moreover, surface sediment layers have fresh food availability. Test morphology as a morphological adaptation to live shallow or deep in the sediment was studied by Corliss (1985) and Corliss and Chen (1988). They found that infaunal species tend to be planispiral, globular or flattened while epifaunal species are planoconvex or biconvex in shape. Furthermore, infaunal species which are tolerant of dysoxia have higher surface area volume ratios than epifaunal species. In the present study, fusiform species such as *Globobulimina affinis*, *G.* aff. *turgida*, *G. turgida*, *Chilostomella oolina*, *C. ovoidea* lived deeper in the sediments than flattened calcareous species such as *Lenticulina* aff. *iota*, *Hoeglundina elegans*. Different foraminiferal species react differently to oxygen and food availability within the sediment. For example, Nomaki et al. (2005) suggested that *Globobulimina* will consume fresh

phytodetritus when it has the opportunity to do so, although not as quickly as shallow-infaunal taxa such as *Uvigerina*.

2.4.6 Foraminiferan and Metazoan: a comparison

Multicorer samples are too small to yield sufficient numbers of metazoan macrofauna, foraminifera are directly compared to published results on metazoans from the same sites (Levin et al. 2000). The metazoan abundance pattern was different from that of foraminifera (Figure 2.5). The 700-m site yielded highest metazoan densities, but it had the lowest foraminiferal abundances. For the metazoans, as mentioned in a previous section, the highest abundance recorded at 700-850 m may reflect an oxygen threshold (0.15-0.20 ml/l) above which macrofauna can take advantage of organically-enriched environments. For the foraminifera, this same phenomenon occur at a slightly greater depth than for metazoans, suggesting a higher critical oxygen concentration (0.2 ml/l) for the foraminiferal macrofauna. Surface-deposit feeding polychaetes (spionids and cirratulids) dominated the metazoan assemblage at 700 m. The foraminiferal assemblage at this station was dominated by the surface-dwelling *Hoeglundina elegans*. It is therefore possible that where the oxygen concentration is high enough for metazoans to occur, they are very abundant and better competitors for the food resources. Below the 700-m peak in metazoan densities where oxygen is not limiting, foraminifera again dominate at 850 m and below. In the core of the OMZ at 400 m, metazoans were fairly abundant (123 individuals per 10 cm^2) and were more abundant than foraminifera (72 individuals per 10 cm^2) (Levin et al. 1997).

2.4.7 Live:dead ratios

The comparison between stained tests (presumably live) and dead tests can give important information on the life processes of foraminifera (Murray 1991; Jorissen and Wittling 1999; Gooday and Hughes 2002). On the Oman margin, there was a decrease in overall live:dead ratios, from 0.05 at 100 m to 1.53 at 3400 m, with water depth. This increase could imply a slower turn over rate of species with depth. However, a more plausible explanation for the higher ratios is the fact that less robust species become more abundant with water depth, in particular at deepest sites. Organic-walled and soft-shelled species are rarely present in the fossil record, while delicate organic-cemented agglutinated tests disintegrate quickly, resulting in under-representation in the dead assemblage (Schroder 1986; Mackensen and Douglas 1989). In these cases, the live assemblage is not accurately represented by the dead assemblage, suggesting that only robust agglutinated and calcareous tests can be used to accurately compare live and dead assemblages. At sites below the CCD, calcitic and aragonite tests are destroyed by dissolution resulting in live assemblages dissimilar to dead ones. This is not the case of our

study area, as the deepest station (3400 m) is well above the CCD which in this area is located at around 5000 m. However, these tests also disintegrate in acidified pore-waters of organic-carbon enriched sediments (Douglas and Woodruff 1981), a destructive process that could operate in central parts of the OMZ.

Where live:dead ratios of calcareous foraminifera are low, it can mean that the turn-over rate is high, i.e. species reproduce rapidly and are short lived, adding dead shells to the sediment at a faster rate than slower growing species. In this case, if samples collection coincides with a period of high organic flux, live:dead ratios could be high as a result of high live abundances. Conversely, longer-lived species have higher live:dead ratios, adding dead tests to the sediment at slower rates, In some cases, species are represented only in the dead assemblage, either meaning that live specimens are rare or that these are short lived species with strong seasonal fluctuations in abundance (Gooday et al. 1990; Gooday and Rathburn 1999). The opposite situation was observed in the case of the calcareous foraminifera *Cancris auriculus* at the 400-m site, which was entirely absent from the dead assemblage down to 5 cm in the sediment. There is no obvious explanation for this observation.

At the 100-m site, there were very high abundances of both live and dead *Uvigerina* ex gr. *semiornata* resulting in fairly small live:dead ratios and indicating fast turnover rates for this species at this site. The *Reophax* and *Psammosphaera* species that were common at 100 m also had relatively small live:dead ratios, again suggesting a fast turnover rate. It has been speculated that deep-water foraminifera reproduce mainly through asexual reproduction (Murray 1991), involving multiple division of the cytoplasm followed by the release of small juveniles. Sexual reproduction also results in the generation of small individuals. This means that studies where only larger size fractions are considered, will not reveal periods of rapid reproduction which generate numerous small juvenile specimens. In those cases, a higher proportion of the live assemblage is represented in the smaller size fractions, and live:dead ratios will be low in the larger size fractions.

It is interesting to note that the 700-m site had the lowest abundance of live foraminifera, of any station across the Oman margin, but the highest abundance of dead foraminifera, and therefore the lowest live:dead ratios. This suggests a fast turn over rate at this site, implying that short lived opportunistic species to inhabit this site.

2.5 Conclusions

As suggested by previous authors, oxygen and food availability are important factors in determining foraminiferal community structure (Jorissen et al. 1995; Van der Zwaan et al. 1999; Gooday 2003). Within OMZs, diversity is typically depressed and a few species dominate the assemblages (Levin 2003). However, the current study did not find highest abundances within the core of the OMZ. This was probably a result of the use of the >300 μm size fraction which excludes the small species typically found within OMZs Instead, the highest foraminiferal abundance was found within the upper boundary of the OMZ (100 m), where huge numbers of *Uvigerina* ex gr. *semiornata* occurred. This sharp peak probably representing an edge effect. A second much less pronounced abundance was peak found at the lower boundary (850 m) of the OMZ. The bottom-water oxygen concentration here was 0.2 ml/l, which seems to be a critical value for foraminifera. The taxonomic composition within the OMZ was typical of low oxygen environments with one important difference. Allogromiids were relatively abundant in the core of the OMZ, something rarely reported. Diversity was depressed between 100 m and 850 m and relatively higher at 1250 and 3400 m sites, further confirming the change in community at 850 m. The vertical distribution of foraminifera in the sediment reflected the response found across the horizontal oxygen gradient. Species were concentrated in the top sediment where bottom-water oxygen concentration were low and found deeper in sediments at higher oxygen concentrations. Foraminifera and metazoan responded similarly to oxygen and food availability, with one main difference. In the case of metazoans, the lower boundary edge effect occurred at 700 m where oxygen concentrations were 0.15 ml/l, compared to 850 m for foraminifera (O_2 = 0.2 ml/l). Live:dead ratios of foraminifera increased with water depth.

CHAPTER 3

Large organic-walled Protozoa (*Gromia*) in the Arabian Sea: morphotype diversity and ecology

3.1 Introduction

Gromiids are large benthic protozoa with filose pseudopodia and an organic, proteinaceous test (Hedley 1960), which includes an inner layer of "honeycomb membranes", a feature unique to this genus (Hedley and Bertaud 1962). One species, *Gromia oviformis*, is the best known representative of this group. It is a cosmopolitan species that inhabits coastal, intertidal and sublittoral waters and is found on the weed of coralline pools, on *Cladophora*, on the walls of rock crevices, undersurfaces of stones, holdfasts of kelp and the surface layer of sandy and muddy sediments (Jepps 1926; Hedley 1958; Hedley and Bertaud 1962; Arnold 1972; Arnold 1982; Pawlowski et al. 1994; Bowser et al. 1996). Although this group is well known from shallow water, it was unknown in the deep sea until the first species was discovered at bathyal depths (between 1200 and 1700 m water depth) on the Oman margin of the Arabian Sea (Gooday et al. 2000). This species was identified as a gromiid on the basis of its wall structure and described as *Gromia sphaerica*. Since then, a variety of undescribed gromiid-like protozoa have been found at other localities on the Oman and Pakistan margins. One of these, a small species that typically lives on elevated substrates, has recently been described as *Gromia pyriformis* Gooday and Bowser, 2005 on the basis of morphological criteria (Gooday and Bowser 2005). An elongate object with attached foraminifera collected from the Santa Catalina Basin off California, identified by Jumars (1976) as a "faecal pellet", closely resembles one of the elongate gromiid morphotypes found in the Arabian Sea. It was found living at 1130 m water depth where the bottom water oxygen concentration was 0.4 ml/l and the bottom temperature 4.02°C. This one probable record suggests that large gromiids may be quite common in bathyal, organically-enriched, mildly dysoxic environments. Moreover, *Gromia*-like species were frequently observed in bathyal polar waters and in fjords on the west coast of Svalbard (Gooday et al. in press), but their relationships to shallow-water *G. oviformis* were not established.

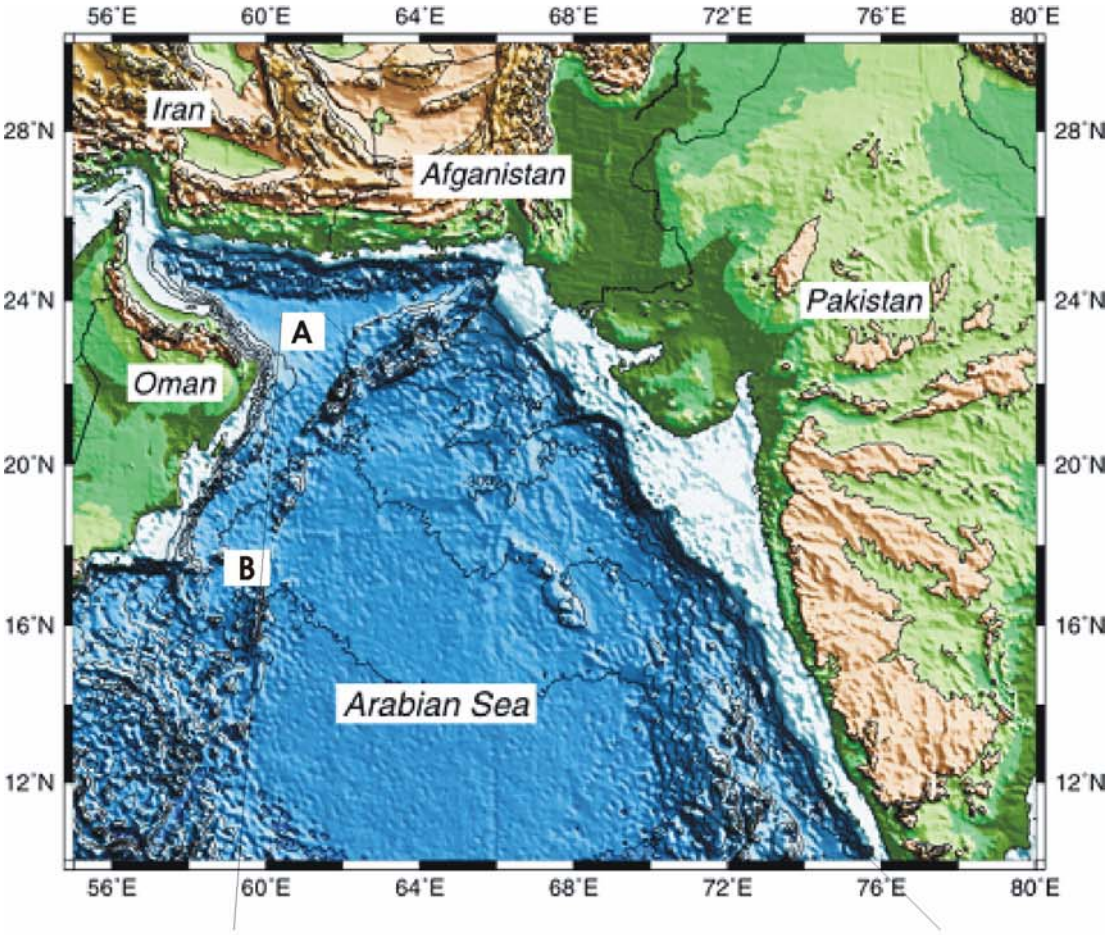
A series of studies of gromiid morphology, ecology and ultrastructure was conducted to address the biology of these important deep-sea protozoa, and to confirm that they are, indeed, gromiids. This chapter describes the abundance, diversity and distribution of gromiids on the Oman and Pakistan margins. A survey of Arabian Sea morphospecies is also presented. Chapter 4 presents the molecular work.

3.2 Materials and Methods

3.2.1 Study site

Specimens were collected from both the Oman and Pakistan margins of the Arabian Sea along transects between 100 m and 3500 m depth during a series of cruises by the British research ship R.R.S *Charles Darwin* (CD) (Figure 3.1). On the Oman margin, samples were collected along a bathymetric transect across the oxygen minimum zone (OMZ) between 22° and 24° N latitude, 58°30’ and 61° E longitude, and during cruise CD 143 in December 2002 (Figure 3.1). The continental slope in this area is heavily dissected by canyons, creating a highly irregular topography. Because not all key environmental characteristics were determined during cruise CD143, we have used the earlier *Discovery* cruise 211 published data to fill the gaps (Table 3.1). Figure 3.1 shows the position of R.R.S. *Discovery* cruise 211 that took place on the south part of the Oman margin during October-November 1994. The Oman margin OMZ (O^2 <0.5 ml/l) occurs between 90 and 1350 m water depth, with minimum oxygen values of 0.2 ml/l at 400 m, rising to 2 ml/l at 2200 m and 3 ml/l at 3500 m (Figure 3.2, Table 3.1). The temperature is around 20°C at 300 m, decreasing steeply with water depth to 2°C at 3000 m and 1.7°C at 3500 m (Figure 3.3). Salinity is highest at the surface, with more than 36.5 ppt, decreases to less than 36 ppt at 150 m, reaches a second high peak of 36.5 ppt at 275 m and then decreases gradually with depth reaching normal levels of 35 ppt at 1600 m (Figure 3.4). Sediments were finer, soupy mud in the core of the OMZ (400 m), with firmer mud at 850 m, but coarser *Globigerina* sands where gromiids were found at 1250 m (Levin et al. 1997).

Figure 3.1 Location of cruises on the Oman and Pakistan margins of the Arabian Sea. RRS *Charles Darwin* cruises: **A** CD 143 and **C** CD 145, 146, 150 and 151. **B** RRS *Discovery* cruise 211.



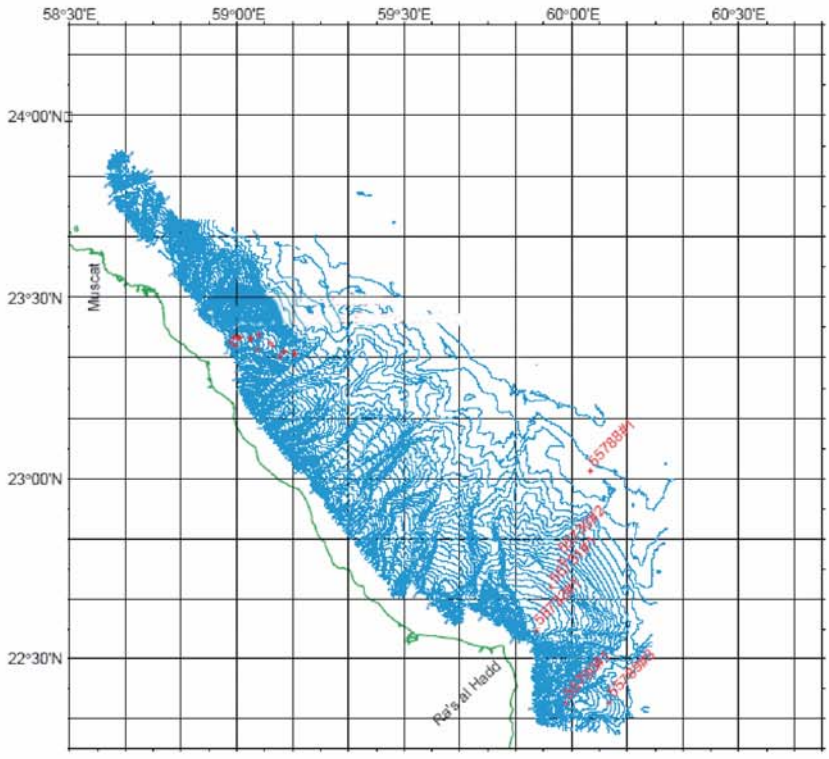


Table 3.1 Physical and chemical characteristics of stations examined on the Oman margin during RRS *Discovery* cruise 211 in October-November, 1994. S.E = Standard Error, TOC = Total Organic Carbon.

Water depth	**400 m**	**850 m**	**1250 m**	**3400 m**
Bottom-water temperature (°C)	13.3	9.6	6.7	1.7
Bottom-water oxygen (ml/l)	0.16	0.20	0.52	3.0
% TOC (0-0.5 cm)	4.99	4.01	2.67	2.72
(S.E.) n=3	(0.44)	(0.16)	(0.07)	(0.12)
C:N (0-0.5 cm)	8.52	8.89	7.82	9.42
(S.E.) n=3	(0.20)	(0.63)	(0.39)	(0.05)
Surface pigment 0-0.5 cm (μg/g)	770	167	68	185
(S.E.)		(39)	(26)	(101)
n		3	3	3
Hydrogen index (0-0.5 cm) (mg Hydrocarbon/g TOC)	490	441	423	366
(S.E.)	(12.5)	(0)	(11.7)	(5.5)
n	2	2	3	2
% Sand (0-1 cm)	22.3	37.6	56.8	21.3
Mean grain size (μm)	42.2	66.6	79.0	42.8
Median grain size (μm)	28.7	47.1	42.1	26.5
(all n = 1)				
% $CaCO_3$ (0-0.5 cm)	55.10	60.50	66.10	34.48
(S.E.) n = 3	(2.5)	(1.7)	(1.0)	(3.29)
Substrate	Fine, soupy mud	Firmer mud	*Globigerina* sand	Phytodetrital layer over fine mud

Figure 3.2 Bottom-water oxygen values (measured by the CTD O_2 sensor and Winkler titrations of core top water) across the OMZ on the Oman margin (**A**), CD 143. Data from Brian Bett.

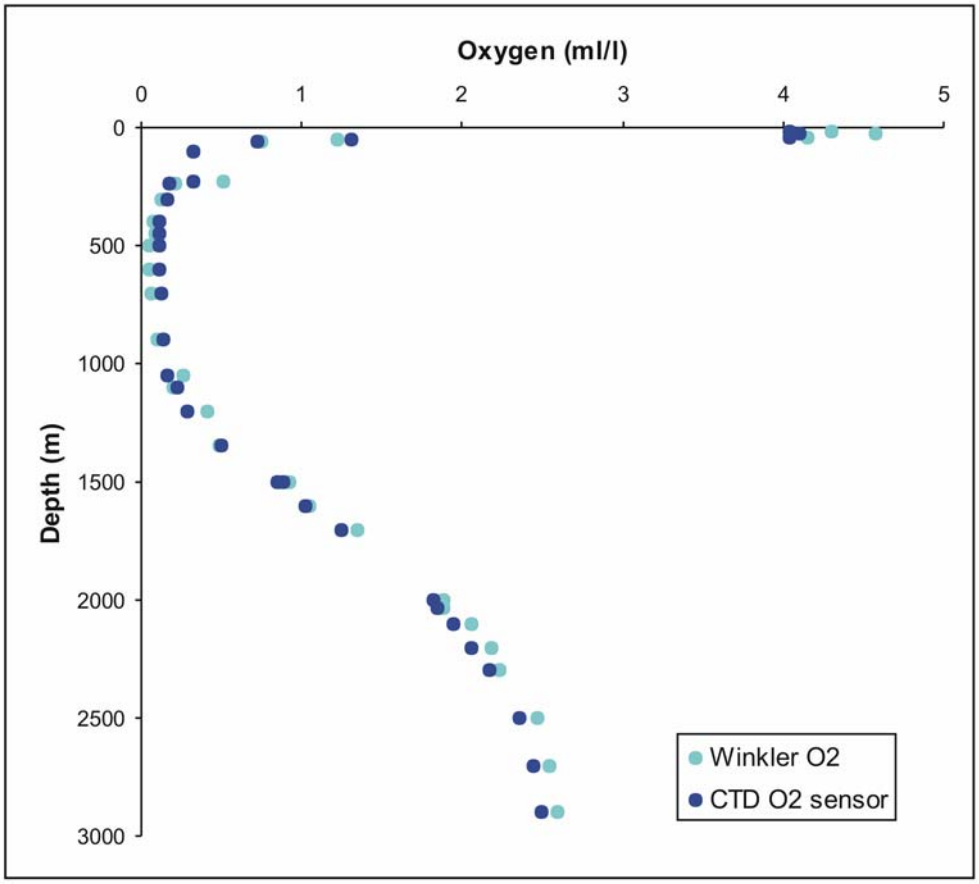


Figure 3.3 Temperature (measured from core top water collected by the CTD) across the OMZ on the Oman margin (**A**) during CD 143. Data from Brian Bett.

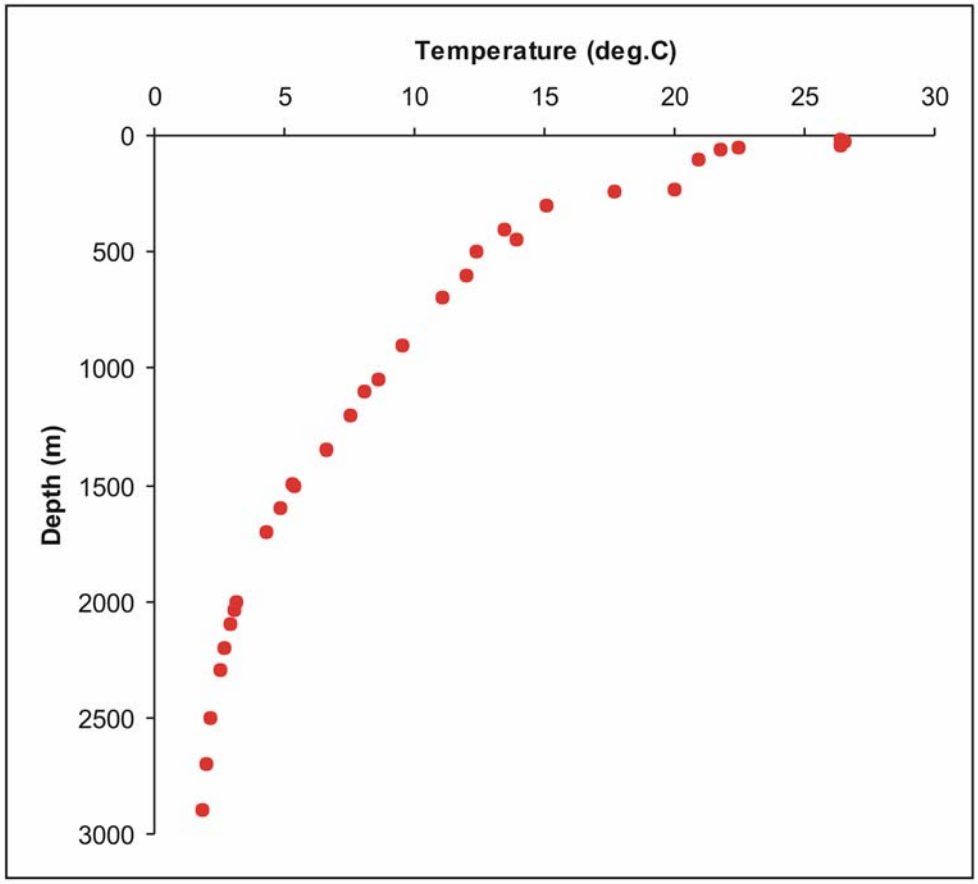
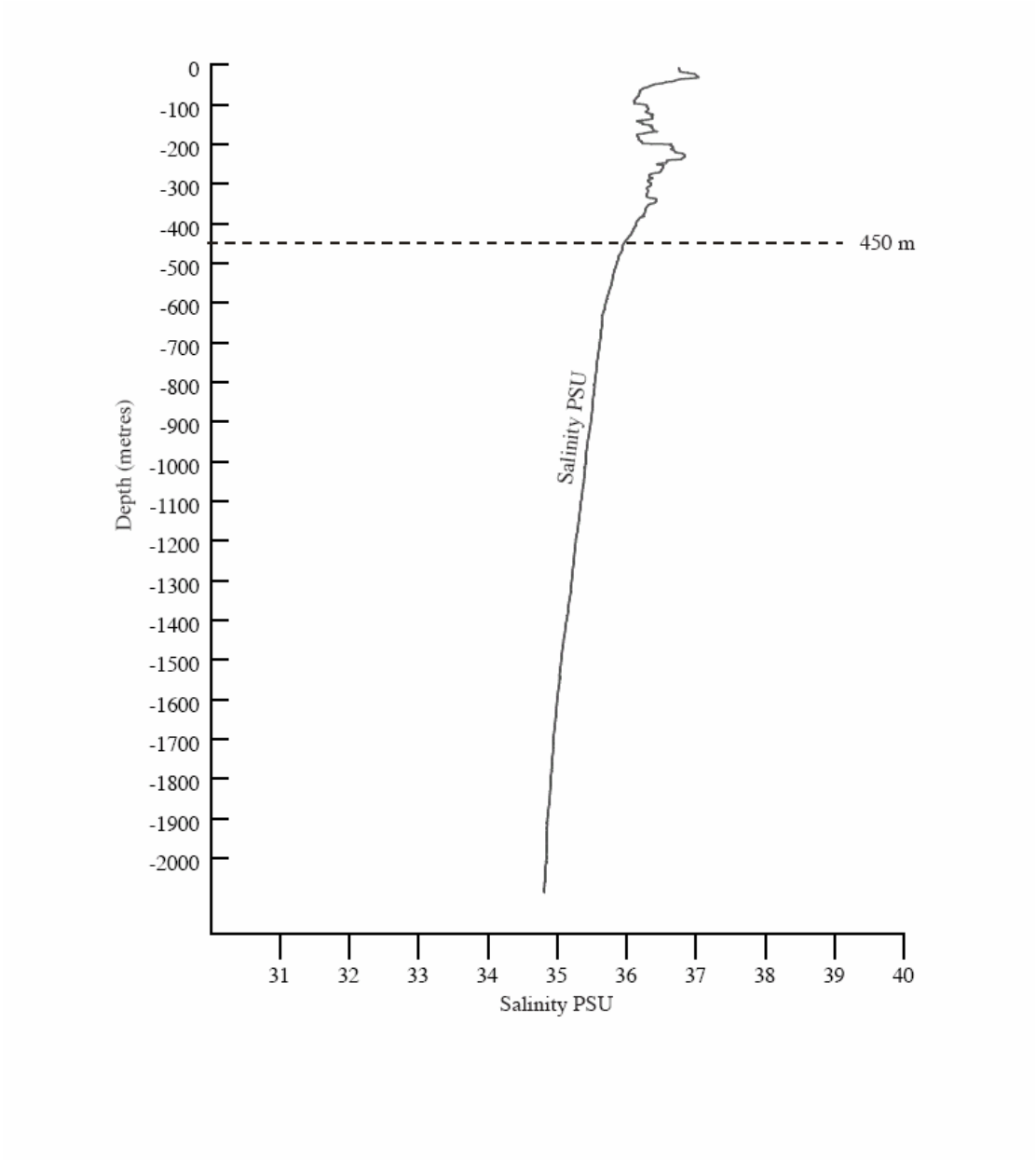


Figure 3.4 Salinity (measured from core top water collected by the CTD) across the OMZ on the Oman margin (**A**) during CD 143. Data from Brian Bett.



On the Pakistan margin, samples were collected in 2003 across the OMZ between 22°40’ and 23°20’ N and 65°40’ and 66°50’ E during cruises CD145 (March-April), CD146 (April-May), CD150 (August) and CD151 (September 2003) (Figure 3.1 and 3.5). In this area, the OMZ impinges on the seafloor between 125 m and 1250 m (Figure 3.6). The Pakistan study site lies on the continental margin (outer shelf and slope), NW of the Indus Canyon. The topography of the slope is smoother than off Oman but it is interrupted by a series of smaller canyons, in addition to the large Indus Canyon. Figure 3.7 shows a lot of structure in the oxygen profiles in the top 100 m during CD 145, with differences in bottom water oxygen concentrations between CTD stations. However, variations were very slight below 1000 m water depth, where gromiids occur. CTD profiles indicate that water temperatures range from 26°C at the surface to 2°C near the seafloor at 3000 m water depth (Figure 3.7). Salinity is highest at the surface, with a second peak at 250 m, then gradually decreasing, to reach 35 ppt at 1500 m water depth (Figure 3.8). The Pakistan study area was further offshore than the Oman study area and the continental slope areas smoother. At 1200 water depth, sediments showed three consecutive layers: a surface phytodetrital layer, brown sediment with numerous fine burrows (2.5 - 3 cm) with compacted sediment below (Bett 2003). At 1850 m water depth, light grey clays were covered by a surface layer of orange/brown flocculent material. In general, sediments were organically enriched, in particular surface sediments from 1000 and 2000 m water depth which exhibited high concentrations of phosphate, silicate and nitrate (Bett 2003).

Figure 3.5 Pakistan **C**, CD cruises 145, 146, 150 and 151 (BSNAP – Bathysnap mooring recovery site, and A3200 – additional work sites). From Bett (2003).

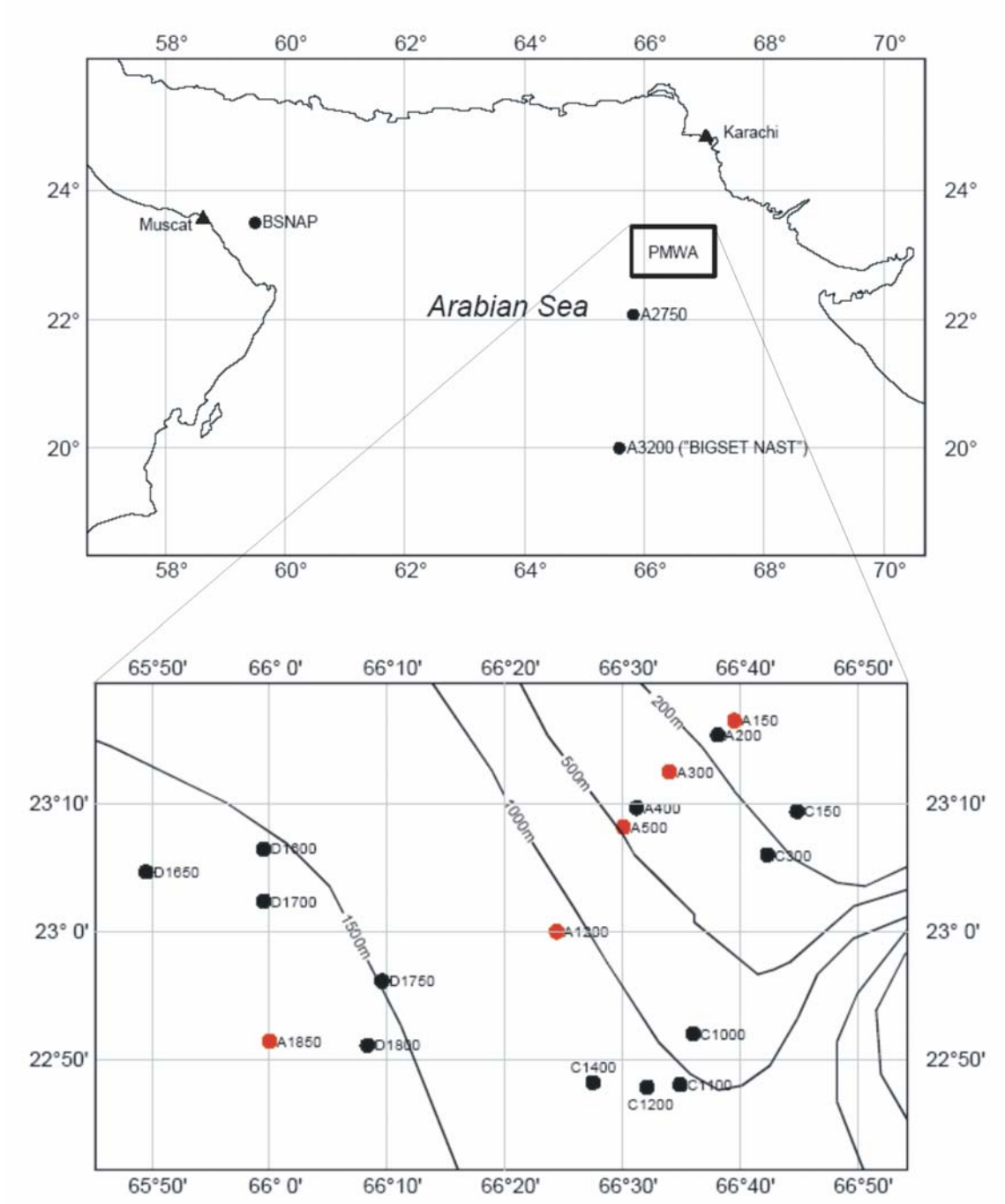


Figure 3.6 Co-plotted oxygen profiles (measured by the CTD Winkler titrations of core top water) from the Pakistan margin, CD 145. From Bett (2003).

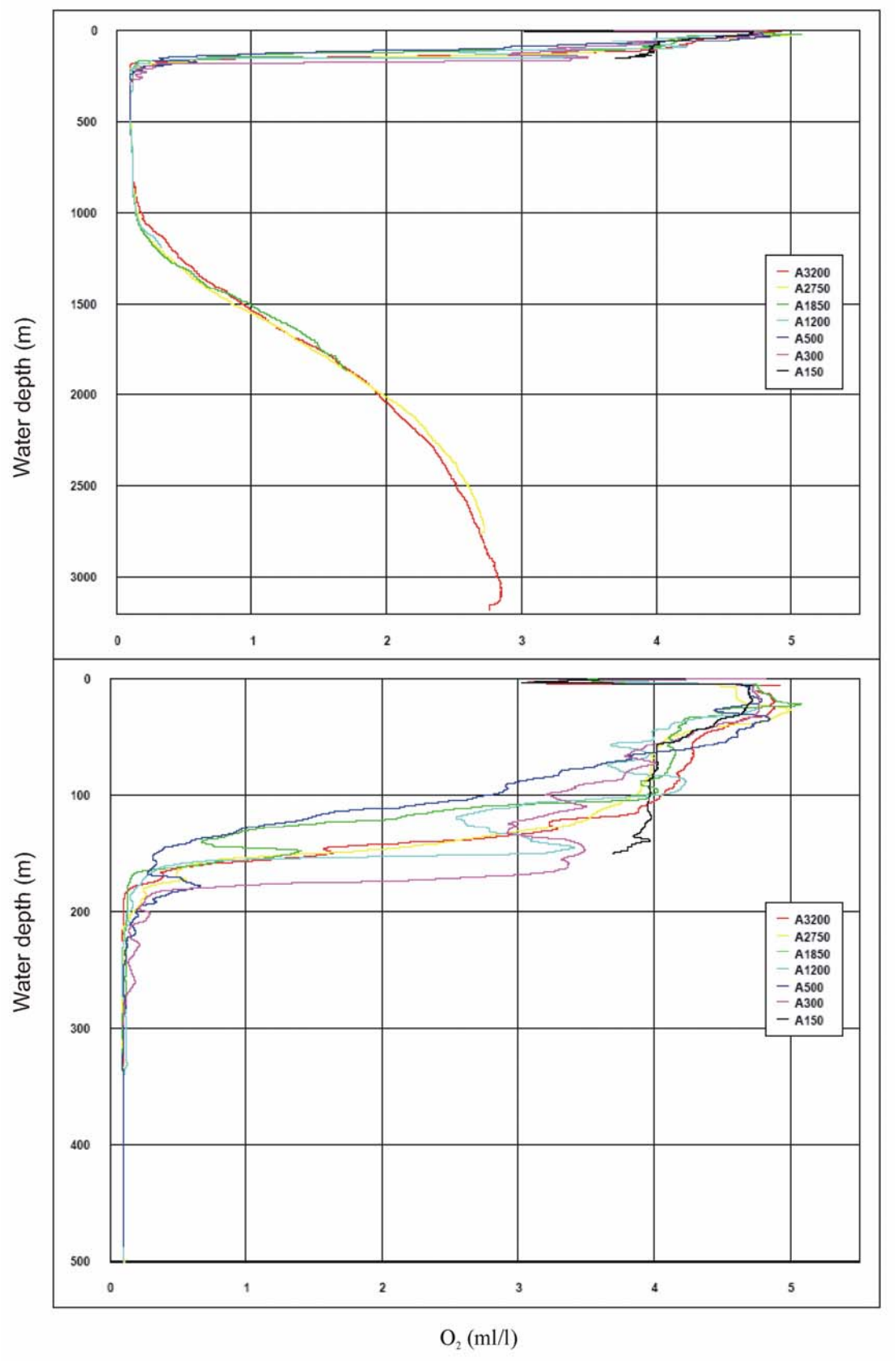


Figure 3.7 Co-plotted temperature profiles (measured from core top water collected by the CTD) from the Pakistan margin, CD 145. From Bett (2003).

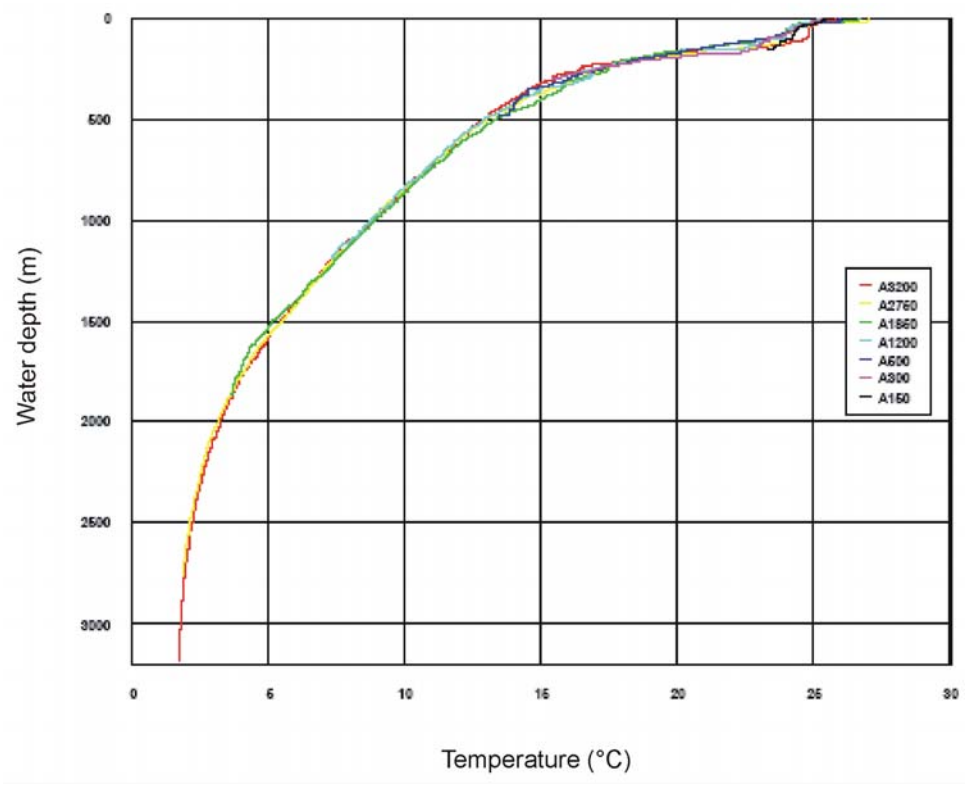
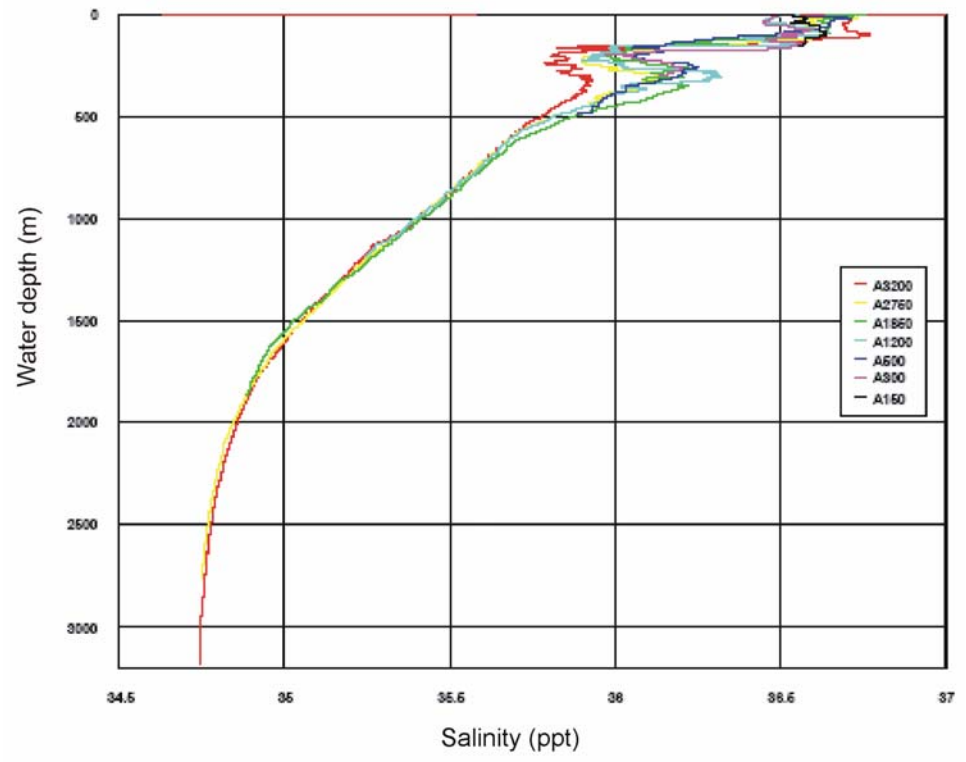


Figure 3.8 Co-plotted salinity profiles (measured from core top water collected by the CTD) from the Pakistan margin, CD 145. From Bett (2003).



3.2.2 Sampling Methods

Samples were obtained using gear appropriate for organism of different size classes. The multicorer (Figure 2.3) was used to collect samples for meiofaunal studies, the megacorer (Figure 3.9) for studies of macrofauna and the Agassiz trawl (Figure 3.10) for megabenthic organisms. Gromiids occurred in all these kind of samples. Core samples were used for quantitative as well as qualitative gromiid studies, while Agassiz trawl samples were used only for qualitative studies.

Initially, all gromiids found on the surface of megacores or multicores were removed, either using a plastic pipette or forceps, and preserved as specified below. Cores were then sliced into 1 cm thick layers down to 3 cm sediment depth. Unsieved sediments were examined under a binocular microscope for any additional gromiids, care being taken to maintain sediments at the same temperature as the sampling area using ice or a cold plate. All material collected using the Agassiz trawl was put into buckets and taken straight to the CT (temperature controlled) laboratory for picking and preservation. The picked gromiids were fixed in 4% formaldehyde solution for morphological work or in 3% cacodylate-buffered glutaraldehyde (Bé and Anderson 1976) for ultrastructure work.

Figure 3.9 Megacorer equipped with 100 mm id plastic core tubes.

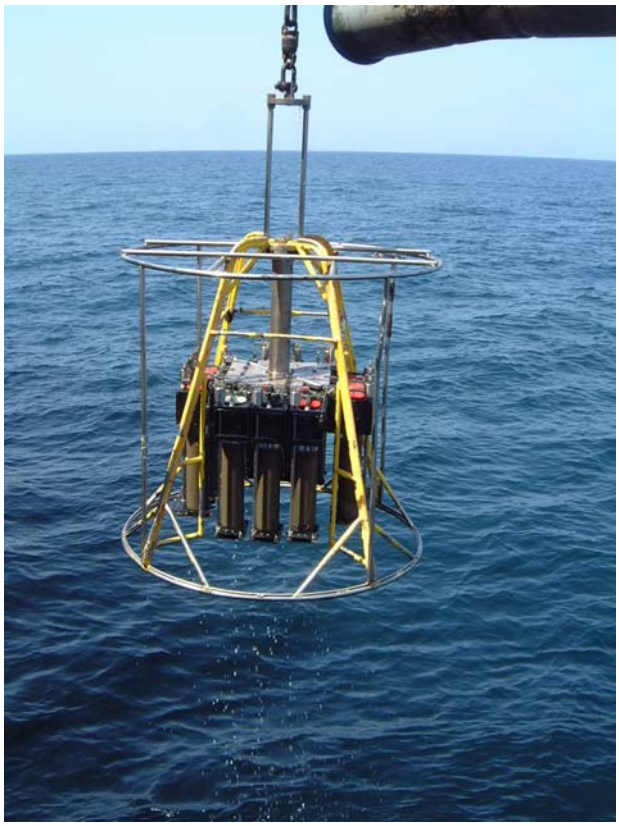


Figure 3.10 Agassiz Trawl.

3.2.3 Morphological Methods

Gromiids preserved in 4% formaldehyde were photographed using a digital camera (Nikon Coolpix 4500) attached to a Wild M5 binocular microscope and counted and described. In addition, 2 specimens were air dried and examined in the Scanning Electron Microscope (SEM).

3.2.4 Ultrastructural Methods

3.2.4.1 *Resin block preparation.*

In the laboratory, individual gromiids were rinsed twice (10 minutes) with the buffer (sodium cacodylate) and post fixed (1 hour) with 1% osmium tetroxide buffered in sodium cacodylate to which 1% NaCl had been added to give a pH of 7.2. Specimens were then rinsed twice (10 minutes) in buffer followed by serial dehydration in ethanol (30% ethanol - 20 minutes, 50% ethanol - 20 minutes, 70% ethanol - 20 minutes, 95% ethanol - 20 minutes, absolute ethanol – 40 minutes, absolute ethanol – 40 minutes, Acetonitrile – 20 minutes). Finally, specimens were embedded in 50:50 Acetonitrile:spur resin that was polymerised at 60°C for at least 24 h.

3.4.2.2 *Histology verification*

Resin blocks were carved manually using razor blades and then polished using glass knives on a microtome. Semi-thin (0.50 µm) sections were cut and stretched using chloroform and were

then placed in distilled water on glass slides that were dried on a hot plate. These were stained with 1% toluidine blue in 1% borax and fast dried, again on a hot plate. Sections were observed under an optical microscope for cell structure, before being examined at higher magnifications in a transmitted electron microscope.

3.4.2.3 *Transmitted Electron Microscopy (TEM) and High Voltage Electron Microscopy (HVEM)*

Ultra-thin (0.50 nm) sections, required for TEM, were cut using a diamond knife. Gromiids have silica grains within their tests and therefore it was difficult to obtain good sections. Semi-thin sections (50 µm) were also cut using a diamond knife. These were examined in the HVEM (Figure 5.2.15), which physically accommodates and visualizes sections up to 1 mm thick. All cut sections were stretched using chloroform and placed on either TEM or HVEM grids that were dried before staining with uranyl acetate for use in either microscope.

3.3 A taxonomic survey of gromiids from the Arabian Sea

Supergroup Rhizaria
Order Gromida Claparède and Lachman, 1859
Suborder Gromiina Delage and Héouard, 1986
Family Gromiidae Reuss, 1862
Genus *Gromia* Dujardin, 1835

Gromia sphaerica Gooday, Bowser, Bett and Smith 2000 (Figure 3.11)
Described by Gooday et al. (2000)
Occurrence: Oman margin CD 143 stations: 55759#1 (1100 m), 55744#1 (1200 m), 55767#1 (1390 m), 55789#3 (2030 m), 55726#1 (2075 m). Pakistan margin CD 145 stations: 55841#1 (1620 m), 55737#1 (1791 m) and 55815#1 (1799 m). Pakistan margin CD 151 station: 56137#12 (1852 m).
Description. Test typically spherical. Five specimens found on megacores were 12 to 20 mm diameter (average 15 mm, S.D. 5). The organic wall is thin, flexible and transparent, covered with multiple apertures of 0.02 mm average diameter. Oman and Pakistan specimens of *Gromia sphaerica* are visually the same, with the slight difference that in the Pakistan specimens the test contents fill the test while in the Oman specimens, the test contents are looser and do not fill the entire test interior.

Gromia sp.1 – grape-shaped (Figures 3.12 and 3.20 **A**)

Occurrence: Oman margin CD 143 stations: 55717#1 (1341 m), 55767#1 (1390 m), 55731#1 (1414 m), 55710#1 (1422 m), 55774#2 (1684 m), 55752#1 (1692 m), 55730#2 (1980 m), 55775#1 (1990 m), 55725#2 (2010 m), 55789#3 (2030 m), 55726#1 (2075 m).

Description:

Light microscope observations. A grape-shaped morphospecies with a thin translucent organic test wall, often with a pinkish reflective stain resembling mother of pearl on one side; test contents often not filling the whole test. The test is broadly oval in outline with smoothly rounded ends and gently curved sides; based on 104 specimens measured, dimensions are as follows: length 0.6 to 5 mm (average 2 mm, S.D. 0.5), width 0.6 to 2.8 mm (average 1.3 mm, S.D. 0.3). Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent, ranging from 0.06 to 0.3 mm diameter (average 0.1 mm, S.D. 0.03).

HVEM observations. Gromia sp.1 (Figure 3.20 A) has a thin outer test, with pores running through it, underlain by a single or multiple honeycomb membranes. This species looks like the classical ultrastructure photographs of *Gromia oviformis* wall structure (Hedley and Bertaud 1962).

Gromia sp.2 – grape-shaped (Figures 3.13 and 2.20 **B**)

Occurrence: Oman margin CD 143 stations: 55717#1 (1341 m), 55767#1 (1390 m), 55731#1 (1414 m), 55710#1 (1422 m), 55774#2 (1684 m), 55752#1 (1692 m), 55725#2 (1980 m), 55730#2 (1980 m), 55775#1 (1990 m).

Description:

Light microscope observations. Morphospecies with droplet-shaped test, oval in general shape but with an evenly rounded aboral end and a more narrowly rounded oral end; based on 110 specimens measured, dimensions are as follows: length 0.6 to 3.4 mm (average 1.7 mm, S.D. 0.6), width 0.5 to 2.8 mm (average 1.4 mm, S.D. 0.5). Very distinctive wall, which has a honeycomb-like structure visible under a binocular microscope. This is not to be confused with the honeycomb membranes only visible in the HVEM. Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent, ranging from 0.02 to 0.4 mm width (average 0.2 mm, S.D. 0.07).

HVEM observations. The rather peculiar honeycomb-like structure of the test wall can be seen very clearly on the HVEM micrographs (Figure 3.20 B). It appears to represent the outer test layer present in other gromiids and is quite rigid. The structure appears to comprise at least 2 layers of polygons. The outer layer is open, so that the outer edges of the walls of the polygon project into the surrounding medium. The walls of the polygon are penetrated by a series of open spaces, which in places beaks the walls up into kind of lattice-like structure. These do not appears to be the same as the pores observed in other species. The outer honeycomb layer is underlain typical honeycomb membranes, arranged in layers parallel to the test.

Gromia sp.3 – sausage-shaped (Figures 3.14 and 3.21)

Occurrence: Oman margin CD 143 stations: 55717#1 (1341 m), 55731#1 (1414 m), 55710#1 (1422 m), 55730#2 (1980 m), 55775#1 (1990 m). Pakistan margin CD 145 stations: 55841#1 (1620 m), 55737#1 (1791 m) and 55815#1 (1799 m). Pakistan margin CD 145 station: 55910#3 (1875 m).

Description:

Light microscope observations. A very elongate gromiid with a sausage-shaped test and a thin translucent organic wall. The test has smooth rounded ends and parallel sides; based on 17 specimens measured, dimensions are as follows: length 1.4 to 11.4 mm (average 6.8 mm, S.D. 4.8), width 0.3 to 4.5 mm (average 1.4 mm, S.D. 0.8). Length:Width ratio = 4.8. Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent, ranging from 0.04 to 0.4 mm width (average 0.4 mm, S.D 0.6).

HVEM observations. It was difficult to obtain good sections for this large morphotype and therefore no HVEM images were obtained. DIC photographs taken by Sam Bowser show that the wall of *Gromia* sp.3 is covered in pores, inlaid by a layer of stercomata, mainly concentrated at the proximal end of the test (Figure 3.21). The oral capsule is clearly illustrated in Figure 3.21.

Gromia sp.4 – spherical (Figure 3.15)

Occurrence: Oman margin CD 143 stations: 55753#1 (1093 m), 55717#1 (1341 m), 55767#1 (1390 m), 55731#1 (1414 m). Pakistan margin CD 145 stations: 55811#1 (1174 m), 55802#7 (1200 m), 55802#4 (1201 m), 55841#1 (1620 m), 55737#1 (1791 m), 55815#1 (1799 m), 55826#2 (1833 m), 55827#4 (1867 m), 55827#3 (1870 m) and 55830#2 (1874 m). Pakistan margin CD 151 stations: 56139#2 (1193 m) and 56140#2 (1859 m).

Description. Test typically spherical, 0.8 to 5.0 mm diameter (average 2.6 mm, S.D. 1.1) with a single aperture of 0.08 to 0.05 mm diameter (average 0.2 mm, S.D. 1); measured from 16 specimens. Oral capsule relatively small compared with other species. The organic wall is thicker and more flexible than in *Gromia sphaerica*. When dropped on the floor this gromiid type bounces like a tennis ball.

Gromia sp.5 – grape-shaped (Figure 3.16)

Occurrence: Oman margin CD 143 station: 55725#2 (2010 m) and Pakistan margin CD 151 stations: 56137#2 (1852 m) and 55910#3 (1875 m).

Description. This morphospecies is based mainly on molecular data rather than morphological data. It is a grape-shaped morphospecies with either a thin, translucent test wall or a thick, opaque test wall, sometimes with a pinkish reflective stain resembling mother of pearl on one side. The test is broadly oval in outline with an evenly rectangular shape, smoothly rounded ends and gently curved sides. However, there are slight variations in test shape which span the

morphologies of the grape-like species (1 and 6) described above and below. Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent.

Gromia sp.6 – grape-shaped (Figures 3.17 and 3.20 **C**)

Occurrence: Oman margin CD 143 stations: 55717#1 (1341 m), 55767#1 (1390 m), 55731#1 (1414 m), 55710#1 (1422 m), 55774#2 (1684), 55752#1 (1692 m), 55725#2 (1980 m), 55730#2 (1980 m), 55775#1 (1990 m), 55789#3 (2030 m), 55726#1 (2075 m).

Description:

Light microscope observations. A grape-shaped morphospecies with a thick, sometimes translucent but generally opaque organic test, sometimes with a pinkish reflective stain resembling mother of pearl on one side; test contents fill all the test. The test is broadly oval in outline with gently concave sides and smoothly rounded ends; based on 624 specimens measured, dimensions are as follows: length 0.6 to 8 mm (average 3.5 mm, S.D. 2.0), width 0.08 to 4.5 mm (average 2.4 mm, S.D. 1.4). Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent, ranging from 0.02 to 0.6 mm width (average 0.3 mm, S.D. 0.2).

HVEM observations. This species possesses a thicker outer test layer than sp.1. Typical honeycomb membranes underlie this outer layer. The cell contained numerous stercomata (Figure 3.20 C). One of the three specimens examined under the TEM and the HVEM, had filamentous bacteria attached to the outer surface of the test. Bacteria were of different types and sizes but further investigation is required for detailed description.

Gromia sp.7 – sausage-shaped (Figures 3.18 and 3.20 **D**)

Occurrence: Oman margin CD 143 stations: 55766#1 (1103), 55717#1 (1341 m), 55767#1 (1390 m), 55731#1 (1414 m), 55710#1 (1422 m), 55775#1 (1990 m), 55789#3 (2030 m), 55726#1 (2075 m). Pakistan margin CD 145 stations: 55841#1 (1620 m), 55737#1 (1791 m) and 55815#1 (1799 m).

Description:

Light microscope observations. An elongate gromiid with a sausage-shaped test and a thin, translucent organic wall, often with a pinkish reflective stain resembling mother of pearl on one side. The test has smooth rounded ends with parallel sides, with a constriction behind the front end. Very similar to Sausage-like *Gromia* sp.3 but with shorter, fatter test and smaller Length:width ratio of 3.1. Based on 136 specimens measured, dimensions are as follows: length 1.1 to 15.4 mm (average 4.7 mm, S.D. 1.8), width 0.4 to 4.1 mm (average 1.5 mm, S.D. 0.3). Test filled with brownish stercomata and loose sediment-like material. Oral capsule prominent, ranging from 0.06 to 0.6 mm width (average 0.3 mm, S.D 0.06). This species is similar to the elongate gromiids reported from the Oman margin by Gooday et al. (2000). Some specimens

closely resemble the “faecal pellet” from the Santa Catalina Basin Basin, illustrated by Jumars (1976).

HVEM observations. The wall ultrastructure of this species was very similar to *Gromia* sp.1 (Figure 3.20 D).

Gromia sp.8 (Figure 3.19)

Occurrence: Oman margin CD 143 stations: 55774#2 (1684 m) and 55775#1 (1990)

Description. Branched organic test with rounded edges and an aperture at the tip of each branch. Overall length of 2 mm. Average branch length of 1.6 mm. Average oral capsule diameter 0.08 mm. Test partially filled with loose sediment.

Figure 3.11 Light photographs of *Gromia sphaerica*. Oman margin: **A1** 1160 m Station 55759#1 specimens 1 and 2, **A2, A3**, **A4** and **A5** specimen 2. B1 and B2 1200 m Station 55744#1 specimen 1, B3 detail of apertures. Pakistan margin: C 1852 m Station 56137#12 specimen 1 and D specimen 2. For other photographic images refer to Gooday et al. (2000). All specimens were preserved in formalin with the exception of specimens in **C** and **D** that were frozen at -70°C for molecular phylogeny studies. The structures visible on specimen in **C** is an artefact from the freezing process followed by defrosting. For HVEM images see Gooday et al. (2000).

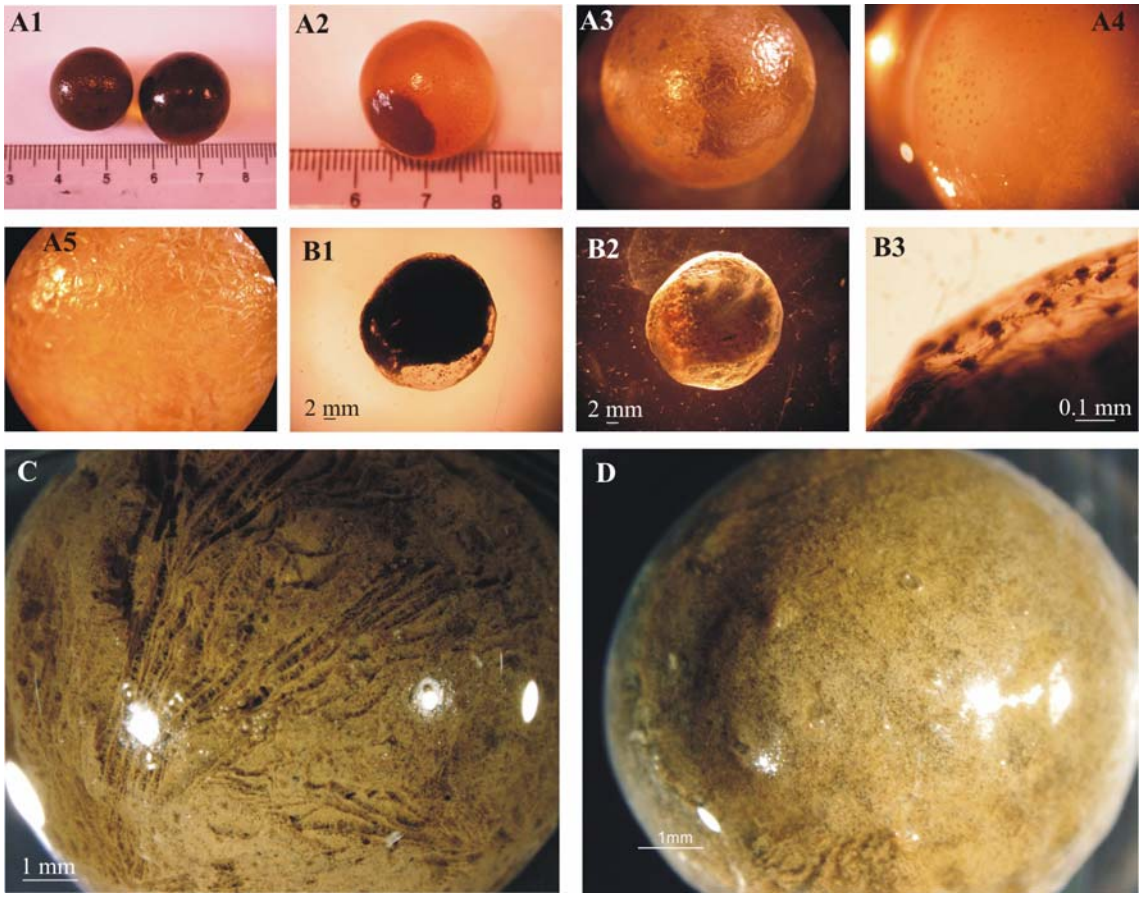


Figure 3.12 Light photographs of *Gromia* sp.1. **A** 1390 m Station 55767#1 specimen 1, **B** specimen 2. **C** 1422 m Station 55710#1 specimen 1, **D** specimen 2. **E1** 1684 m Station 55774#1 specimen 1, **E2** detail of the oral capsule. **F** 1691 m Station 55752#1 specimen 1. **G** 1980 m Station 55730#2 specimen 1, **H** specimen 2. **I** 2030 m Station 55789#3 specimen 1. **J** 2075 m Station 55726#1 specimen 1, **K** specimen 2. All specimens were preserved in formalin with the exception of specimen in C that was frozen at -70°C for molecular phylogeny studies.

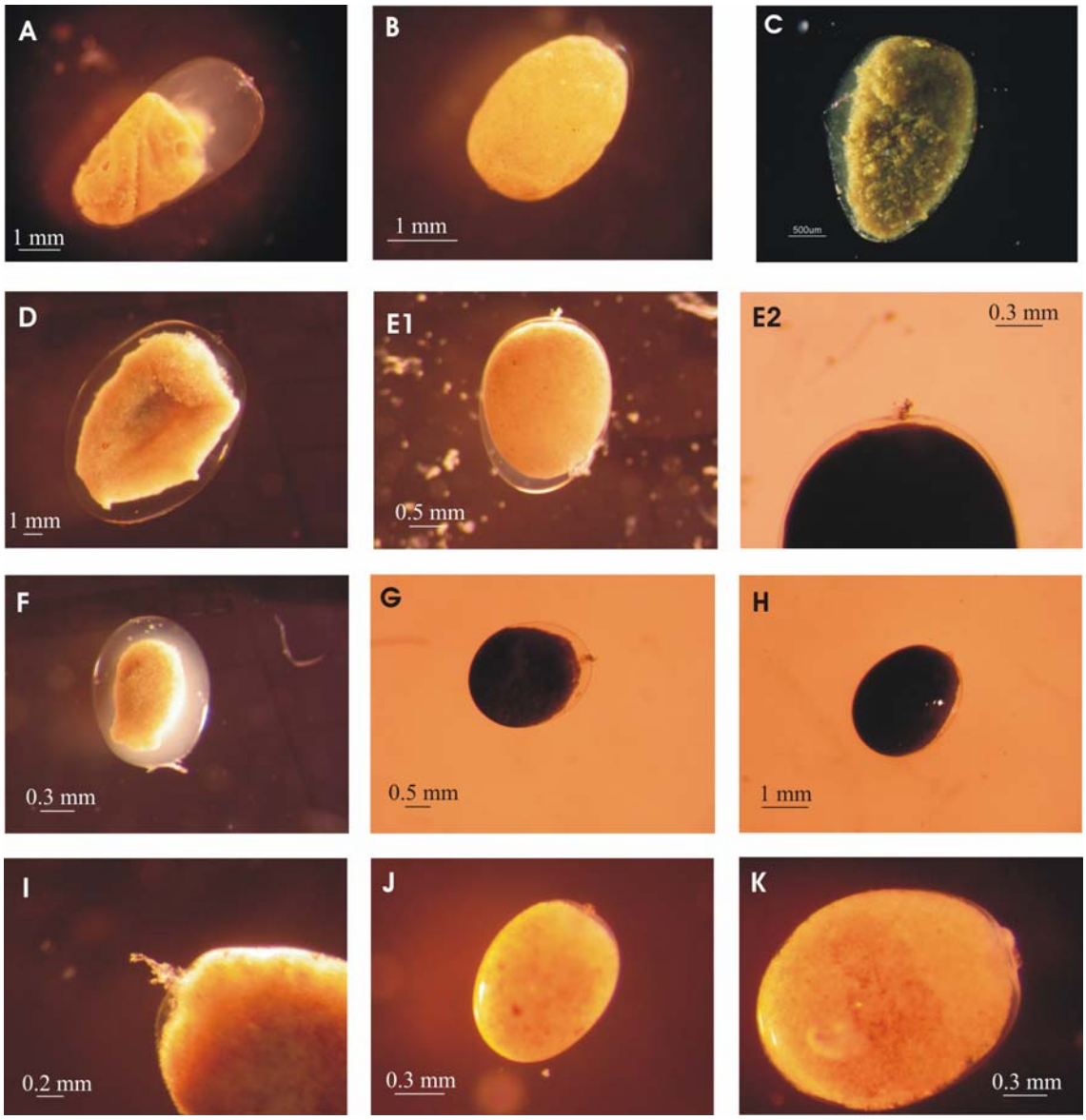


Figure 3.13 Light photographs of *Gromia* sp.2. **A1** 1341 m Station 55717#1 specimen 1, **A2** detail of the wall, A3 detail of the oral capsule, **B** specimen 2. **C1** 1390 m Station 55767#1 specimen 1, **C2** detail of the oral capsule, **D1** specimen 2, **D2** detail of the oral capsule. **E** 1414 m Station 55731#1 specimen 1. **F1** 1422 m Station 55710#1 specimen 1, **F2** detail of the oral capsule, **G** specimen 2, **H1** specimen 3, **H2** detail of the wall. **I** 1684 m Station 55774#1 specimen 1, **J** specimen 2. **K** 1691 m Station 55752#1 specimen 1. **L1** 1980 m Station 55730#2 specimen 1, **L2** detail of the wall, **L3** detail of the oral capsule. All specimens were preserved in formalin with the exception of specimens in H and L that were frozen at -70°C for molecular phylogeny studies.

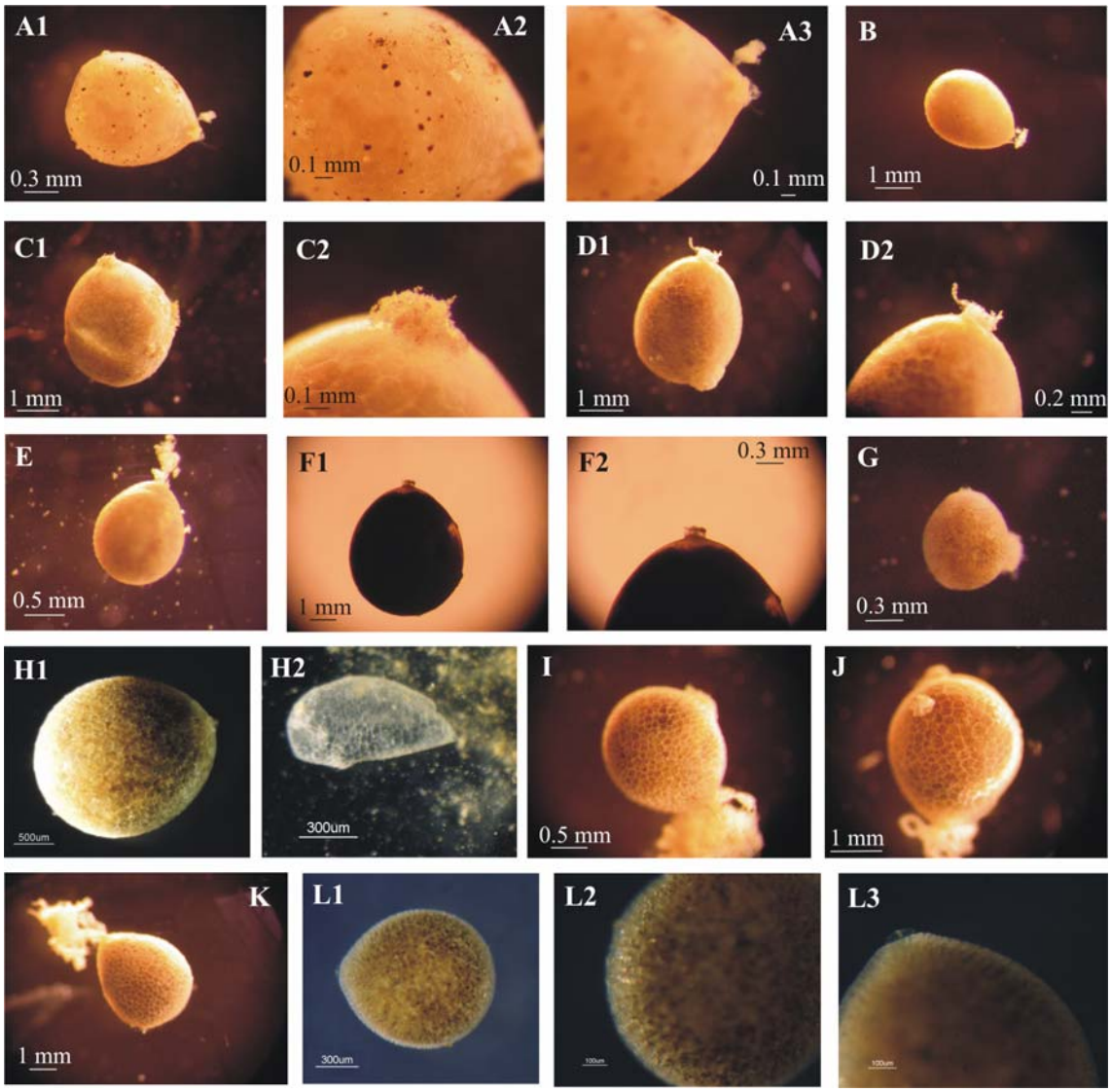


Figure 3.14 Light photographs of *Gromia* sp.3. **A1** 1341 m Station 55171#1 specimen 1, **A2** detail of the oral capsule, **B** specimen 2. **C** 1414 m Station 55731#1 specimen 1, **D1** specimen 2, **D2** detail of the left oral capsule, **D3** detail of the right oral capsule. **E** 1422 m Station 55710#1 specimen 1. **F1** 1692 m Station 55752#1 specimen 1, **F2** detail of the oral capsule. **G1** 1980 m Station 55730#1 specimen 1, **G2** detail of the oral capsule, **H1** specimen 2, **H2** detail of the oral capsule, **I1** specimen 3, **I2** detail of the oral capsule, **J1** specimen 4, **J2** detail of the oral capsule, **K1** specimen 5, **K2** detail of the oral capsule, **L1** specimen 6, **L2** detail of the oral capsule. **M** 1875 m Station 55910#3 specimen 1, **N** specimen 2. All specimens were preserved in formalin with the exception of specimens in **M** and **N** that were frozen at -70°C for molecular phylogeny studies.

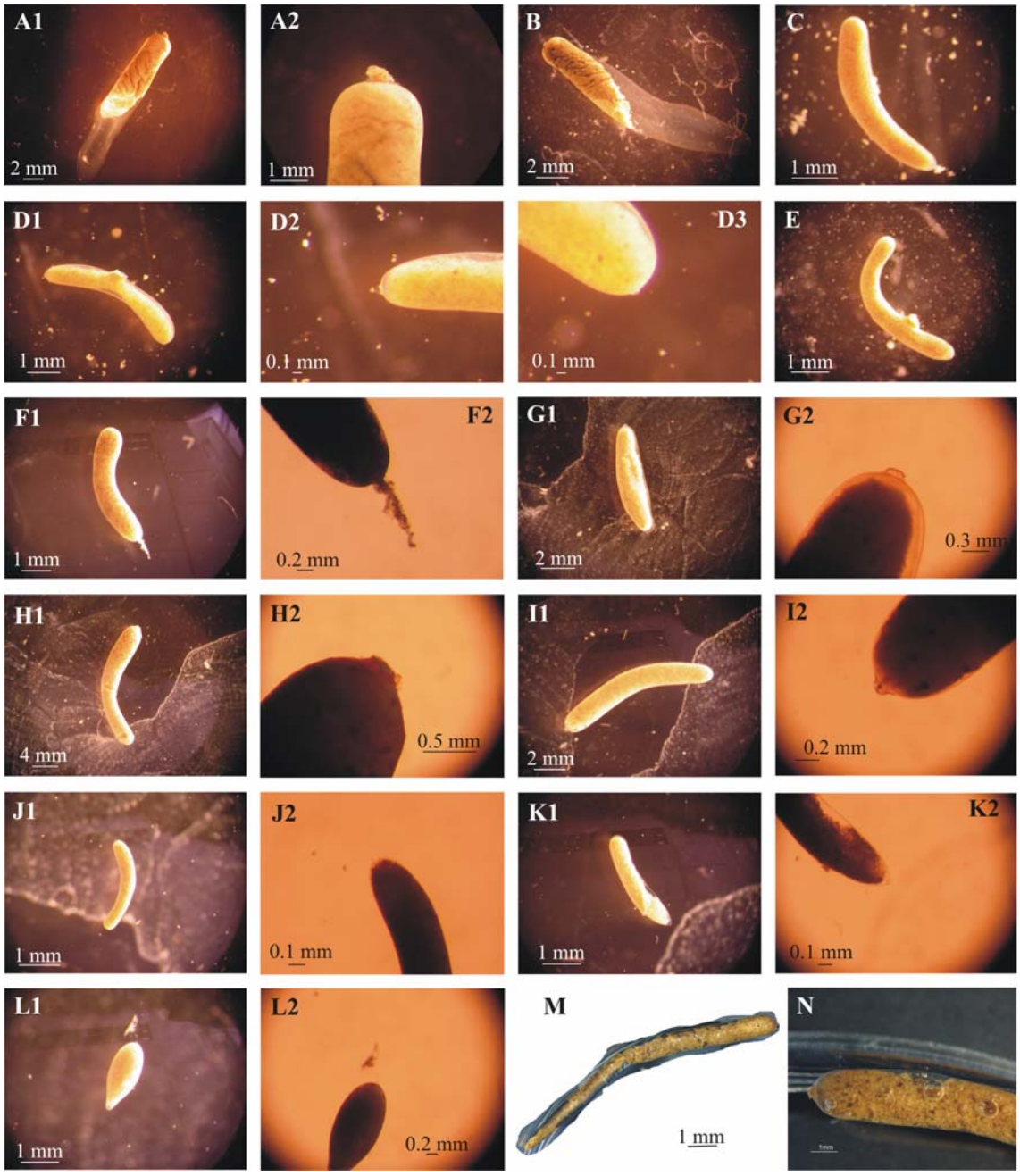


Figure 3.15 Light photographs of *Gromia* sp.4. Oman margin: **A** 1093 m Station 55753#1 specimen 1, **B** specimen 2. **C** 1341 m Station 55717#1 specimen 1, **D** specimen 2, **E** specimen 3, **F** specimen 4, **G1** specimen 5, **G2** detail of the oral capsule, **H1** specimen 6, **H2** detail of the oral capsule, **I** specimen 7. **J** 1390 m Station 55767#1 specimen 1, **K** specimen 2. **L** 1414 m Station 55731#1 specimen 1, **M** specimen 2, **N1** specimen 3, **N2** detail of the oral capsule or attached gromiid. Pakistan margin: **O1** and **O2** 1193 m Station 56139#2 and **P** 1859 m station 56140#2 specimen 1. All specimens were preserved in formalin with the exception of specimen in O that was frozen at -70°C for molecular phylogeny studies.

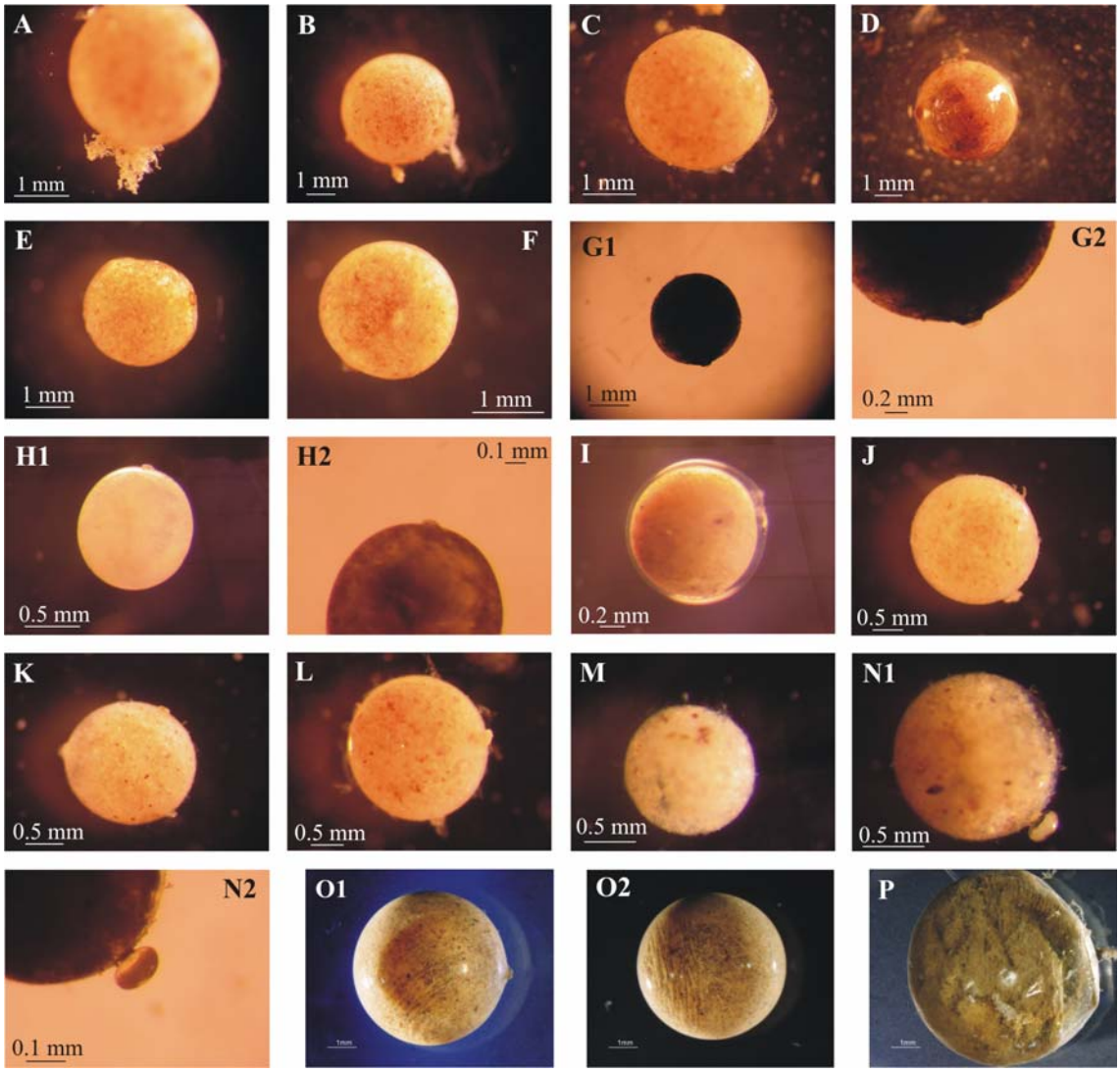


Figure 3.16 Light photographs of *Gromia* sp.5. Oman margin: **A** 2010 m Station 55725#2 specimen 1. Pakistan margin: **B** 1852 m Station 56137#2 specimen 1, **C** 1875 m Station 55910#3 specimen 1 **D** and specimen 2. All specimens were frozen at -70°C for molecular phylogeny studies. The bubbles seen in the pictures are the result of the defrosting of the specimens for photography.

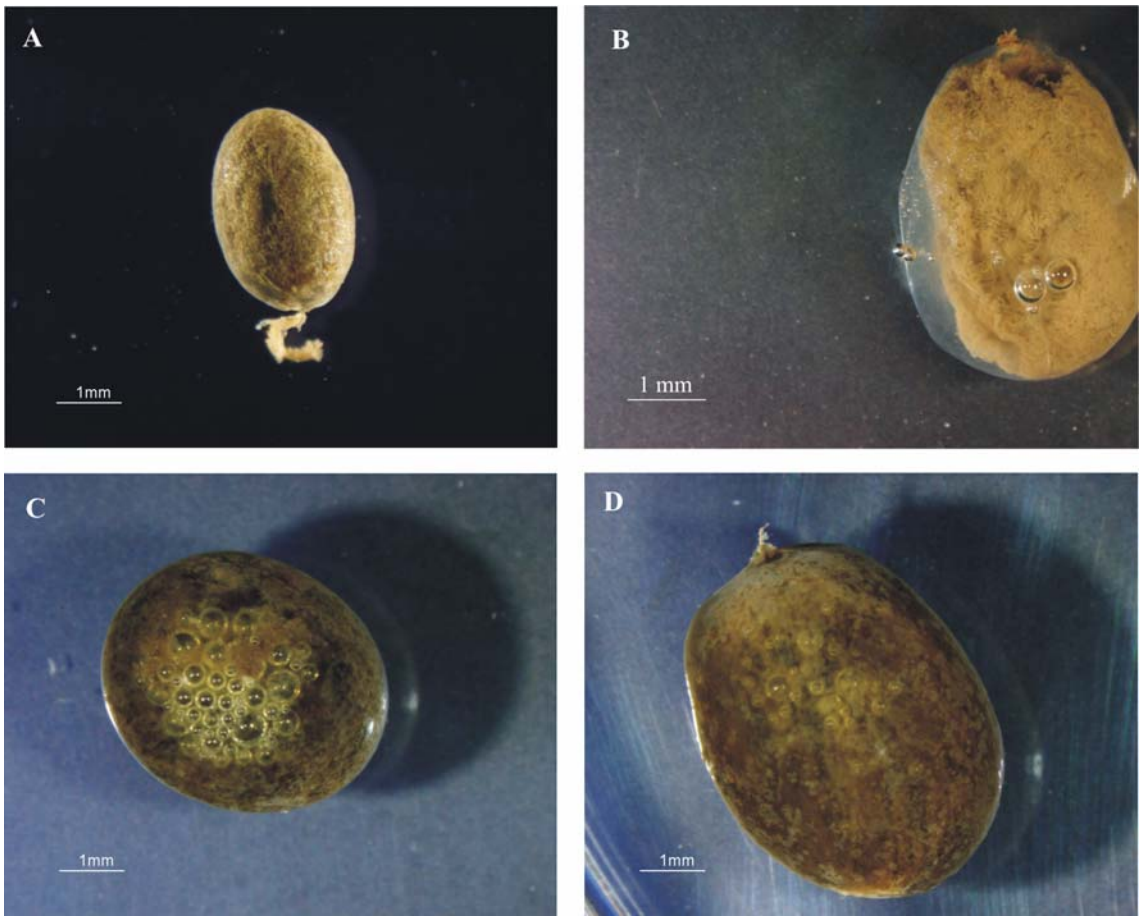
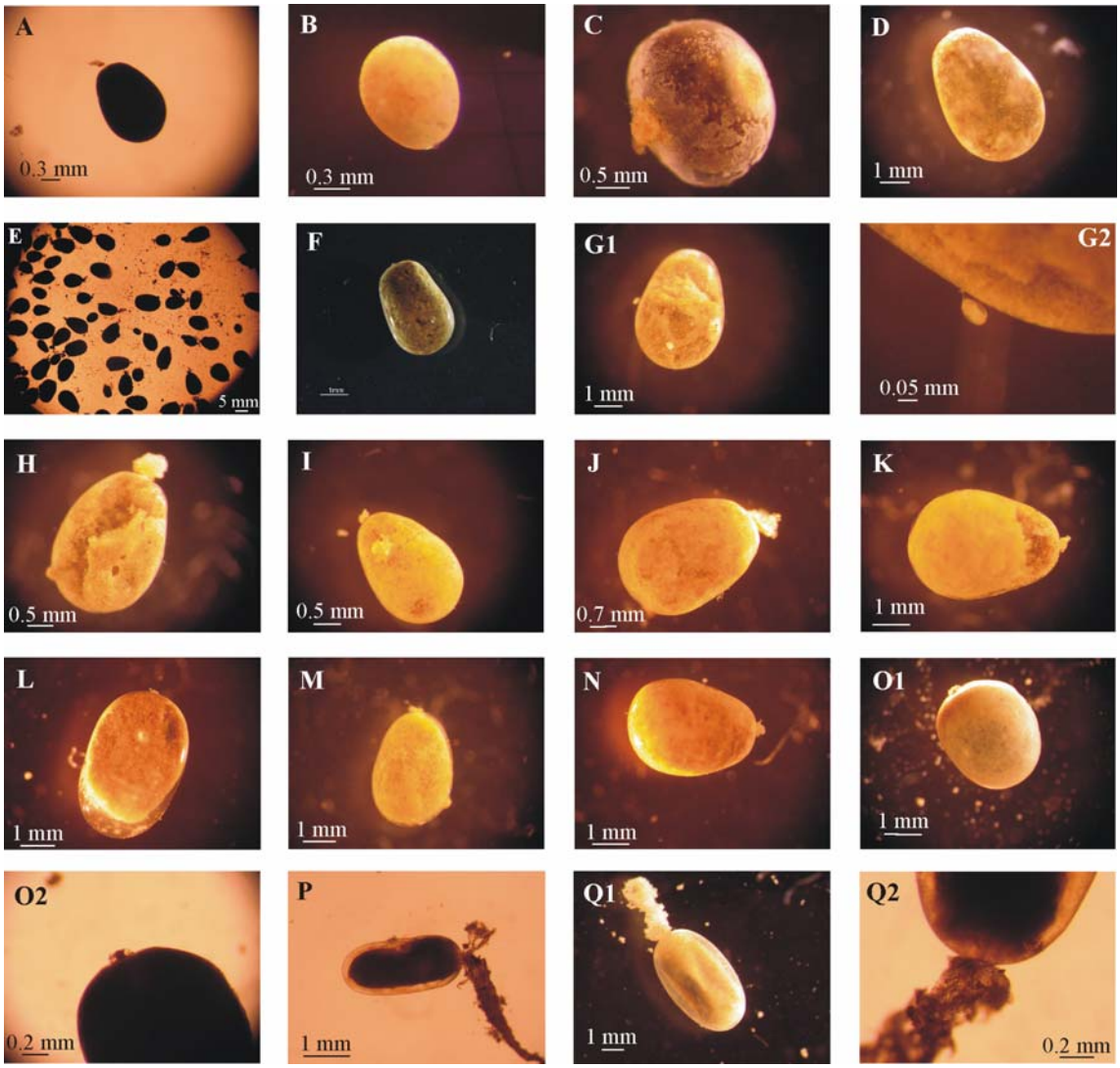


Figure 3.17 Light photographs of *Gromia* sp.6. **A** 1341 m Station 55717#1 specimen 1, **B** specimen 2, **C** specimen 3 and **D** specimen 4. **E** 1390 m Station 55767#1, **F** specimen 1, **G1** specimen 2, **G2** detail of attached gromiid, **H** specimens 3, **I** specimen 4, **J** specimen 5, **K** specimen 6, **L** specimen 7, **M** specimen 8, **N** specimen 9, **O1** specimen 10, **O2** detail of the oral capsule. **P** 1414 m Station 55731#1 specimen 1, **Q1** specimen 2, **Q2** detail of the oral capsule. **R** 1422 m Station 55710#1 specimens 1, **S** specimen 2, **T** specimen 3, **U** specimen 4, **V** specimen 5, **W** specimen 6, **X** specimen 7, **Y** specimen 8, **Z** specimen 9. **Aa** 1684 m Station 55774#2 specimens 1, **Ab** specimen 2 and **Ac** specimen 3. **Ad1** 1692 m Station 55752#1 specimen 1, **Ad2** detail of the oral capsule. **Ae1** 1980 m Station 55730#2 specimen 1, **Ae2** detail of the oral capsule, **Af1** specimen 2, **Af2** detail of the oral capsule. **Ag1** 2030 m Station 55789#3 specimen 1, **Ag2** detail of the oral capsule. **Ah1** 2075 m Station 55726#1 specimen 1, **Ah2** detail of the oral capsule, **Ai1** specimen 2, **Ai2** detail of the oral capsule. All specimens were preserved in formalin with the exception of specimens in **F**, **T**, **U** and **L** that were frozen at -70°C for molecular phylogeny studies.



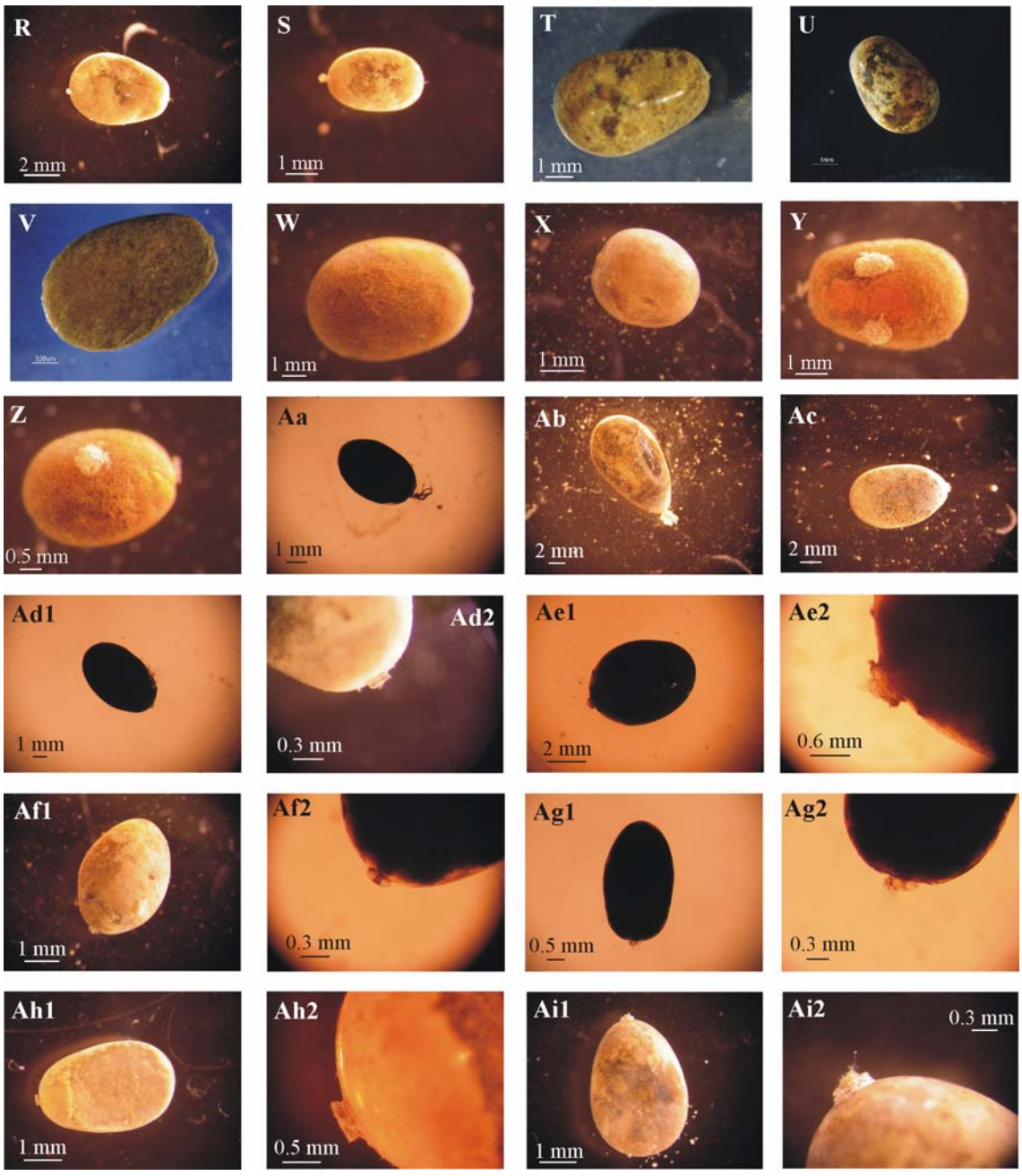

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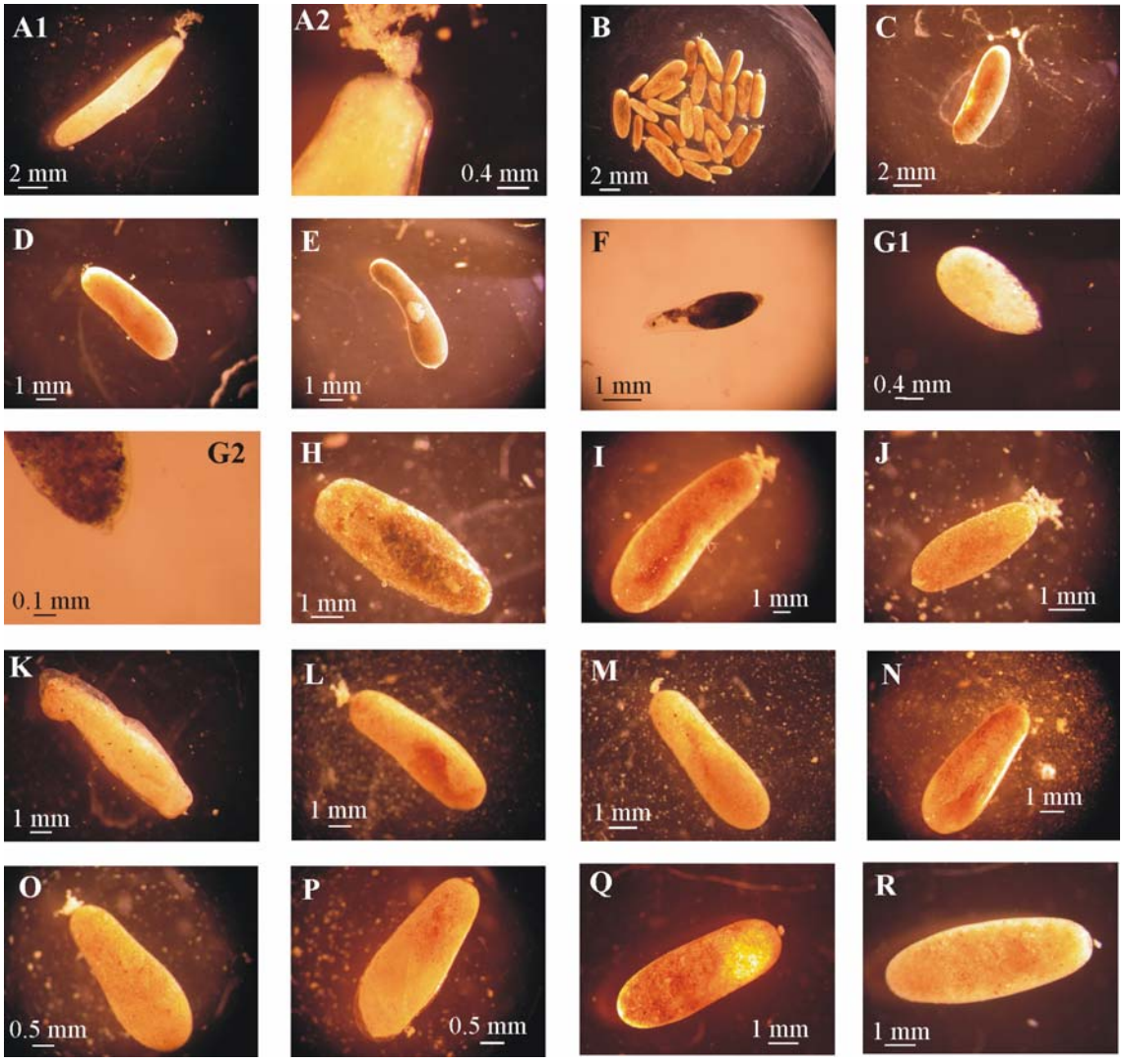
Figure 3.18 Light photographs of *Gromia* sp.7. **A1** 1102 m Station 55766#1 specimen 1, **A2** detail of the oral capsule. **B** 1341 m Station 55717#1 several specimens, **C** specimen 1, **D** specimen 2, **E** specimen 3, **F** specimen 4, **G1** specimen 5, **G2** detail of the oral capsule, **H** specimens 6, **I** specimen 7, **J** specimen 8, **K** specimen 9, **L** specimen 10, **M** specimen 11, **N** specimen 12, **O** specimen 13, **P** specimen 14, **Q** specimen 15, **R** specimen 16, **S1** specimen 17, **S2** detail of the oral capsule, **T** specimens 18. **U** 1390 m Station 55767#1 several specimens, **V** specimen 1, **W** specimen 2, **X** specimen 3, **Y** specimen 4, **Z** specimen 5, and **Aa** specimen 6. **Ab** 1414 m Station 55731#1 specimens 1, **Ac** specimen 2, **Ad** specimen 3, **Ae** specimen 4, **Af** specimen 5, **Ag** specimen 6 and **Ah** specimen 7. **Ai1** 1422 m Station 55710#1 specimen 1, **Ai2** detail of the oral capsule, **Aj1** specimen 2, **Aj2** detail of the oral capsule, **Ak1** specimen 3, **Ak2** detail of the oral capsule, **Al1** specimen 4, **Al2** detail of the oral capsule, **Am** specimens 5, **An** specimen 6 and **Ao** specimen 7. **Ap1** 2030 m Station 55789#3 specimen 1, **Ap2** detail of the oral capsule, **Aq** specimen 2. **Ar** 2075 m Station 55726#1 specimen 1. All specimens were preserved in formalin.



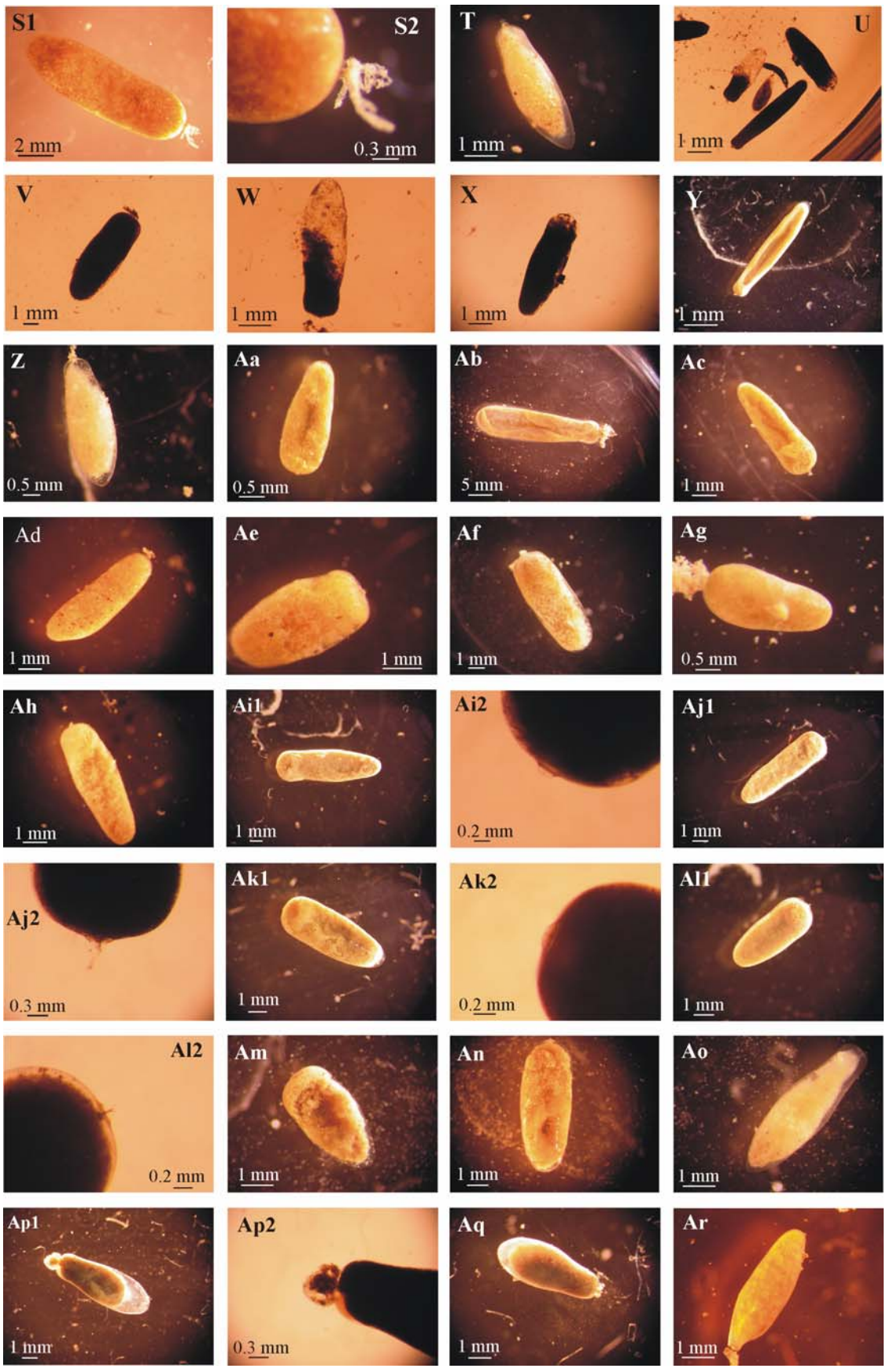

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Figure 3.19 Light photographs of *Gromia* sp.8. **A1** and **A2** 1684 m Station 55774#2 specimen 1, **A3** and **A4** detail of the bottom left aperture, **A5** and **A6** detail of the right aperture and **A7** and **A8** detail of the top left aperture. **B** 1990 m Station 55775#4 specimen 1. Both specimens were preserved in formalin.

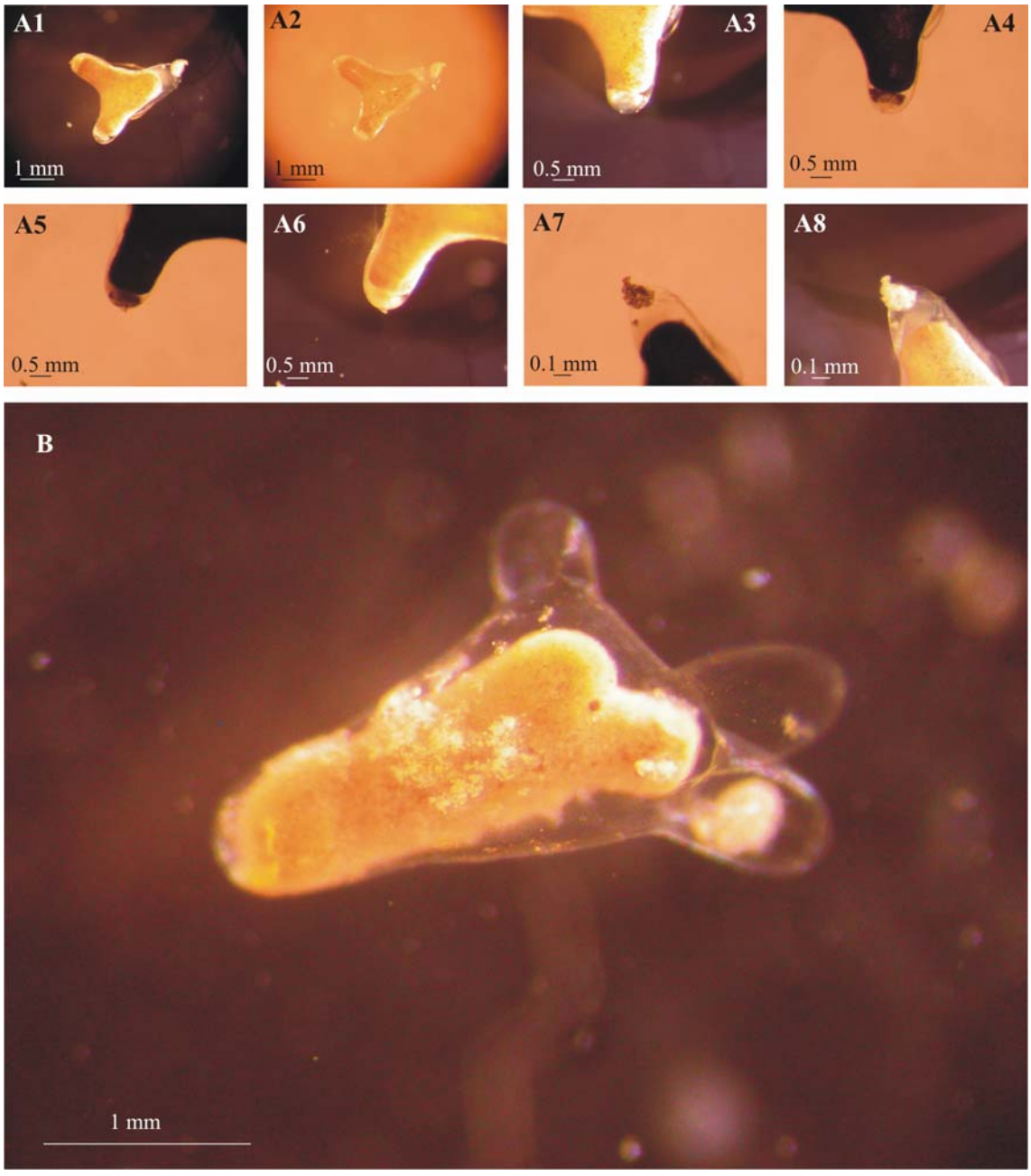


Figure 3.20 High-voltage transmission electron micrographs of 0.5 nm thick sections through the test wall. *Gromia* sp.1: **A1** cross-section showing the honeycomb membrane (hm) and the cytoplasm (c) (x5000), **A2** Closer view of the honeycomb membranes (hm) (x25000). *Gromia* sp.2: **B1** detail of honeycomb wall structure (hw) (x1600), **B2** end of honeycomb wall structure (hw), honeycomb membrane (hm) and cytoplasm (c) (x4000). *Gromia* sp.6 cross section of outer wall (ow), cytoplasm (c) (x5000), C2 bacteria (b) attached to the outer wall (ow) (x20000) and **C3** honeycomb membranes (hm), cytoplasm (c) and stercomata (s) (x8000). **D** *Gromia* sp.7: cytoplasm (c), honeycomb membrane (hm)? (x31500). **E** *Gromia* sp.5 outer wall (ow), honeycomb membranes (hm), cytoplasm (c) and stercomata (s) (x2500).

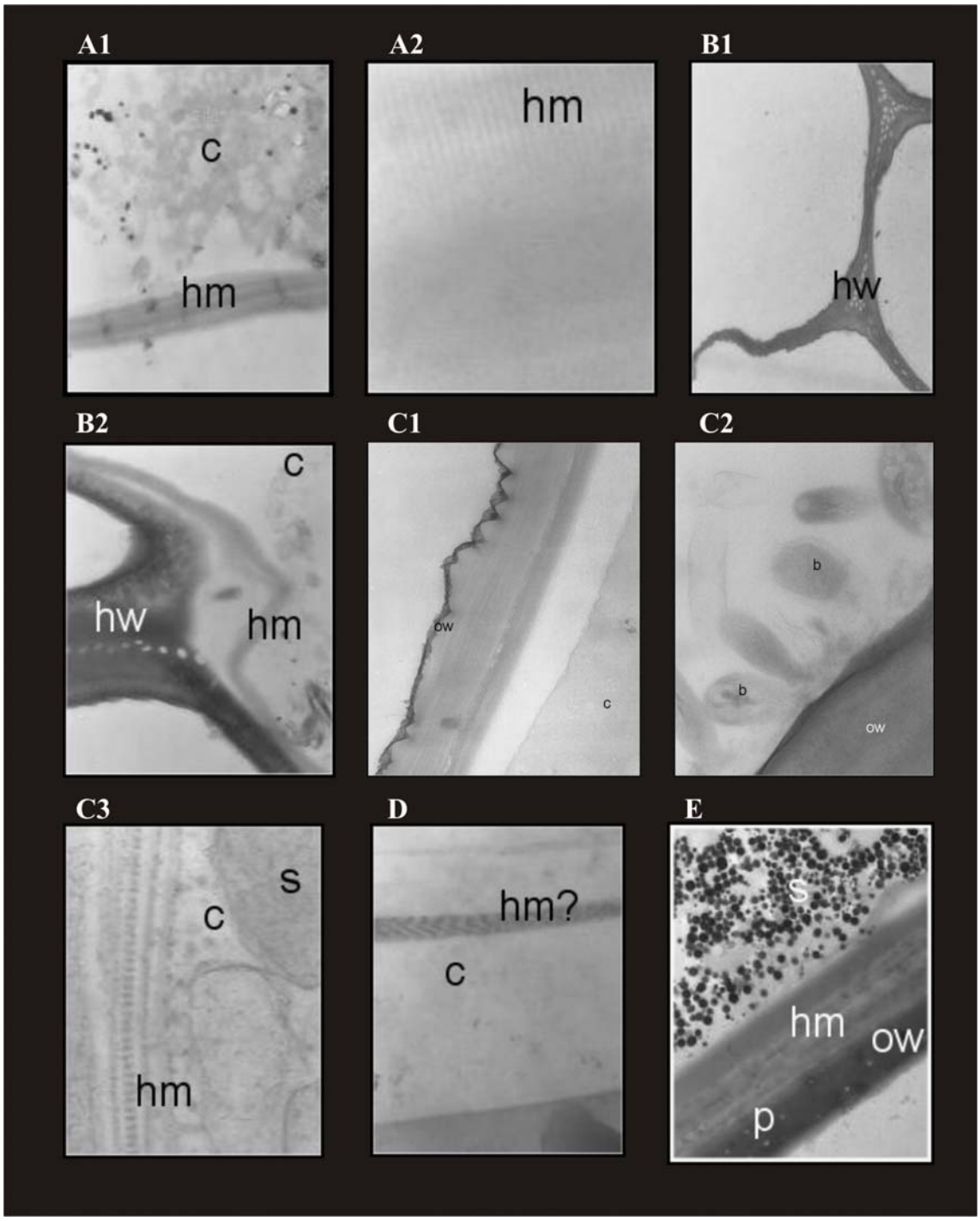
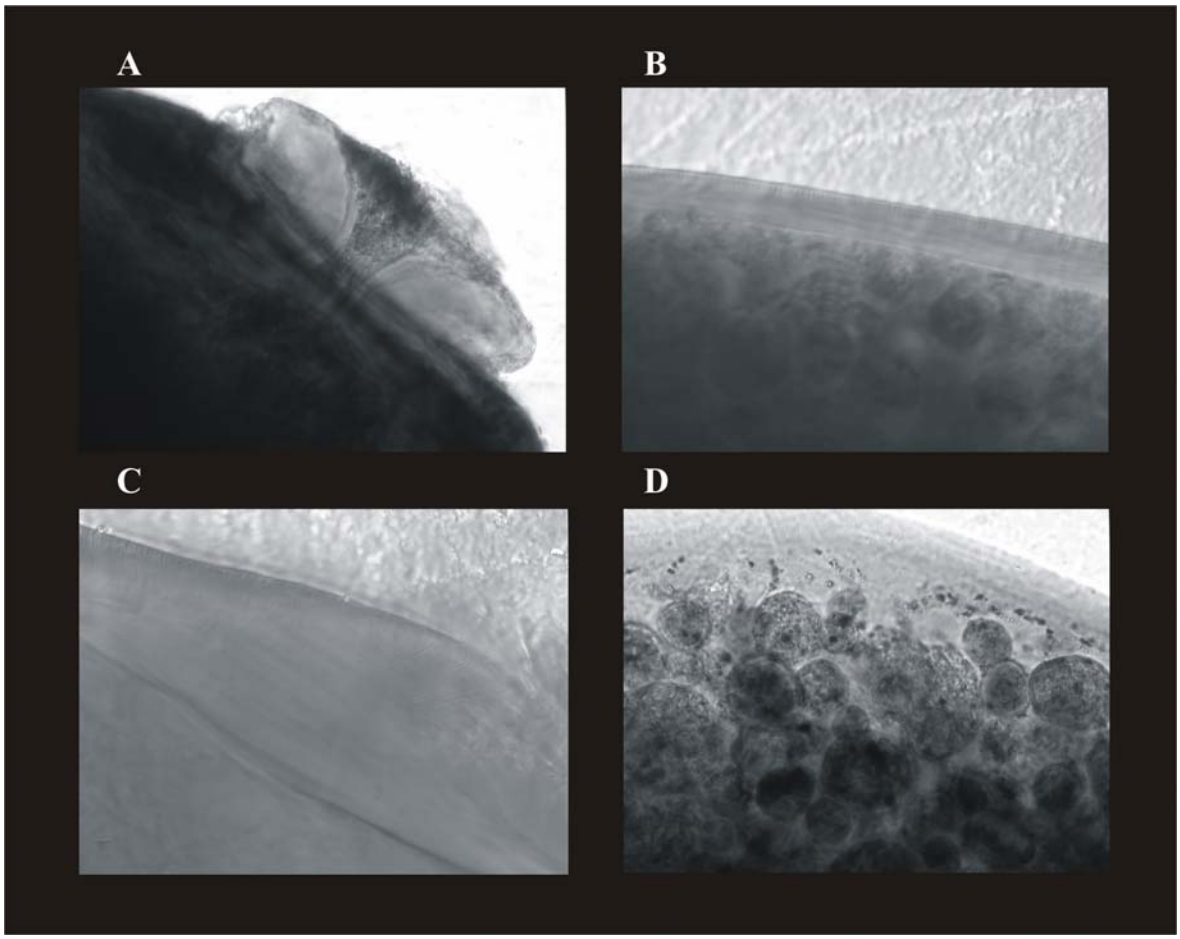


Figure 3.21 Differential contrast photograph from *Gromia* sp.3. **A** detail of oral capsule (x10), **B** and **C** detail of wall covered in pores (x20) and **D** stercomata (x20).



3.3 Results

3.3.1 Abundance

On the Oman margin, gromiids were found on the surface of megacore samples collected between 1093 m and 2075 m water depth where oxygen levels were > 0.5 ml/l. Total gromiid abundance (Figure 3.22, Table 3.2) was highest at the 1400 and 1700 m stations, ranging respectively from 10.7 to 27.5 individuals and 17.9 to 33.2 individuals per core (surface area 78.5 cm^2). Densities were considerably lower (0 to 3.3 specimens per core) at the deepest station (2000 m), and lowest at 1100 m, where only 0.3 to 0.6 gromiids were present per core. There was considerable patchiness between deployments as well as between cores within deployments. For example, at 1400 m, mean densities varied between 10.7 and 27.5 specimens per core between deployments (Table 3.2) and within one individual 8-core deployment, densities ranged from 6 to 71 specimens per core (Table 3.3).

On the Pakistan margin, different gromiid morphoptypes were abundant in trawl samples from 1620 to 1799 m but were observed only occasionally in megacore samples, one specimen per deployment being typical (Table 3.4). This implies that gromiids are much more abundant on the Oman margin than the Pakistan margin of the Arabian Sea.

Figure 3.22 Mean abundance of gromiids found on the surface of megacores (78.5 cm^2) on the Oman margin, CD 143.

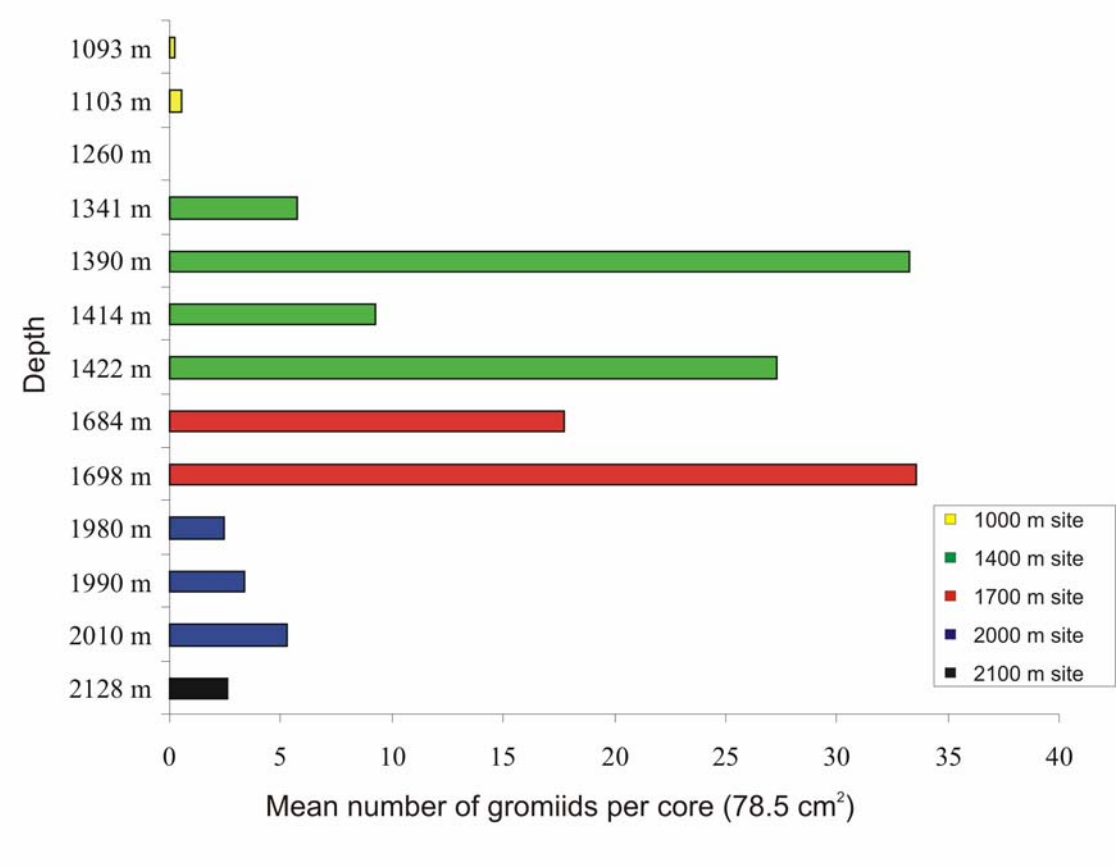


Table 3.2 Mean abundance of gromiids found on the surface of megacores (78.5 cm^2) and collected by the Agassiz trawl on the Oman margin, CD 143.

Depth (m)	1093	1103	1260	1341	1390	1414	1422	1684	1698	1980	1990	2010	2128
Station number	55753#1	55766#1	55759#1	55717#1	55767#1	55731#1	55710#1	55774#1	55752#1	55730#2	55775#1	55725#2	55726#1
Number of cores	8	7	Trawl	4	8	7	7	8	9	7	8	4	7
Morphotypes:													
Sausage-like				1.0		3.0	8.0				1.0		
Carrot-like				17.0	59.0	7.0	15.0						1.0
Grape-like	2.0	4.0		4.0	205.0	53.0	166.0	141.0	298.0	16.0	22.0	21.0	16.0
Honeycomb-like					1.0	2.0			1.0	1.0			
Gromia sphaerica			Numerous		1.0								1.0
Other				1.0			2.0	1.0	3.0		4.0		
Total per deployment	2.0	4.0	0.0	23.0	266.0	65.0	191.0	142.0	302.0	17.0	27.0	21.0	18.0
Mean per core (78.5 cm^2)	0.3	0.6		5.8	33.3	9.3	27.3	17.8	33.6	2.4	3.4	5.3	2.6
Mean per 10 cm^2	0.0	0.1	ND	0.7	4.2	1.2	3.5	2.3	4.3	0.3	0.4	0.7	0.3

Table 3.4 Mean abundance of gromiids found on the Pakistan margin, CD 145. ND: no data.

Depth (m)	1174-1177	1192	1193	1620-1660	1791-1814	1799-1852	1826	1861	1864	1868
Station number	55811#1	55802#7	55802#4	55841#1	55837#1	55815#1	55826#2	55827#4	55827#3	55830#2
Sampling Equipment	Agassiz Trawl	Megacorer (78.5 cm^2)	Multicorer (25.5 cm^2)	Agassiz Trawl	Agassiz Trawl	Agassiz Trawl	Megacorer (78.5 cm^2)	Megacorer (78.5 cm^2)	Megacorer (78.5 cm^2)	Multicorer (25.5 cm^2)
Number of cores		1	1				12	4	1	5
Morphotypes:										
Sausage-like				Numerous	Numerous	Numerous				
Carrot-like				Numerous	Numerous	Numerous				
Grape-like				Numerous	Numerous	Numerous				
Spherical	Numerous	2.0	1.0	Numerous	Numerous	Numerous	1.0	3.0	1.0	2.0
Gromia sphaerica				Numerous	Numerous	Numerous				
Total per deployment	ND	2.0	1.0	ND	ND	ND	1.0	3.0	1.0	2.0
Mean per core	ND	2.0	1.0	ND	ND	ND	0.1	0.8	1.0	0.4
Mean per 10 cm^2	ND	0.3	0.4	ND	ND	ND	0.0	0.1	0.1	0.2

Table 3.3 Mean number of gromiids per core (78.5 cm^2) visible on the surface of megacores collected at Station 55767#1 at 1390 m on the Oman margin.

Surface gromiids	**C1**	**C2**	**C3**	**C4**	**C5**	**C6**	**C7**	**C8**	**Total per core (78.5 cm^2)**	**Mean pe 10 cm^2**
Carrot-like	6	15	6	6	4	9	1	12	59	8
Grape-like	18	53	16	17	7	32	4	59	206	26
Honeycomb-like		1							1	0
Gromia sphaerica							1		1	0
Total per core (78.5 cm^2)	24	69	22	23	11	41	6	71	267	34
Total per 10 cm^2	3	9	3	3	1	5	1	9	34	4

3.3.2 Diversity and distribution of gromiid morphotypes on the Oman margin (CD 143)

On first examination, two very distinct gromiid morphotypes, grape-shaped and sausage-shaped were visible on the surface of undisturbed megacore samples (Figure 3.23). Closer examination under the microscope revealed a variety of different types ranging from sausage-shaped to grape-shaped and spherical forms, all found just below the OMZ (O_2 >0.5 ml/l). The total number of morphotypes recognized was between 1 and 8 found at any one water depth (Table 3.2). Detail of species found in different depth zones are as follows.

1100 m. Cores from two megacore deployments (Station 55753#1, 1093 m and Station 55766#1, 1103 m) yielded occasional specimens of *Gromia* sp.4 (1093 m) (Figure 3.15 A and B) and *Gromia* sp.7 (1103 m) (Figure 3.18 A), typically 0 to 1 specimen per core (Table 3.2).

1100 - 2000 m. Gromia sphaerica was sampled with the megacorer on one occasion (Station 55789#3, 2030 m), and only one specimen was collected. However, it was abundant in two Agassiz trawl deployments at 1100 m (Station 55759#1) and 1200 m water depth (Station 55744#1). Apart from the irregularly shaped *Gromia* sp.8, this is the only gromiid found to have a test with multiple apertures (Figure 3.11 A and B).

1400 m. Four deployments at around 1400 m (stations 55717#1, 1341 m; 55767#1, 1390 m; 55731#1, 1414 m and 55710#1, 1422 m) yielded 5 gromiid morphotypes (Table 3.5): *Gromia* sp.7, (Figure 3.18 B to Ao), *Gromia* sp.3 (Figure 3.14 A to E), *Gromia* sp. 1 (Figure 3.12 A to D) and *Gromia* sp. 6 (Figure 3.17 A to Z). There was also a distinct morphotype, *Gromia* sp.2 (Figure 3.13 A to H) found in very small numbers during ship board examination of samples. Only 3 specimens of this species were picked at sea, but more detailed laboratory examination showed a total of 93 specimens spread across all four deployments. *Gromia* sp.6 was the most abundant morphotype (42.1%) at this site, followed by *Gromia* sp.7 (24.5%), *Gromia* sp.2 (17.6%), *Gromia* sp.1 (10.8%), *Gromia* sp.4 (3%), and *Gromia* sp.3 (1.9%) (Table 3.5).

1700 m. Two deployments at 1700 m (stations 55774#1, 1684 m and 55752#1, 1692 m) yielded mostly *Gromia* sp.6 (Figure 3.17 Ab to Ad), which accounted for 88.2% of the total assemblage at the site (Table 3.5). *Gromia* sp.1 (Figure 3.12 E and F) represented 7% of the total assemblage, followed by *Gromia* sp.2 (3.8%) (Figure 3.13 I to K), *Gromia* sp.4 (0.5%) and the least abundant morphotypes, *Gromia* sp.3 (Figure 3.14 F) and *Gromia* sp.8 (Figure 3.19 A) which each accounted only for 0.2% of the total assemblage (2 and 1 specimens respectively).

2000 m. Six gromiid morphotypes were sampled at 2000 m water depth (stations 55730#2, 1980 m; 55775#1, 1990 m; 55725#2, 2010 m; 55789#3, 2030 m and 55726#1, 2075 m). *Gromia* sp.1 (Figure 3.12 G to K) accounted for 38.1% of the total gromiid assemblage (42 specimens), followed by *Gromia* sp.6 (28.6%) (Figure 3.17 Ae to Ai), *Gromia* sp.3 (Figure 3.14 G to N) and *Gromia* sp.7 (Figure 3.18 Ap to Ar) (each 14.3%). *Gromia sphaerica* was present at the deepest site, accounting for 2.4% of the total assemblage. *Gromia* sp.8 (Figure 3.19 B) was also present at this site and also accounted for 2.4% of the total assemblage.

Figure 3.23 Gromiids visible on the surface of an undisturbed megacore collected at Station 55767#1 from the Oman margin during CD 143.

Table 3.5 Percentage abundance of gromiid morphotypes on the Oman margin. * numbers expressed as % per deployment

Depth (m)	1093	1100	1103	1200	1341	1390	1414	1422	**1400**	1684	1692	**1700**	1980	1990	2010	2030	2075	**2000**
Station number	55753#1	55759#1	55766#1	55744#1	55717#1	55767#1	55731#1	55710#1	**Total**	55774#2	55752#1	**Total**	55730#2	55775#1	55725#2	55789#3	55726#1	**Total**
Number of cores	8.0	Trawl	7.0	Trawl	4.0	8.0	7.0	7.0	**26.0**	8.0	9.0	**17.0**	7.0	8.0	4.0	12.0	7.0	**38.0**
Morphotypes: *																		
Sausage-like sp.1	0.0		100.0		70.7	24.5	10.7	8.9	**24.5**	0.0	0.0	**0.0**	0.0	0.0	0.0	57.1	18.2	**14.3**
Sausage-like sp.2	0.0		0.0		2.7	0.0	4.0	3.2	**1.9**	0.0	0.3	**0.2**	26.1	0.0	0.0	0.0	0.0	**14.3**
Grape-like sp.1	0.0		0.0		1.3	3.2	6.7	28.0	**10.8**	4.9	8.0	**7.0**	39.1	0.0	0.0	14.3	54.5	**38.1**
Grape-like sp.2	0.0		0.0		4.0	15.5	42.7	15.3	**17.6**	2.1	4.7	**3.8**	0.0	0.0	0.0	0.0	0.0	**0.0**
Grape-like sp.3	0.0		0.0		6.7	55.9	32.0	44.6	**42.1**	92.3	86.3	**88.2**	34.8	0.0	0.0	14.3	27.3	**28.6**
Spherical-like sp.1	100.0		0.0		14.7	0.9	4.0	0.0	**3.0**	0.0	0.7	**0.5**	0.0	0.0	0.0	0.0	0.0	**0.0**
Gromia sphaerica	0.0		0.0		0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	**0.0**	0.0	0.0	0.0	14.3	0.0	**2.4**
Irregular sp.1	0.0		0.0		0.0	0.0	0.0	0.0	**0.0**	0.7	0.0	**0.2**	0.0	100.0	0.0	0.0	0.0	**2.4**
Total per deployment	2.0	0.0	4.0	0.0	75.0	220.0	75.0	157.0	**527.0**	143.0	299.0	**442.0**	23.0	1.0	0.0	7.0	11.0	**42.0**
Mean per core (78.5 cm2)	0.3		0.6		18.8	27.5	10.7	22.4	**79.4**	17.9	33.2	**51.1**	3.3	0.1	0.0	0.6	1.6	**5.6**
Mean per 10 cm2	0.0	ND	0.1	ND	2.4	3.5	1.4	2.9	**10.1**	2.3	4.2	**6.5**	0.4	0.0	0.0	0.1	0.2	**0.7**

3.3.3. Diversity and distribution of gromiid morphotypes on the Pakistan margin (CD 145)

1200 m. A single morphotype was collected at this site, *Gromia* sp.4, which is spherical in shape and has a single oral capsule (Figure 3.15 8 O). Although the Agassiz trawl at station 55811#1 (1174 m) collected numerous specimens, only one specimen (Figure 3.24) was obtained at each of stations 55802#7 (1200 m megacorer) and 55802#4 (1201 m multicorer).

1620 – 1874 m. Figure 3.25 shows the material retained in a 2 mm sieve from a trawl sample collected at Station 55837#1 (1791 m). Two very distinct morphotypes can be distinguished, grape-shaped specimens about 5 mm diameter and sausage-shaped ones 20 to 30 mm in length. Once more, although numerous specimens were sampled with the Agassiz trawl, only 1-3 specimens were collected per deployment when sampling with either the multicorer or the megacorer (Table 3.4).

Figure 3.24 Single *Gromia* sp.4 collected by the megacorer at Station 55826#2 (1826 m), CD 145 form the Pakistan margin.

Figure 3.25 Gromiids collected by the Agassiz trawl at Station 55837#1 (1800 m) CD 145 on the Pakistan margin.

3.3.4. Ecological observations

SHRIMP video images from CD 143 unfortunately, were not clear enough to see gromiids clearly and as such some rough observations are presented. At 1100 m, images showed a *Globigerina* sand empty of gromiids, suggesting a sparse distribution on the seabed. At the 1400-m and 1700-m stations, gromiid densities were high (Table 3.4) with regular aggregates of gromiids spread across the seabed. At 2000 m the number of gromiids reduced again (Table 3.4) and they were scarcely seen. Pakistan WASP video images unfortunately were too far from the seabed to spot even the large gromiids, such as *G. sphaerica* and therefore, there are no in situ images, aside from the undisturbed megacores and multicores.

Specimens were found mainly living on or just below the sediment surface with their apertures directed into the organic rich surface layer, which seems to suggest that they are probably feeding on it (Figure 3.23). The tests were frequently surrounded by a halo of lighter-coloured sediment.

Specimens were found living above the OMZ where oxygen levels start to return to normal in both Oman and Pakistan margins of the Arabian Sea. However, they do not occur at depths

greater than 2100 m water depth (Figure 3.26), where oxygen levels start to reach levels greater than 2 ml/l.

3.3.4.1 *Gromiids as substrate for other protozoans*

Most gromiid specimens found on the Oman margin had organisms attached to their walls, mainly little dome-shaped protists (presumed to be foraminifera). However, gromiid specimens collected from the Pakistan margin did not have any organisms attached to their tests.

Gromia sp.1 had no organisms attached to its surface (Figure 3.12). Dome-shaped organisms, believed to be foraminifera (Gooday pers. comm.), encrusted on some specimens of *Gromia* sp.2 (Figure 3.27 A1 to A10), *Gromia* sp.6 (Figure 3.27 B1 to B3 and B5 to B10), *Gromia* sp.7 (Figure 3.27 C1 and C2), *Gromia* sp.3 (Figure 5.4.5 D1 and D2) and *Gromia* sp.4 (Figure 3.27 E1 and E2). In two separate occasions, very small oligochaete cases attached to gromiid tests (Figure 3.27 B4 and E3), once attached to *Gromia* sp.6 at Station 55767#1 (1390 m) and once attached to *Gromia* sp.4 at Station 55731#1 (1414 m).

Figure 3.26 Gromiid morphotypes found below the OMZ in the Oman and Pakistan margins.

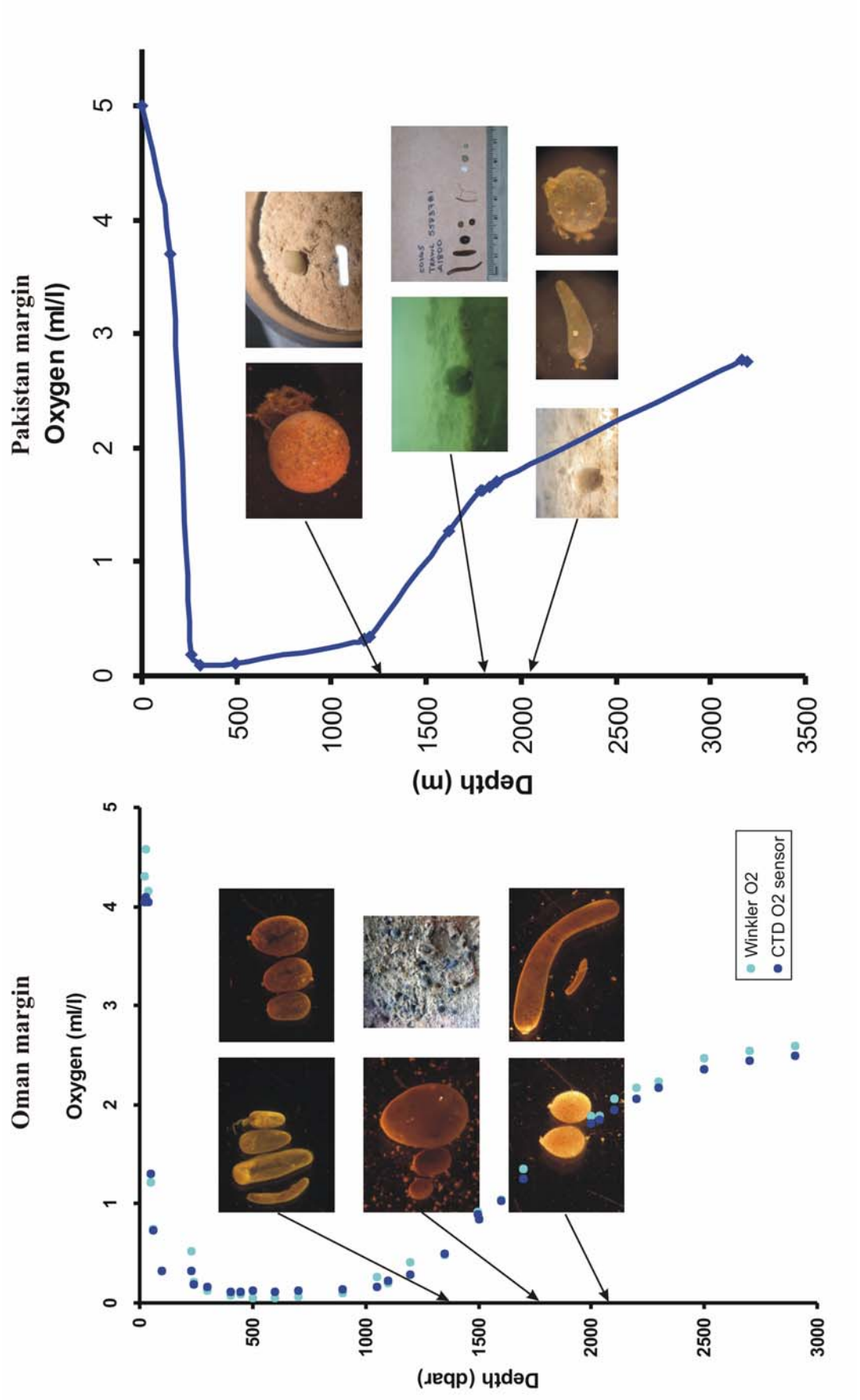
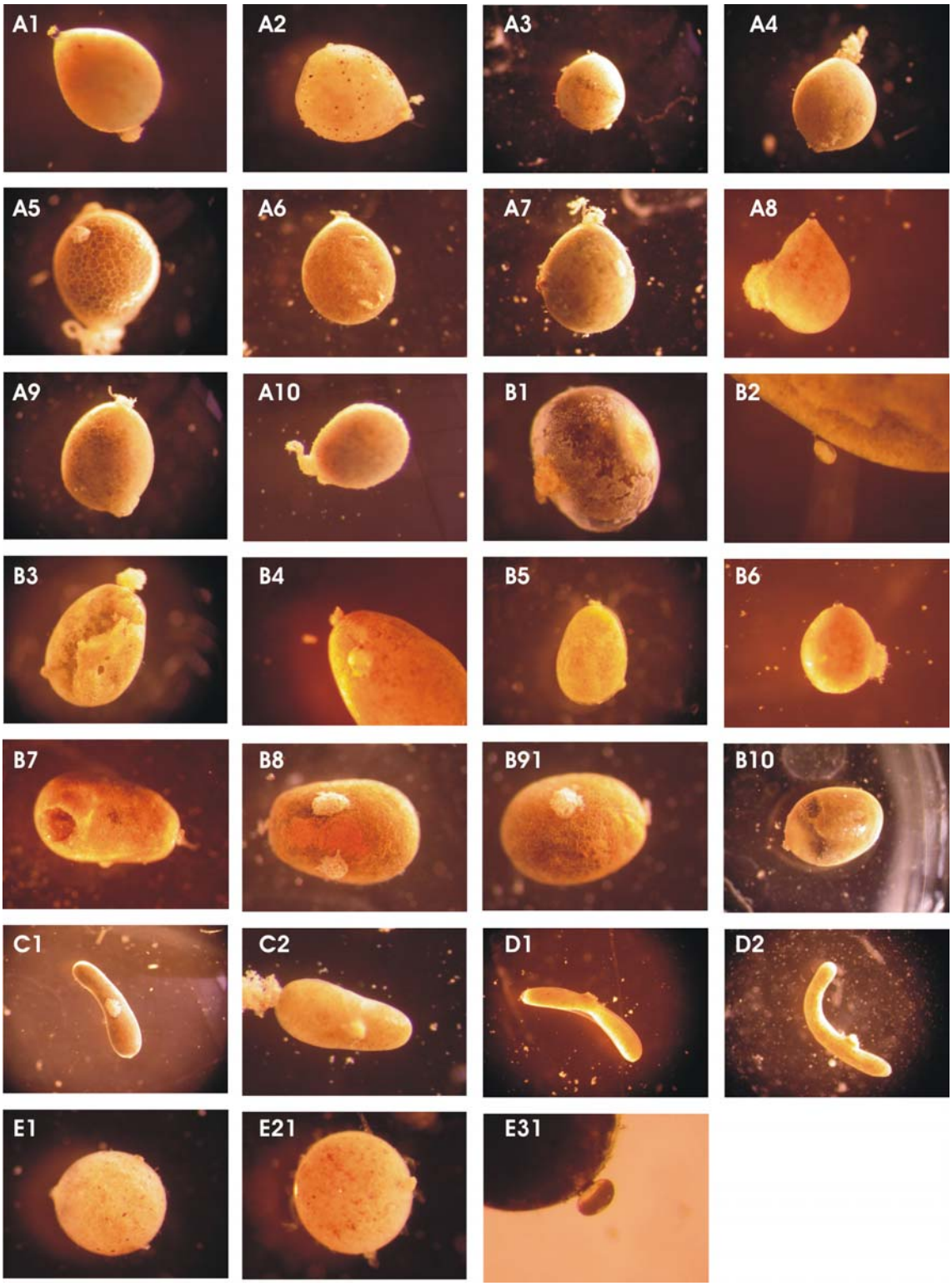


Figure 3.27 Gromiids found with other organisms attached to the test from the Oman (CD 143) and Pakistan (CD 145) margins of the Arabian Sea. Light photographs illustrating organisms attached to the wall of *Gromia* sp.2 **A1** - **A10**, *Gromia* sp.6 **B1** - **B5**, *Gromia* sp.7 **C1** and **C2**, *Gromia* sp.3 **D1** and **D2** and *Gromia* sp.4 **E1** and **E2**.



3.5 Discussion

Although *Gromia oviformis* is widely reported from shallow waters (Jepps 1926; Hedley 1958; Hedley and Bertaud 1962; Arnold 1972; Bowser et al. 1996; Burki et al. 2002), gromiids were previously unknown from the deep sea, with the exception of *Gromia sphaerica*, a species described by Gooday et al. (2000) from the Oman margin and more recently *Gromia pyriformis* that has been described from the bathyal Pakistan margin of the Arabian Sea (Gooday and Bowser 2005). The current study has therefore enhanced considerably our knowledge of gromiids in general and deep-sea gromiids in particular, adding 8 new morphospecies to the 3 currently described deep sea gromiids.

3.5.1 Morphology-based diversity

Morphologically, there are seven new and distinct deep-sea gromiid species, *Gromia* sp.1, sp.2, sp.3, sp.4, sp.6, sp.7 and sp.8 (Figures 3.12-3.15, 3.17-3.19). *Gromia sphaerica* (Figure 3.11), known previously from Oman (Gooday et al. 2000), is here reported for the first time from the Pakistan margin of the Arabian Sea. Molecular work presented in the following chapter has revealed one additional species *Gromia* sp.5, characterized purely by molecular analysis. The general criteria used in distinguishing *Gromia* species were shape of the organic-walled test (ovoid to spherical or elongate) and the size of the oral capsule that in the case of *Gromia* sp.4 and sp.8 is very small. The wall structure was also a distinguishing feature, as in the case of *Gromia* sp.2.

Gromia sp.1 and sp.6 (Figures 3.12 and 3.17) are morphologically very similar to *G. oviformis* (Arnold 1972). At first sight, there is no difference between *Gromia* sp.1 and sp.6. However, closer microscopic examination revealed that sp. 1 has a thinner translucent test. *Gromia* sp.6, on the other hand, has a thicker, more opaque test with test contents filling the whole test. The wall ultrastructure of *Gromia* sp.1 and sp.6 further separates the two species. Both species have an inner layer of honeycomb membranes, but *Gromia* sp.1 has a thinner outer layer than *Gromia* sp.3 and also has numerous pores. *Gromia* sp.6 is also the only species known to have filamentous bacteria attached to the surface of the wall. However, these epibionts were observed in only one specimen, and so we cannot draw definite conclusions. *Gromia* sp.2 is distinguished from *Gromia* sp.1 and 6 by the more pointed apertural end and the very distinctive honeycomb structure of the test wall. The rigidity of the honeycomb-like structure may confer some robustness to the test, perhaps as a defence against predators or possible adverse environmental conditions. This feature has not been reported in any other gromiid, either from shallow or deep

water. *Gromia* sp.7 resembles an elongated form of *Gromia* sp.1. *Gromia* sp.3 is an elongated form of *Gromia* sp.6, similar to *Gromia* sp.7 but with an even more elongated test, a thicker and more opaque wall, and sometimes with dome-shaped foraminifera attached to wall the surface. These two sausage-shaped morphotypes are very similar to specimens collected under the Ross Ice Shelf (Pawlowski and Bowser per. com.). These are the first reported elongated gromiids. *Gromia* sp.3 is well defined using morphological characters and also forms a distinctive clade C, based on molecular criteria (Figure 4.3). Ultrastructure images of this species were not obtained because of the difficulty of sectioning such a large organism. *Gromia* sp.7, on the other hand, was not sequenced but there is a good morphological basis for considering it as a separate species. Although *G. sphaerica* and *Gromia* sp.4 have the same perfect spherical shape, *G. sphaerica* has multiple apertures and the average test diameter is 15 mm, while *Gromia* sp.4 has a single aperture and a much smaller diameter (average 2.6 mm). *Gromia* sp.8 is a very distinctive lobate morphotype, and not previously reported from the deep sea. Only 2 specimens were found at two stations (55774#2, 1684 m and 55775#4, 1990 m) on the Oman margin. Its occurrence at these stations expands the range of gromiid morphotypes found on the Oman margin. Rather similar lobed forms of *G. oviformis* were reported by Jepps (1926), who found these forms to be very common in thick tangles of the algae *Corallina* sp.

The Oman margin gromiids were more rounded or grape-shaped while on the Pakistan margin, more elongated sausage shaped forms were more common. In the Pakistan megacore samples, only one type of gromiid (*Gromia* sp.4) was observed, the other morphotypes were found in the trawls. *Gromia sphaerica* from the Oman margin was also found mainly in trawl samples and typically only one specimen was found per deployment on the surface of megacores. The Agassiz trawl samples a wider area, which explains the large number of gromiids in the trawl catches. My results suggest that *G. sphaerica* and the Pakistan gromiids occur sparsely on the sediment (or are found in aggregations and perhaps because of its large size and randomness of sampling it is poorly sampled with the megacorer).

In general, foraminifera are much more abundant and diverse than gromiids (Gooday 1999). Chapter 2 looks at foraminiferal abundances and diversity form the same area and abundances are one order of magnitude higher than gromiid abundances. Although gromiids are single-celled organisms, they are relatively large, falling into the macro- and megafaunal fractions and as a consequence this may limit their abundance. Xenophyophores are an example of another large protist typically found in low numbers (Gooday 1996). Moreover, xenophyophores have less elaborate tests than foraminifera, and gromiids are much less elaborate.

3.5.2 Relation to environmental parameters

Figure 3.26 shows an overview of the different morphotypes found across the OMZ on both the Oman and Pakistan margins. Gromiids first appear below the OMZ, where oxygen concentrations start to rise (0.5 ml/l). They are absent in the core regions of the OMZ on both sides of the Arabian Sea. Interestingly, gromiids were not found at two stations located at 110 m (Oman margin) and 140 m (Pakistan Margin) water depth, above the OMZ. These depths lie within the known bathymetric range of *G. oviformis* which has a maximum reported depth of occurrence of 270 m (Arnold 1972). However, only two stations were sampled above the OMZ and therefore their absence from this region cannot be concluded. The bottom temperatures were higher at these stations (22°C at 110 m and 20°C at 140 m) and this may be a limiting factor in the distribution of gromiids. However, Arnold (1972) reported that *G. oviformis* tolerates temperature from 0°C to 30°C. It is interesting to note that gromiids were found where the sediment is muddy and soupy, often with greenish coloration, and smelling of hydrogen sulphide. This observation suggests that they feed on the organic-enriched sediment.

3.5.3 Ecological significance

Evidence from SHRIMP images and core samples, indicates that gromiids live with the apertural end embedded in the organic rich surficial sediment. Their tests are also full of stercomata which are composed of fine sediment particles and are spread throughout the cell organelles. These observations, as stated above, indicate that they are ingesting sediment and associated organic detritus and are possibly important in the degradation of fresh organic matter reaching the seafloor. If this assumption is correct then, because they are the most abundant macrofaunal organism at many stations, they have a considerable influence on organic carbon cycling at the sediment-water interface. In addition, they may have a direct impact on the smaller size classes organisms that live in the sediments such as smaller foraminifera, through predation, or mechanical disturbance. Moreover, gromiids deploy pseudopodia to feed and this may play an important role in stabilizing and structuring the sediment environment, creating greater sediment heterogeneity (Nyholm and Gertz 1973).

Microscopic observations also revealed that dome-shaped agglutinated foraminifera encrust the test wall of gromiids. This seems to suggest that gromiids may act as substrates for other organisms, mainly foraminifera, creating a firm micro-habitat within the soft OMZ sediments for encrusting organisms. These observations suggest that, rather than having a uniform deep-

sea OMZ soft-sediment, there is at least one micro-system of harder substrate provided by gromiids that enable encrusting organisms to also live there.

3.6 Conclusions

The current study has enhanced considerably the knowledge of gromiids in general and deep-sea gromiids in particular. Eight new deep-sea gromiid species have been added to the 3 previously know species: *Gromia* sp.1, *Gromia* sp.2, *Gromia* sp.3, *Gromia* sp.4, *Gromia* sp.5, *Gromia* sp.6, *Gromia* sp.7 and *Gromia* sp.8. Morphological characterization of gromiid species is adequate with the exception of grape-shaped species which lack sufficient characters to separate different species. In the Arabian Sea, gromiids are more abundant on the Oman rather than the Pakistan margin, and while grape-shaped specimens dominate the Oman margin, sausage-shaped gromiids are more abundant on the Pakistan margin. On both margins, gromiids occur below the OMZ, when oxygen concentrations are higher than 0.5 ml/l. However, they were not found above the OMZ at similar oxygen levels. Gromiids live on the sediment surface with apertures facing down, possibly feeding on the organic-enriched sediments. As a consequence they may play an important role in carbon cycling. In addition, they act as microhabitats for microbial organisms, and possibly are important in contributing to sediment heterogeneity, through the use of pseudopodia for feeding.

Chapter 4

High diversity of deep-sea *Gromia* from the Arabian Sea revealed by small subunit rDNA sequence analysis.

4.1 Introduction

The taxonomic position of *Gromia* has been debated for many years. Early authors confused *G. oviformis* with *Allogromia ovoidea* (Hedley 1958). Later, Rhumbler (1904) showed that gromiids were distinct from allogromiids in having filose rather than reticulose pseudopodia. He therefore assigned them to the Filosea, a group of testate amoebae with filose pseudopodia, an assignment followed later by Bovee (1985). Patterson et al. (2000) regarded *Gromia* as an "amoeba of uncertain affinities". The first molecular data available for *Gromia* were based on a partial sequence of the gene coding for the Large SubUnit ribosomal DNA (LSU rDNA); this showed that *Gromia* branches within the eukaryotic crown (Pawlowski et al. 1994). More recently, Burki et al. (2002), showed that *Gromia* is closely related to the Cercozoa, based on Small SubUnit ribosomal DNA (SSU rDNA) gene sequences. In addition to the shallow-water gromiid, *G. oviformis*, the Cercozoa include the "athalamid", reticulose *Gymnophrys cometa* (Nikolaev et al. 2003) and the haplosporidian and paramyxid parasites of bivalves (Cavalier-Smith and Chao 2003). Various other amoeboid and/or flagellated organisms also belong to the Cercozoa (Atkins et al. 2000; Bhattacharya and Oliveira 2000; Kuhn et al. 2000; Bulman et al. 2001; Vickerman et al. 2002; Wylezich et al. 2002; Cavalier-Smith and Chao 2003). A position close to the Cercozoa was confirmed by other analyses of SSU rDNA (Berney and Pawlowski 2003; Cavalier-Smith and Chao 2003). More recent multigene phylogenetic analyses indicate that *Gromia* branches as a sister group to the Foraminifera or Haplosporidia (Longet et al. 2003; Longet et al. 2004). The latest classifications based on molecular phylogenetic data placed *Gromia* in the supergroup Rhizaria (Cavalier-Smith 2002; Cavalier-Smith and Chao 2003; Nikolaev et al. 2004; Simpson and Roger 2004). The group includes the morphologically heterogeneous Cercozoa, and two important lineages of amoeboid protists, the Foraminifera as demonstrated by actin (Keeling 2001; Archibald et al. 2003; Archibald and Keeling 2004), polyubiquitin (Archibald et al. 2003), RNA polymerase II (Longet et al. 2003), and revised SSU rRNA (Berney and Pawlowski 2003) analyses and the radiolarians shown to be related to the Cercozoa-Foraminifera clade (Burki et al. 2002; Cavalier-Smith 2002; Cavalier-Smith and Chao 2003; Polet et al. 2004).

The studies reviewed above were based on shallow-water *Gromia*. Here, we report the first molecular data on species of *Gromia* from the bathyal deep sea. Our new molecular results are consistent with earlier morphological and ultrastructural evidence (Gooday et al. 2000) and clearly establish that gromiids inhabit deep-water environments. All the Arabian Sea specimens have an aperture enveloped by an oral capsule (Arnold 1952) and at least some have pores on the organic wall surface. Another basic characteristic of gromiids, the layer of honeycomb membranes in the wall, is present in all specimens that we examined using HVEM (Chapter 3).

4.2 Materials and Methods

4.2.1 Study area

Study area is the same as in chapter 3. The study area on the Oman margin was sampled on CD 143 (Figure 3.1) during December 2002. Samples from the Pakistan margin were collected during a series of cruises during 2003: CD 145, 146, 150 and 151 (Figures 3.1 and 3.5).

4.2.2 Sampling

Gromiid specimens were collected as in chapter 3 using either a megacorer equipped with 100 mm id plastic core tubes, or a multicorer equipped with 57 mm id core tubes. Both devices obtain samples in which the sediment-water interface is virtually undisturbed, maintaining gromiids and other organisms in their life positions. At some depths, numerous gromiids were also collected using an Agassiz Trawl. Station details are summarised in Table 4.1.

As soon as possible after recovery, samples were taken to a shipboard temperature-controlled laboratory adjusted to the appropriate bottom water temperature. All gromiids found on the core surfaces were removed using a plastic pipette or forceps and frozen at either -20°C or -80°C for molecular analysis. Cores were then sliced into 1 cm thick layers down to 3 cm sediment depth. The sediments slices were examined for additional gromiids under a binocular microscope with ice packs used to keep the samples cool. All gromiids found were frozen as above.

Table 4.1 Details of stations on the Oman and Pakistan margins of the Arabian Sea where gromiids were collected from molecular genetic analysis.

Station and series	Latitude	Longitude	Water depth (m)	Specimens
Oman:				
55710#1	23°21.83'N	59°06.03'E	1422	1, 2, 3, 4, 15 and 17
55725#2	23°20.31'N	59°09.85'E	2010	11
55759#1	23°23.37'N	59°03.67'E	1260	8
55767#1	23°22.10'N	59°05.60'E	1390	16
Pakistan:				
55910#3	22°52.24'N	66°00.09'E	1875	5, 6, 12 and 13
56137#12	22°52.39'N	66°00.00'E	1852	7, 9 and 14
56140#2	22°52.42'N	66°59.97'E	1859	10

4.2.3 DNA extraction, amplification, re-amplification, cloning and sequencing

Specimens removed from the -80°C freezer were allowed to defrost slightly before being documented photographically (Figure 4.1). Specimens were then cut into 4-8 pieces depending on size (for example, a specimen 4.5 mm in diameter was cut into 4 pieces) and each small piece was pippetted into a tube containing 400 µm of preheated (65°C) lysis buffer. Fragmentation of *Gromia* cells was necessary to avoid the inhibition of PCR amplifications, which occurred regularly when complete cells were extracted. As the amplifications were successful for only few extracts from each cell, we have deduced that the majority of examined *Gromia* contained only one nucleus.

4.2.3.1 *DNA extraction*

DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Basel, Switzerland). The specimens in the preheated lysis buffer were first mechanically disrupted and then the enzyme RNase was added to digest the RNA (Ribonucleic acid) in the sample that was allowed to lyse at 65°C. After lysis, proteins and polysaccharides and detergents were salt precipitated by incubation on ice with added buffer AP2. Cell debris and precipitates were removed with a brief spin through a QIAshredder column. The cleared lysate was then transferred to a new tube where binding buffer and ethanol were added to the DNeasy membrane column. This column allowed the DNA to be bound to a membrane while contaminants such as proteins and polysaccharides are washed through with buffer AP3. The pure DNA on the membrane was then eluted using a preheated (65°C) low-salt Elution buffer.

4.2.3.2 *PCR (Polymerase Chain Reaction) Amplification and re-amplification*

PCR reactions were prepared by using a mix of water, PCR buffer (Roche), DNTP and a pair of Primers. Two µl of DNA extract were added to each reaction making a total volume of 50µl. The PCR amplification profile consisted of 40 cycles, with 30 s at 94°C, 30 s at 50°C and 2 min at 72°C, followed by 5 min at 72°C. For the re-amplification, a PCR reaction was prepared again, adding 1µl of the product of the first PCR (amplification), making a total of 50 µl. The PCR re-amplification profile consisted of 25 cycles, with 30 s at 94°C, 30 s at 52°C and 2 min at 72°C, followed by 5 min at 72°C for the final extension. A gel electrophoresis was then conducted on the products, and wherever a positive signal was obtained, products were purified using High Pure PCR purification kit (Roche, Rotkreuz, Switzerland).

4.2.3.3 *Sequencing*

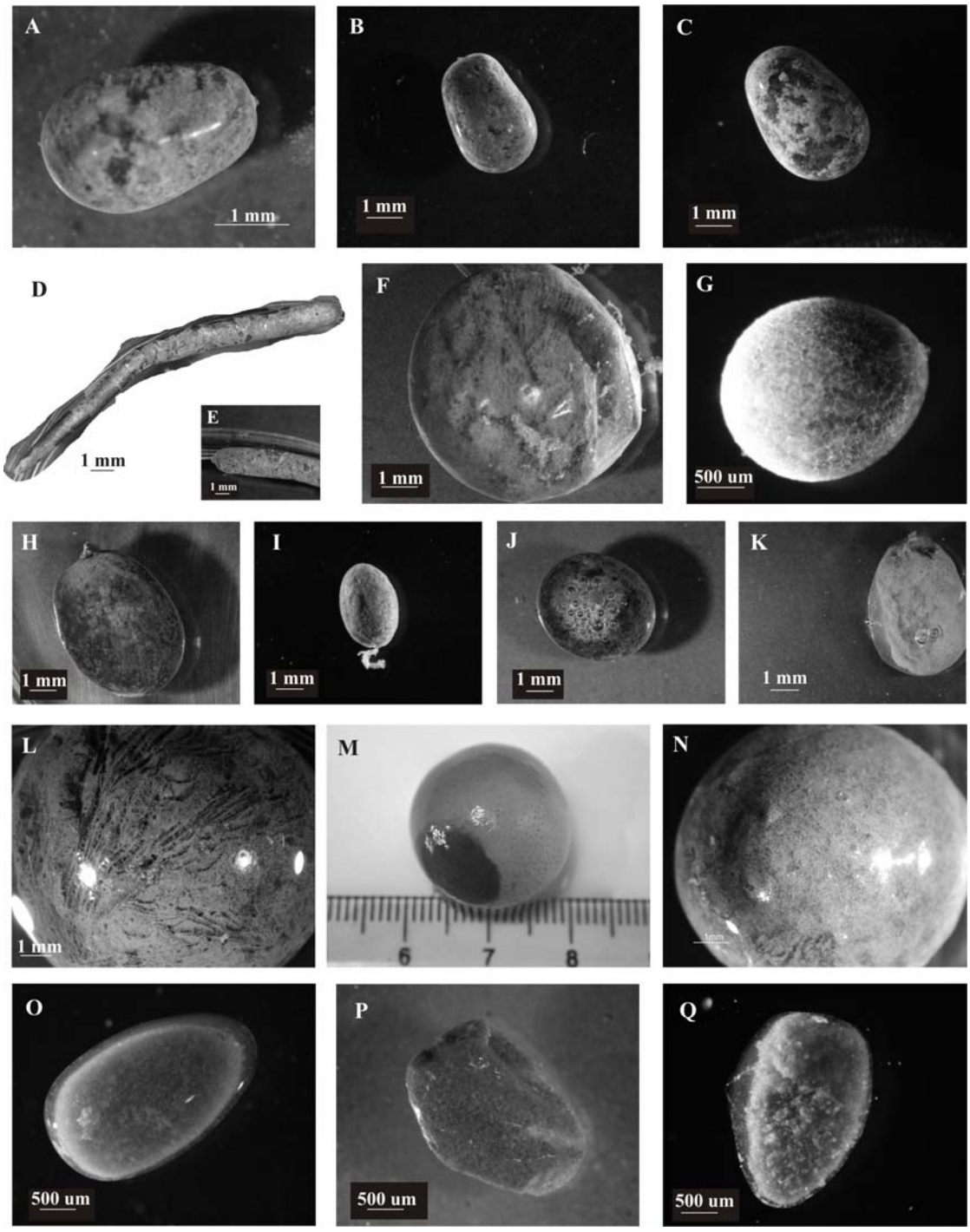
Whenever possible, products were sequenced directly using the ABI-PRISM Big Dye Terminator Cycle sequencing Kit and analysed with an ABI-3100 DNA sequencer (Applied Biosystems, Rotkreuz, Switzerland), all according to the manufacturer's instructions.

4.2.3.4 *Cloning*

When direct sequencing failed, purified products were ligated into pGEM Vector system (Promega, Wallisellen, Switzerland), cloned in XL-2 Ultracompetent Cells (Stratagene, Basel, Switzerland) and sequenced as above.

First, a fragment of the SSU rDNA gene was amplified for all possible specimens using the universal primer pair S12.2 and SB (Table 4.2). Then the PCR products were re-amplified first using the universal primers pair S14 and SB (Table 4.2). Secondly, the re-amplification was done using the Cercozoa specific primer S16Ce and the universal primer SB. Lastly, the re-amplification was conducted using the *Gromia* specific primer S13r_Gro and SB. Initially, universal primers were used to test that the bands obtained with the *Gromia* specific primers were accurate. Morover, initially a positive control was used, *G. oviformis* DNA from Burki et al. (2002) and a negative control (water) to test the quality of the DNA.

Figure 4.1 Light photographs of extracted specimens for phylogenetic analysis. Specimens [DNA number]: **A** 17 [4319, 4320], **B** 16 [4433], **C** 15 [4390], **D** 5 [4331], **E** 6 [4440], **F** 10 [4421], **G** 4 [4399], **H** 12 [4338], **I** 11 [4363, 4364 and 4366], **J** 13 [4333], **K** 14 [4298], **L** 9 [4353, 4357, 4358], **M** 8 [4375], **N** 7 [4466], **O** 2 [4396], **P** 3 [4411] and **Q** 1 [4385, 4386].



The amplification of ITS fragment was attempted for selected isolates. The first amplification with S12.2 and L5 and to re-amplify with S13r_Gro and L5 (Table 4.2) was unsuccessful. However, amplification was successful with S12.2 and GRLSU1, a *Gromia* specific primer designed by Burki et al. (2002), and consequent re-amplification with S13r_Gro and GRLSU1 (Table 4.2). Because of the length of the fragment and the difficulty in sequencing, two forward primers close r to the 3' end of the SSU: S19Gr and S20Gr (Table 4.2) were designed. The following combinations of primers were then attempted: 1) PCR I: S20Gr + GRLSU1; 2) PCR I: S19Gr + GRLSU1, PCR II: S20Gr + GRLSU1 and 3) PCR I: S13r_Gro + GRLSU1, PCR II: S20Gr + GRLSU1. The first combination of primers failed, but the last two worked and last one was chosen (PCR I: S13r_Gro + GRLSU1, PCR II: S20Gr + GRLSU1) as the best. All results presented on the ITS region are based on it.

Using specific primers was necessary because *Gromia* isolates contained DNA of some other eukaryotes, related to *Crythecomonas longipes*, *Labyrinthuloides haliotidis*, *Gymnophrys cometa*, *Trinema enchelys*, *Massisteria marina* and uncultured eukaryote isolates C1_E023, C2_E025, C5_E006, E170 and clones Bola471 and Sey017, as indicated by BLAST comparison of sequenced PCR products obtained with universal primers.

Table 4.2 Position and specificity of the various primers.

Name	Orientation	Specificity	Position	Composition
6Gr	D	*Gromia*	600	GGGCAAGTCTGGTGC
12.2	D	Broad	1500	GATYAGATACCGTCGTAGTC
13r_Gr	D	*Gromia*	1600	CTGTGGATAGGACTCG(CT)TCAG
20Gr_F	D	*Gromia*	1800	CTACCGATGGAACGATCC
GRSSU1	R	*Gromia*	1900	TCCAAAGTTTTCACCGGATC
B	R	Broad	2000	TGATCCTTCTGCAGGTTCACCTAC
GRLSU1	R	*Gromia*	3100	TGACATCACATTCCAATGAA

5.2.4 Phylogenetic analysis

Evolutionary trees were inferred using the neighbor-joining (NJ) (Saitou and Nei 1987) and maximum likelihood (ML) (Felsenstein 1981) methods. *Gromia* SSU rDNA sequences and their eukaryotic homologs were aligned using Clustal X (Thompson et al. 1994), and further adjusted by eye with Seaview (Galtier et al. 1996). To infer the phylogenetic position of *Gromia* among eukaryotes, we used an alignment of 32 SSU rDNA sequences (comprising 8 *Gromia* sequences) and 799 unambiguously aligned sites. The alignment of *Gromia* sequences consisted of 27 sequences and 445 sites. We used PHYLO_WIN program to obtain the NJ trees, with distances corrected using K2, HKY and LogDet models (Galtier et al. 1996). The maximum

likelihood approach was achieved with PhyML v2.1b1, using GTR model (Guindon and Gascuel 2003). The proportion of invariable sites and the shape of the gamma distribution were adjusted to maximize the likelihood of the phylogeny. The reliability of internal branches was assessed using the bootstrap method (Felsenstein 1985) with 1000 bootstrap replicates for NJ tree and 100 bootstrap replicates for ML trees.

4.3 Results and Discussion

A total of 153 isolates were extracted from 34 gromiid specimens collected from the Oman and Pakistan margins of the Arabian Sea, making an average of 4.5 extractions per specimen. A total of 6 out of 153 isolates were amplified using the primer pair S12.2 + SB, of which only two sequences of *Labyrinthuloides haliotides* were obtained. Re-amplification using the *Gromia* specific primer S13r_Gr and SB was more successful with 52 isolates re-amplified, of which 40 *Gromia* sequences were obtained, and 15% unsuccessful sequences with high ambiguity from direct sequencing. Using specific primers was necessary because *Gromia* isolates contained DNA of some other eukaryotes. Nonetheless, even with *Gromia* specific primers, other organisms were sequenced. Out of the 52 isolates, the following non *Gromia* organisms were sequenced: *Crythecomonas longipes*, *Labyrinthuloides haliotidis*, *Gymnophrys cometa*, *Trinema enchelys*, *Massisteria marina* and uncultured eukaryote isolates C1_E023, C2_E025, C5_E006, E170 and clones Bola471 and Sey017. From the 52 isolates re-amplified with primer pair S13r-Gr and SB, 15 were re-amplified using S6Gr + GRSSU1, for the almost complete SSU rRNA. Out of these, 27% *Gromia* sequences were obtained, 46% sequences of Uncultered eukaryote isolates C1_E023, C5_E006, C2_E025 and E170, clones Bola471 and Sey017 and an uncultures marine alveolate Group II DH148-EKD; and 27% failed by being too ambiguous. For the ITS rDNA gene, out of the 52 isolates, 13 were re-amplified using the primer pair S20Gr + GRLSU1. Seven *Gromia* sequences were obtained and 6 failed by showing high ambiguity.

4.3.1 Monophyly of Gromiida

Sequences of about 2/3 of the whole length of the SSU rDNA for three different isolates were obtained, representing *G. sphaerica* [4466] from Pakistan, *Gromia* sp. 6 [4319] from Oman and *Gromia* sp. 3 [4440] from Pakistan. The length of the sequences ranged from 1215 to 1286 and the base composition was 46.73 – 47.42 % GC. These sequences were compared to five previously published *Gromia* sequences (Burki et al. 2002), 11 sequences of Cercozoa, 3 plasmodiophorids, 4 haplosporidians and 7 Foraminifera (Table 4.3).

The maximum likelihood (ML) and neighbour-joining (NJ) analyses give congruent results showing that all *Gromia* sequences form a monophyletic group, branching between Plasmodiophora and Haplosporidia (Figure 4.2). The monophyly of Gromiida is supported by 100% bootstrap values in both analyses. The genetic divergence between *Gromia* sequences is remarkably low and ranges from 0.6 to 6.2%, with mean value of 3.06%. This low level of genetic variations corresponds in some sense to the morphological homogeneity of the genus, which is composed mainly of similar large grape or sausage-shaped morphotypes. However, it is surprising to find such low sequence divergence given the rather broad ecological and geographical settings from which the examined *Gromia* were obtained. This result could suggest that the Gromiida is a relatively recently evolving group, which was very successful in colonizing practically all marine habitats. Alternatively, it is possible that *Gromia* is characterized by unusually slow rates of SSU rDNA evolution. This idea can be examined by further testing of their protein coding genes.

The phylogenetic position of Gromiida, branching between Haplosporidia and Plasmodiophora, differs slightly from the initial study of *Gromia* (Burki et al. 2002) in which Haplosporidia where not included. It differs also from some analyses of Cercozoa phylogeny (Cavalier-Smith and Chao 2003), in which *Gromia* branches within the clade formed by Plasmodiophora and Haplosporidia. However, given that our analyses are based on partial SSU rDNA sequences, with relatively limited taxon sampling, the phylogenetic position of Gromiida cannot be firmly established and we cannot exclude the possibility that *Gromia* is a sister group to Foraminifera or Haplosporidia as indicated by some other studies (Berney and Pawlowski 2003; Longet et al. 2003; Longet et al. 2004).

4.3.2 Molecular and morphological diversity of Arabian Sea *Gromia*

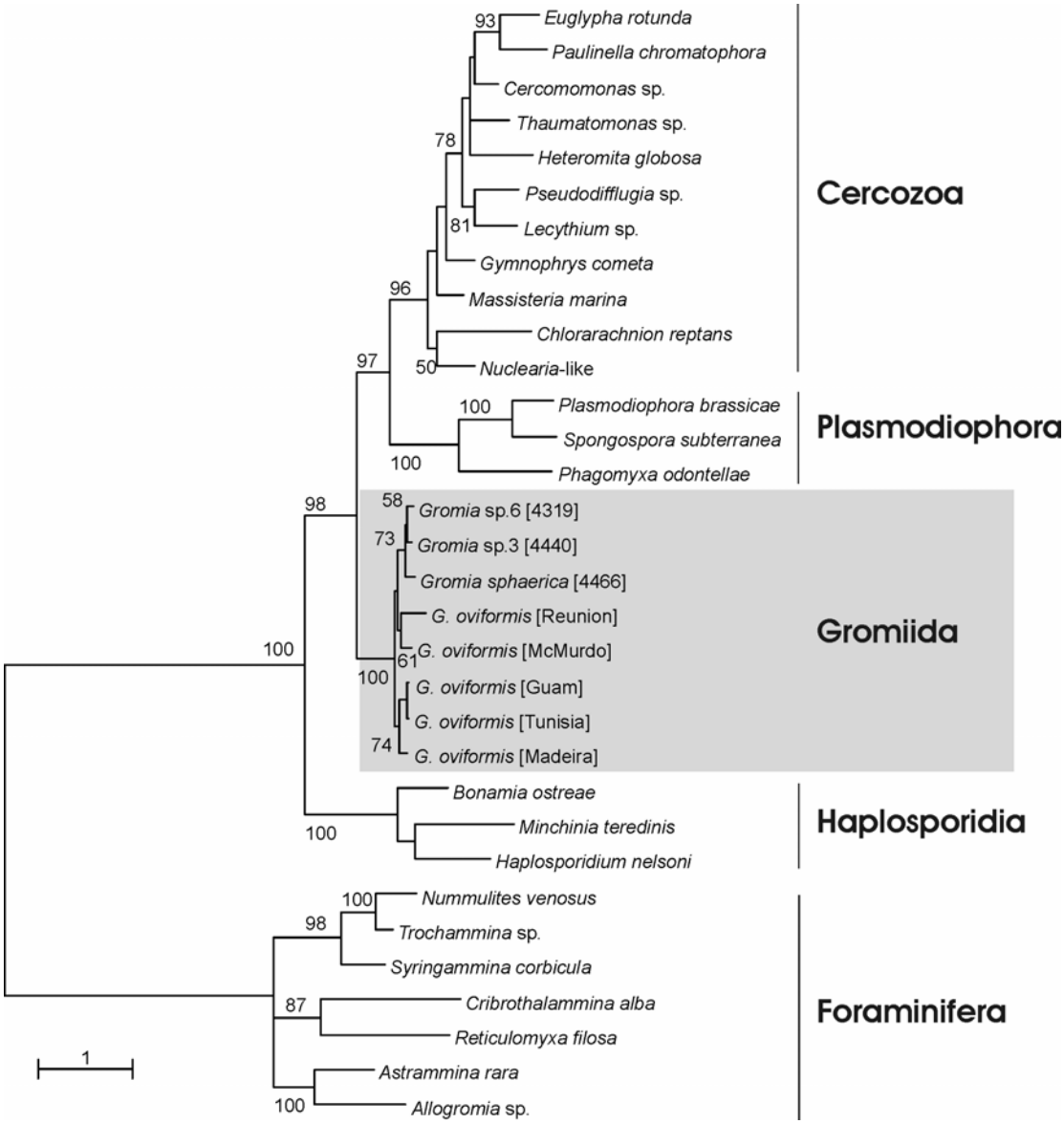
A fragment of the SSU rDNA of the length averaging 760 nucleotides was sequenced for 23 *Gromia* isolates from Arabian Sea. The phylogenetic analysis of these sequences revealed seven distinctive clades or lineages (Figure 4.3). One of them (clade D) corresponds to previously described species *G. sphaerica* (Gooday et al. 2000). Five other clades can be defined morphologically on the basis of their test morphology and wall structure (Chapter 3). Molecular and morphological descriptions of each clade are given below.

Table 4.3 List of previously published sequences used in our analysis.

Taxonomic position	Species name	Accession number
Gromiida	*Gromia oviformis* (Madeira)	AJ457811
	Gromia oviformis (Reunion)	AJ457812
	Gromia oviformis (McMurdo)	AJ457813
	Gromia oviformis (Guam)	AJ457814
	Gromia oviformis (Tunisia)	AJ457815
Cercozoa	*Euglypha rotunda*	X77692
	Paulinella chromatophora	X81811
	Cercomonas sp.	U42448
	Thaumatomonas sp.	U42446
	Heteromita globosa	U42447
	Pseudodifflugia sp.	AJ418794
	Lecythium	AJ514867
	Nuclearia-like	AF289081
	Gymnophrys cometa	AJ514866
	Massisteria marina	AF174369
	Chlorarachnion reptans	X70809
Plasmodiophora	*Plasmodiophora brassicae*	U18981
	Spongospora subterranea	AF310899
	Phagomyxa odontellae	AF310904
Haplosporidia	*Bonamia ostreae*	AF262995
	Minchinia teredinis	U20319
	Haplosporidium nelsoni	X74131
Foraminifera	*Astrammina rara*	AJ318223
	Allogromia sp.	X86093
	Nummulites venosus	AJ318226
	Trochammina sp.	X86095
	Syringammina corbicula	AJ514856
	Cribrothalammina alba	AJ318225
	Reticulomyxa filosa	AJ132367

Clade A is composed of four sequences obtained from grape-shaped gromiids from Oman (Figure 4.3). Their tests are very similar to shallow-water *G. oviformis* except that they have a thin translucent organic wall (Figure 3.12). The four sequences are almost identical and form a clade supported by 100% bootstrap values. The position of this clade at the base of the tree and its distance from all other gromiids, strongly suggests that this is a distinctive species, called here *Gromia* sp. 1.

Figure 4.2 Phylogenetic position of *Gromia* among Rhizaria inferred from partial SSU rDNA sequences, using the maximum likelihood method. The numbers at the nodes represent percentage of bootstrap support greater than 50 % following ML and NJ data re-sampling.



Clade B is represented in the tree by a single sequence of *Gromia* from Oman, but more partial sequences are available (data not shown). At first sight, this species, described here as *Gromia* sp. 2 (Figure 3.13), closely resembles *Gromia* sp. 1. However, the aperture end of the test is more pointed and a honeycomb-shaped structure (not to be confused with the honeycomb membrane) is visible under a binocular microscope within the thickness of the wall. This structure may confer some rigidity to the test, perhaps as a defence against predators or possible adverse environmental conditions. According to the analyses, *Gromia* sp.2 branches independently between *Gromia* sp. 1 and the shallow water *G. oviformis*. It seems weakly related to *Gromia* from coastal waters in McMurdo Sound, Antarctica. The position of *Gromia* sp. 2 close to the shallow-water gromiids may suggest that this species colonized the bathyal deep sea independently from other Arabian Sea gromiids.

Clade C is represented by a sausage-shaped form with a thick and opaque wall. This elongate morphotype, which was designate here as *Gromia* sp. 3 (Figure 3.14), is unique among Arabian Sea gromiids. Similar but smaller morphotypes have been observed in fjords in Western Svalbard (Arctic Ocean) (Gooday et al. in press) and in the samples from under the Ross Ice Shelf (Pawlowski et al. 2005), but none of these species has been sequenced yet. This study is therefore the first report of molecular data from an elongate gromiid morphotype. Its position as a sister group to the grape-shaped and spherical species is not stable and in some NJ analyses, it was found to branch between clades F and G. However, in all analyses, the clades C to G together form a strongly supported (92-99% bootstrap values) group, composed exclusively of Arabian Sea gromiids.

Clade D corresponds to *G. sphaerica*, a large protozoan (average test diameter of 15 mm) with characteristic multiple test apertures (Figure 3.11). This species has been described previously from the Oman margin (Gooday et al. 2000). Here it is reported for the first time from the Pakistan margin. The sequence divergence within this clade ranges from 0.2 to 0.8% between sequences 4358, 4353, 4357 and 4375, with one fast evolving sequence 4466, which differs from others by 5.7%. Almost all differences are in the SSU region V7 following the nomenclature of Neefs et al. (1993). Among five sequences representing this species, four originate from Pakistan and one originates from Oman. However, the Oman sequence (4375) is almost identical to two of the Pakistan sequences (4353, 4357), suggesting that there are no barriers between the two regions (see below).

Clade E is represented by a single sequence obtained from small (average test diameter 2.6 mm), spherical specimens, which were designated as *Gromia* sp. 4 (Figure 3.15). This species resembles *G. sphaerica*, in being characterized by the perfect spherical shape; the main differences are that *G. sphaerica* has a large test with multiple apertures while *Gromia* sp.4 is

smaller and with a single aperture. The SSU rDNA sequence was obtained from only one specimen, which forms a sister group to *G. sphaerica*, but its position is not supported.

Clade F is the most diverse group and contains six grape-shaped forms from the Oman and Pakistan margins. In contrast to all other clades, this group cannot be defined by any specific morphological features. The test wall is either thin and translucent or thick and opaque and the test morphologies span those of the other grape-shaped species described here. It is considered as a separate species, *Gromia* sp. 5 (Figure 3.16), because the clade is relatively well supported (76% bootstrap values) and the divergence between 6 sequences is relatively low.

Clade G is represented by a grape-shaped gromiid similar to *Gromia* sp. 1 but with a much thicker wall. This species, called here *Gromia* sp. 6 (Figure 3.17), is morphologically distinctive. Its sequences form a strongly supported clade in ML analysis (95% bootstrap values), but it is supported only by 58% in NJ analysis, probably due to the presence of the fast evolving sequence 4433, which differs from others by 1.5-2.0%.

Prior to this study, three gromiid morphotypes were described, the oval or spherical shaped *G. oviformis* (and some other related shallow-water species), the spherical *G. sphaerica* and the pear-shaped *G. pyriformis*. Excluding *G. pyriformis*, for which molecular data are not available, the current study has expanded the number of deep-sea gromiid species to at least seven, comprising at least five basic morphotypes. Within *Gromia*, 7 clades were identified, 6 of which (A, B, C, D, F, and G) are well defined morphologically. The spherical (clades C and D) and sausage-shaped (clade F) gromiids are relatively well defined on molecular criteria and have good morphological support. On the other hand, grape-like species are more difficult to distinguish morphologically and there is some confusion between specimens belonging to clades A, E and G. Indeed, the clade E is defined purely on molecular characteristics and includes specimens that look identical to individuals from clades A, and G. The presence of clade E indicates the likely existence of cryptic species and suggests that species diversity is higher than indicated by test morphology. Nevertheless, the fact that most of the molecular clades correspond to test morphotypes gives credibility to the molecular results.

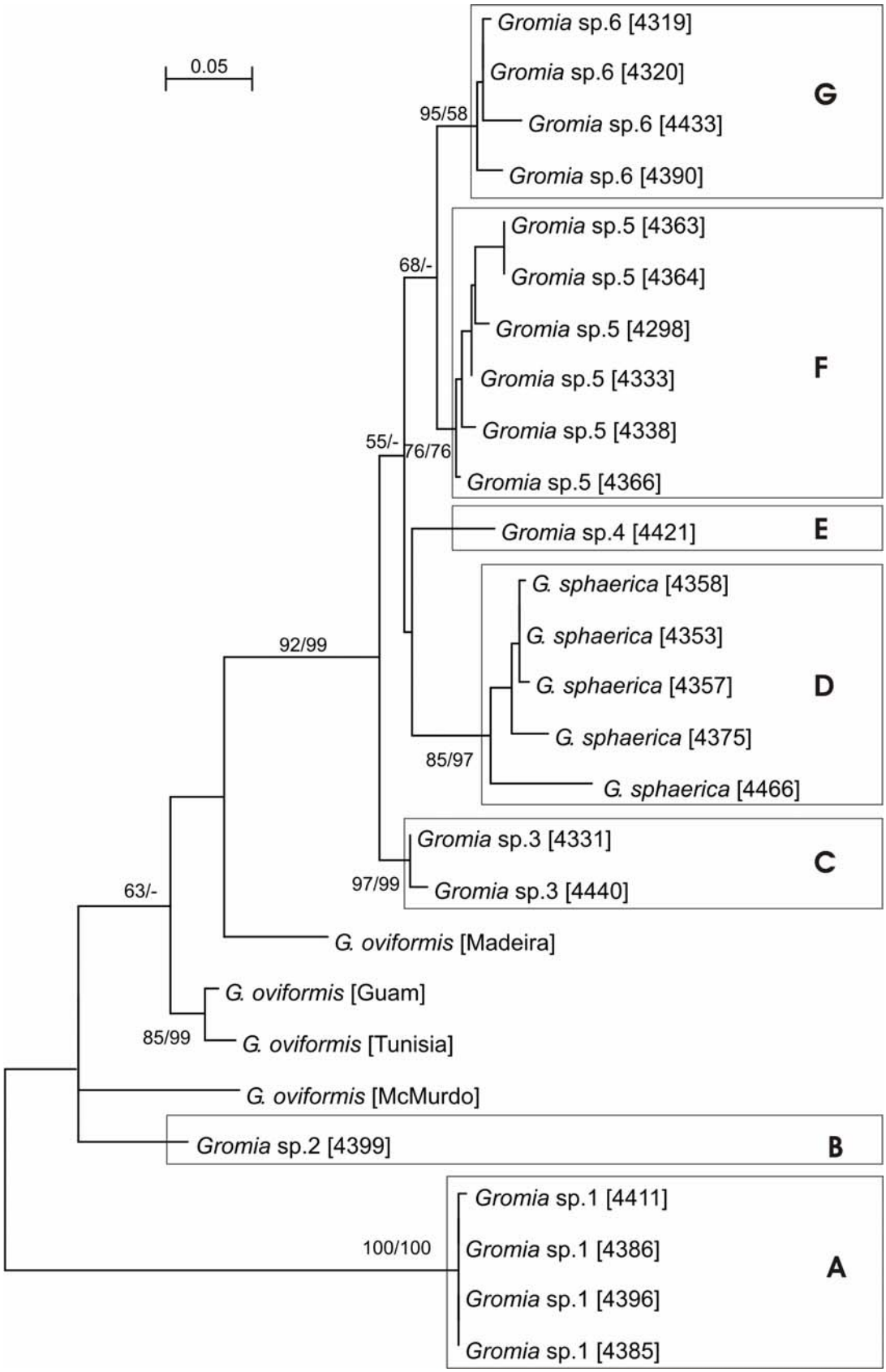
4.3.3 Biogeography of Arabian Sea *Gromia*

Gromiids occurred in core and trawl samples from the Oman and Pakistan margins of the Arabian Sea. They were more abundant in the Oman margin (Chapter 3) than in the Pakistan margin. Figure 4.3 shows 7 clades, representing at least 7 groups of Arabian Sea gromiids. Three of these 7 clades (A, B, and G) were confined to the Oman margin; two (clades E and C) were only found in the Pakistan margin and two (clades D and F) occurred on both margins.

However, although an extensive collection of material was obtained for molecular work, not all the specimens could be sequenced and therefore the data are incomplete. For example, sequences from morphological representatives of clades E and C on the Oman margin were not obtained. Although, gromiid abundance is higher on the Oman than on the Pakistan margin, there is no evidence that diversity (species numbers) is different between the two margins.

In order to compare species that are common to both margins, a fragment of the ITS rDNA, the most variable region of rDNA genes, was amplified for *Gromia* sp. 5 from the Oman and Pakistan margins. *Gromia* sp. 5 isolates 4364 from Pakistan and 4338 from Oman were cloned and sequences from at least 3 clones from each of the PCR products were obtained. The length of the sequences varied between 1056 and 1080 nucleotides and the base composition was 40.96% GC. All sequences were similar (< 1.2%), showing few differences between and within the clones from the two specimens. A clear difference between specimens from the opposite margins was not found, suggesting that there is probably a gene flow between the two regions. However, this should be repeated with a larger number of specimens from different clades in order to ensure that this result is not confined to one gromiid species. If the lack of difference between Oman and Pakistan populations is confirmed, it can be predict that the same gromiids will be found along the Makran margin, which forms the northern border of the Arabian Sea between Oman and Pakistan.

Figure 4.3 Maximum likelihood tree of Arabian Sea gromiids based on partial SSU rDNA sequences. The analysis includes 23 deep sea *Gromia* and 4 shallow water *Gromia* (from Burki et al. 2002). The numbers at the nodes represent percentage of bootstrap support greater than 50 % following ML and NJ data re-sampling.



4.4 Conclusions

The current study has enhanced considerably the knowledge of gromiids in general and deep-sea gromiids in particular. This study confirmed that the shallow and deep-water gromiids are closely related and form a monophyletic group within the Rhizaria. As shown by the analyses, several species of *Gromia* inhabit bathyal depths on the Oman and Pakistan margins. The Oman margin assemblages are more abundant, but not necessarily more diverse than those from the Pakistan margin. Some *Gromia* species inhabit both margins. To a large extent, the diversity of the Arabian Sea gromiids is expressed in test morphology. However, results also reveal evidence for cryptic speciation, suggesting morphology alone will underestimate species numbers, and that molecular data is essential when evaluating diversity within this group.

Chapter 5

Conclusions

5.1 Questions addressed

- **Are benthic foraminiferal trends (abundance, diversity and taxonomic composition) related to dominant environmental variables, such as bottom-water oxygen concentrations and organic carbon concentrations?** Yes. Foraminiferal abundances were higher where oxygen concentrations were higher above the OMZ (100 m) and also at the lower boundary (850 m) of the OMZ at 0.2 ml/l, which seems to be the critical value for foraminifera.

- **Are taxonomic trends observed across the OMZ mirrored by changes in sediment penetration?** Yes. Vertical distribution in the sediment reflected responses found across the horizontal gradient, with species concentrated in the top sediment where bottom-water oxygen concentrations were low. Conversely, species were found deeper in sediments at higher bottom-water oxygen concentrations.

- **Are foraminiferal macrofaunal trends comparable to those of macrofaunal metazoans (data from published sources) across the OMZ?** Both groups responded to oxygen and food availability, but responses were not exactly the same. Metazoan macrofaunal abundances were high within the OMZ and low at higher oxygen concentrations. Another difference was the depth of the lower boundary edge effect. For metazoans, abundance was enhanced at 700 m (O_2 = 0.15 ml/l) compared to 850 m (O_2 = 0.2 ml/l) in the case of foraminifera.

- **Are there similarities between the lifestyle of gromiids (large organic-walled protists, genus *Gromia*) in the deep Arabian Sea and shallow water setting?** Yes. *Gromia* live with the apertures facing the organic rich sediment, possibly feeding on the organic detritus being important in the degradation of fresh organic matter reaching the seafloor in this area.

- **Are there differences between *Gromia* populations from the Oman and the Pakistan margins of the Arabian Sea?** Yes. The Oman margin assemblages are more abundant, but not necessarily more diverse, than those from the Pakistan margin. Some *Gromia* species inhabit both margins, but others are restricted to one of the margins. Although, sausage-shaped morphotypes are more abundant on the Pakistan margin, they occur on both margins. *Gromia sphaerica* occurs on both margins and these separate populations are related. Grape-shaped specimens occur on both margins. Molecular work shows that they represent three different species, two of which are confined to the Oman margin of the Arabian Sea.

- **What is the phylogenetic relation between *Gromia* and other Protista?** Molecular phylogenetic work showed that *Gromia* species constitute a monophyletic group that branches next to the plasmodiophorids and the core Cercozoa. Although the position of *Gromia* is slightly different from that suggested by other studies (Cavalier-Smith 2002; Cavalier-Smith and Chao 2003; Nikolaev et al. 2004; Simpson and Roger 2004), there is no doubt that this group belongs to Rhizaria. The main point to emerge from this analysis is that all *Gromia* species form a monophyletic clade. This clade includes *G. sphaerica*, a species that is unusual in possessing multiple apertures but nevertheless branches with other deep-sea *Gromia*, as well as the shallow-water *G. oviformis*.

- **What does molecular analysis reveal about diversity within *Gromia*?** Eight different deep-sea gromiid morphospecies can be recognized in the Arabian Sea material. Molecular analyses revealed at least 7 different deep-sea gromiids, 6 of which are well defined morphologically. Thus, using a combination of morphological, ultrastructural and molecular tools, a total of 9 different deep-sea gromiids can be recognized in the Arabian Sea. This represents substantial increase in the total number of previously known gromiid species in the world's oceans (3).

5.2 Wider implications of current work

5.2.1 Paleoceanography

Studies on modern OMZ foraminifera are highly relevant to the interpretation of ancient dysoxic environments, particularly in the Cretaceous, when oceanic dysoxia was extremely developed during certain periods. Benthic foraminifera feed on particulate organic matter deposited on the seafloor. Their tests are preserved in the fossil record and their life processes can be directly compared to modern morphotypes. As a consequence, benthic foraminiferal communities are useful as bioindicators of change in paleoproductivity and oxygenation of

oceanic water masses. For example, Thies and Kuhnt (1995) compared two OMZs, a modern upwelling area on the Indian-Pakistan continental margin and Cretaceous organic-rich deposits of the NW African continental margin. They found these two systems to be similar in terms of community succession across the oxygen gradient, with low diversity and high dominance and abundances of calcareous foraminifera within the OMZ, followed by agglutinated faunas at deeper, well oxygenated locations below the OMZ. The shallow region above the OMZ also had low diversity and high abundance, but an even higher dominance of one single species. This result coincides with what was found during the present study in the Oman margin OMZ.

Three oceanic anoxic events occurred during the Cretaceous and studying the distribution patterns of low-oxygen tolerant fauna is very important to evaluate and reconstruct the regional and paleoceanographic settings in which such events occurred. One such studies by Koutsoukos et al. (1990) looked at two latest Cenomanian-earliest Turonian stratigraphic sequences from the south (Sergipe Basin) and north (western Anglo-Paris Basin) Atlantic, in order to evaluate the similarity between morphotypes commonly found in mid-Cretaceous oxygen-depleted sediments. They found that under presumed highly oxygen-depleted conditions, benthic microfauna were not very diverse, and the few species that were able to survive were mostly “opportunistic” r-selected species. Another study by Koutsoukos and Hart (1990) on the upper Aptian to Maastrichtian succession of the Sergipe Basin, Brazil, found a strong relationship between the distribution patterns of foraminiferal associations, trophic adaptations (such as community feeding strategy, dwelling habits and substrate niche patterns) and water-mass conditions (also depth related). In shallower areas where organic matter derived from surface productivity sank to the bottom with consequent oxygen depletion from pelagic respiration, benthic foraminiferans were dominated by r-selected low-diversity, stress-tolerant species with “opportunistic” omnivorous deposit-feeding strategies. Conversely, in aerobic mesotrophic areas in the open shelf, calcareous epifaunal deposit feeding foraminiferans were dominant, and assemblages highly diverse with a low abundances of k-selective species.

Modern studies on foraminiferal assemblages are essential to validate assumptions made when studying patterns among fossil assemblages such as those discussed above. Test morphology in relation to oxygen depletion has been used to interpret fossil characteristics (Corliss 1985; Bernhard 1986; Corliss and Chen 1988). However, Holbourn et al. (2001) compared modern and fossil assemblages from low-oxygen environments and found that present day morphologies did not necessarily occur in fossil assemblages, and more importantly, that the success of species in dysoxic settings depended on many interrelated biotic and abiotic factors including predation, reproductive strategies, bacterial symbiosis, vertical migration of redox boundary, preference for different carbon flux rates, duration and intensity of dysoxic periods, rather than morphological adaptation to low oxygen alone. She also proposed that evolutionary changes in

wall structure may have had more impact on the ability of benthic foraminifera to cope with low oxygen/high productivity environments than changes in test shape.

Interpretation of Cretaceous OMZ assemblages are hampered by the fact that none of the foraminiferal species in the deposits live in modern oceans. Also, Cretaceous OMZs were much more extensive, raising the possibility that modern OMZs are not exact analogues (Rogers 2000). For example, the distributions of dysoxic-tolerant species was more extensive than in modern oceans. Foraminifera can be used in a more direct way to interpret changes in existing OMZs during the severe climatic fluctualtions that characterize the Pleistocene. The work of den Dulk et al. (1998) and Cannariato and Kennett (1999) and Cannariato et al. (1999) provide a good examples.

Clearly, different aspects of foraminiferal assemblages are useful in different geological periods. Species level data can be used in the Pleistocene whereas in the Cretaceous, diversity, dominance and abundances, as well as taxonomic and morphotype composition provide more useful tools.

5.2.2 Biodiversity and Biogeography

Foraminifera are one of the most abundant groups of deep-sea benthic organisms (Gooday 1986), found at all depths in the ocean, including the Challenger Deep at 10,896 m in the Marianas Trench (Todo et al. 2005). Additionally, although there has been extensive research on foraminifera, particularly with regards to calcareous and robust agglutinated species, organic-walled and soft-shelled foraminifera are often overlooked, even though they can account for 10-20% of the abundance and diversity of foraminiferal species in the deep-sea or even higher than 90% in arctic coastal areas (Gooday 2002). When considering global biodiversity, it is therefore important to include these diverse and abundant protists. The current study includes all organisms found in the >300 µm fraction, including soft-shelled and organic-walled foraminifera, adding to the scarce data set.

Most studies of foraminiferan faunal distribution have been conducted in temperate regions of the world and to properly understand the global distribution of species, it is necessary to collect data from all regions. The Arabian Sea lies within the subtropical part of the Indian Ocean. The Indian Ocean foraminiferal fauna is now relatively well known from several studies except for the monothalamous component. When looking at large scale patterns of biodiversity and biogeography, it is therefore important to have a complete dataset without gaps in regional sampling.

The Oman margin of the Arabian Sea is characterized by an intense OMZ. These environments are stressful for many organisms and are believed to influence speciation in the deep sea, either through the geographical restriction of populations of OMZ-tolerant species, the creation of barriers to the dispersal of oxyfilic species or through selection for tolerance to oxygen deficiency (Rogers 2000). As mentioned in the previous section, during periods of Earth's history characterized by global warming, species adapted to life in hypoxic conditions may have been more widespread. With the development of cooler atmospheric conditions, these species became restricted to OMZs associated with localized upwelling and areas of high productivity and poor circulation. These dysoxic areas resemble islands separated by geographical barriers, creating the potential for allopatric speciation and the development of endemic species (Rogers 2000). *Uvigerina* ex. gr. *semiornata* may be a good example of endemism. In the current study, this species occurred in exceedingly high abundances, at shallow depths (100 m) on the Oman margin. Maas (2000) also reported this species from shallow waters (230 m) on the Pakistan margin, but there are no convincing records of it from anywhere else, suggesting it to be restricted to the Arabian Sea OMZ.

Cryptic speciation has been well documented in planktonic foraminifera (Darling et al. 1996; Darling et al. 1997; Darling et al. 2000) but in the case of benthic foraminifera it is poorly understood. This study revealed the presence of cryptic species of the rhizarian protist *Gromia* in the Arabian Sea, reflecting genetic differentiation which is not expressed morphologically. Other studies have found evidence for cryptic speciation in the widespread foraminiferal genus *Ammonia* (Pawlowski et al. 1995; Holzmann 2000; Holzmann and Pawlowski 2000), a problem that was resolved by Hayward et al. (2004) using a combination of morphological and molecular tools. Besides test morphology, molecular and ultrastructural features can create a better understanding of the diversity of testate protists. In this study, it was particularly essential in the case of *Gromia*, which has relatively few morphologically distinctive characteristics. The number of *Gromia* species would have been underestimated if morphology alone had been used to recognize them. Cryptic speciation reveals greater diversity than hitherto appreciated and as a consequence it is essential to detect its occurrence in diversity studies. Without some information about the extent of cryptic speciation in benthic protists and other organisms, it will be impossible to accurately determine biogeographic patterns and the full extent of biodiversity at regional and global scales.

5.2.3 Anthropogenic implications

Historical records of foraminiferal tests preserved in sediments may provide evidence for recent changes in extent of modern dysoxia. This is particularly true in sediments which are laminated, implying the absence of macrofauna bioturbation and with high rates of sediment deposition.

Such conditions exist in fjords and off major rivers. Alve (2000) looked at live and dead foraminiferal assemblage composition, species diversity, the numerical density of tests and re-colonization processes in ^{14}C dated cores from the Frierfjord, Norway and compared it to historical periods of pollution related to industrial developments since 1870, These are good examples of how information on foraminiferal responses to low oxygen and high productivity can be useful, not only to interpret past geological records, but also more recent historical events, and possibly predict future changes. By studying foraminifera in locations where there has been increased anoxia from anthropogenic inputs, we can evaluate impacts, through changes in species abundances and diversity. With global warming and increased anoxia in the world's oceans, foraminifera are potentially good proxies for benthic community responses to pollution. The present study was conducted in a low oxygen area of high productivity and yielded information that adds to the foraminiferal dataset from dysoxic environments. The comparison of foraminiferal and metazoan responses to organic enrichment dysoxia is potentially very important. If the two groups show similar responses, we can use foraminifera as proxies for the way in which entire benthic communities have behaved in the past and are likely to behave in the future. Most monitoring of faunal change in response to environmental change in modern oceans has involved the use of metazoan data. Conversely, our understanding of faunal responses to environmental change in ancient oceans has involved the use of foraminifera. Linking responses by the two groups by studying them together is a crucial step in developing a unified approach to benthic responses to disturbances in past and present oceans.

5.2.4 Gromiids and carbon cycling in organically enriched environments

Gromiids are very abundant in the Oman margin of the Arabian Sea, occurring just below the OMZ, where oxygen concentrations start to increase. They live with their apertures facing the organic-enriched sediment suggesting that they feed on it. They are large in size and one of the main megafaunal components. Nothing is known of the biology of deep-sea gromiids and any speculations can only be based on comparison to the coastal gromiid *Gromia oviformis* which has been extensively studied (Jepps 1926; Arnold 1972). The very similar lifestyle adopted by *Gromia oviformis* in shallow-water sedimentary environments (Nyholm and Gertz 1973) suggests that the general ecology of gromiids is similar in shallow- and deep-water settings. I speculate that deep-water gromiids may play an important role in carbon cycling as they tend to occur in high abundances in organically-enriched environments. However, information about aspects of their biology, such as metabolic rates and feeding preferences are required in order to better understand their ecological role. At the moment there is very little published information available.

5.3 Future directions

5.3.1 Foraminifera in OMZs

- For the Oman margin OMZ transect, finer (< 150 µm and < 63 µm) fractions should be analysed to complete the dataset.
- There is considerable need for the description of new species using a combination of molecular, ultrastructural and morphological approaches. This applies particularly to monothalamous taxa which are undocumented in dysoxic settings and display relatively few taxonomic characteristics.

5.3.2 Deep-sea gromiids

- It is important, first of all, to clarify the phylogenetic position of gromiids in relation to other Rhizaria.
- The genetic variability within the group across geographical areas.
- The functional significance of gromiid test morphotypes is a subject to explore. More than one morphotype co-exists in the same locations, suggesting that subtle differences may exist in their ecologies.
- Gromiids seem to be microhabitats for bacteria and other microbial organisms. Again, this is a subject to explore, using a combination of ultrastructural and molecular tools.

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Appendix A

Live foraminifera (>300 μm) picked from samples collected during D211, from the 0-5 cm and 0-1 cm sediment layers. () number of fragment individuals.

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
	Allogromiida																
1	Allogromiid sp.1									2	2						
2	Allogromiid sp.2									3	3						
3	Allogromiid sp.3									1	1						
4	Allogromiid sp.4									1	1						
5	Allogromiid sp.6									1							
6	Allogromiid sp.7									1							
7	Allogromiid sp.8									1							
8	Allogromiid sp.9									1							
9	Allogromiid sp.10									1							
10	Allogromiid sp.13												5	4			
11	Allogromiid sp.14												3	3			
12	Allogromiid sp.15												1	1			
13	Allogromiid sp.16												1	1			
14	Allogromiid sp.17												1	1			
15	Allogromiid sp.18												1	1			
16	Allogromiid sp.19												1	1			
17	Allogromiid sp.20												(4)	(4)			
18	Allogromiid sp.21						5	4									
19	Allogromiid sp.22						1	1									
20	Allogromiid sp.23	17 (1)	17 (1)														
21	Allogromiid sp.24	4	4														
22	Allogromiid sp.25	4	4														
23	Allogromiid sp.27				2	2											
24	Allogromiid sp.28				1	1											
25	Allogromiid sp.29				1												
26	Allogromiid sp.30				1												
27	Allogromiid sp.31				1												
28	Allogromiid sp.32				1												
29	Allogromiid sp.33				1												
30	Allogromiid sp.34				1												
31	Allogromiid sp.35				1												
32	Allogromiid sp.36				1												
33	Allogromiid sp.37															2	2
34	Allogromiid sp.38															1	1
35	Allogromiid sp.39															1	1
36	Allogromiid sp.40															1	1
37	Allogromiid sp.41															1	
38	Allogromiid sp.45															1	
39	Allogromiid sp.46								1								
40	Allogromiid sp.47								2								
41	Allogromiid sp.48														1		

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
42	Allogromiid sp.49														1		
43	Allogromiid sp.50														2		
44	Allogromiid sp.51											1					
45	Allogromiid sp.52											1					
46	Allogromiid sp.53											1					
47	Allogromiid sp.54											1					
48	Allogromiid sp.55											1					
49	Allogromiid sp.56											(1)					
50	Allogromiid sp.57											(1)					
51	Allogromiid sp.58											1					
52	Allogromiid sp.59											(1)					
53	Allogromiid sp.60											(1)					
54	Allogromiid sp.61											(1)					
55	Allogromiid sp.62											(1)					
56	Allogromiid sp.63	4															
57	Allogromiid sp.64			4 (1)													
58	Allogromiid sp.65																
59	*Micrometula* sp.1				8	8											
60	*Nemogullmia longevariabilis*									6	6						
	Total	**29 (1)**	**25 (1)**	**4 (1)**	**19**	**11**	**6**	**5**	**3**	**18**	**13**	**6 (6)**	**13 (4)**	**12 (4)**	**4**	**7**	**5**
	Astrorhizida: Astrorhizacea: Saccamminidae: soft-shelled																
61	Saccamminid sp.1									6	6						
62	Saccamminid sp.2									1	1						
63	Saccamminid sp.3									1	1						
64	Saccamminid sp.4									1							
65	Saccamminid sp.6												1	1			
66	Saccamminid sp.7												1	1			
67	Saccamminid sp.8												1				
68	Saccamminid sp.9	74	74		8	8											
69	Saccamminid sp.12								1								
70	Saccamminid sp.13											1					
71	Saccamminid sp.14			1													
	Total	**74**	**74**	**1**	**8**	**8**	**0**	**0**	**1**	**9**	**8**	**1**	**3**	**2**	**0**	**0**	**0**
	Astrorhizida: Astrorhizacea: Saccamminidae: Lagenammina																
72	*Lagenammina* sp.1									16	3						
73	*Lagenammina* sp.2									10		1					
74	*Lagenammina* sp.3												9	6	5		
75	*Lagenammina* sp.4												2		10		
76	*Lagenammina* sp.6				15	15											
	Total				**15**	**15**	**0**	**0**	**0**	**26**	**3**	**1**	**11**	**6**	**15**	**0**	**0**

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
	Astrorhizida: Astrorhizacea: Psammosphaeridae: spheres and domes																
77	*Psammosphaera fusca*												7	4			
78	*Psammosphaera* sp.2												2	2			
79	*Psemmosphaera* sp.3	122	26														
80	*Psammosphaera* sp.4	4	4														
81	*Psammosphaera* sp.5	835	119	77													
82	Very distinctive sphere															1	
83	Indeterminate sp. 7 – spheres and domes												13				
84	Indeterminate sp.8	4	4														
85	Indeterminate sp.12															1	
86	Indeterminate sp.13															1	
	Total	**965**	**153**	**770**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**22**	**6**	**0**	**3**	**0**
	Astrorhizida: Astrorhizacea: Bathysiphonidae																
87	*Bathysiphon* sp.1												3	3			
88	*Bathysiphon* sp.2	26	26		39	38	4	4	6								
89	*Bathysiphon* sp.3	22	22	41	23	23	1	1	11								
90	*Bathysiphon* sp.4															3	3
	Total	**48**	**48**	**41**	**62**	**61**	**5**	**5**	**17**	**0**	**0**	**0**	**3**	**3**	**0**	**3**	**3**
	Astrorhizida: Astrorhizacea: Hippocrepinacea: Hippocreppinidae: Hyperammina																
91	*Hyperammina friabilis*															(1)	
92	*Hyperammina* sp.1												1	1			
93	*Hyperammina* sp.2															(3)	
	Total	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0 (4)**	**0**
	Astrorhizida: Komokiacean-like																
94	Chains sp.1															(17)	(9)
95	*Crambis* sp.1															(1)	
96	Komokiacean												(10)				
97	*Reticulum* sp.1															(113)	(50)
	Total	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**(10)**	**0**	**0**	**(131)**	**(59)**
	Other Tubes																
98	*?Pelosina* sp.1							(5)	(29)			(11)					(1)
99	*Pelosina* sp.2						(6)						(9)	(9)			
100	*Rhizammina* sp.1															(5)	
101	*Rhizammina* sp.2															(50100)	(50000)
102	Tubes sp.1				(57)	(3)										(153)	(100)
103	Tubes sp.2																(8)
104	Tubes sp.3															(13)	
105	Indeterminate sp.3												(444)	(33)		(1)	
106	Indeterminate sp.5												(178)				
	Total	**0**	**0**	**0**	**(57)**	**(3)**	**(6)**	**(5)**	**(29)**	**0**	**0**	**(11)**	**(631)**	**(42)**	**0**	**(50272)**	**50109**
	Various Astrorhizida																
107	*Crithionina hispida*															1	1

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
108	*Crithionina* sp.1															1	1
109	"*Crithionina*" sp.2															7	1
110	*Crithionina* sp.3															10	
111	*Crithionina* sp.4												1	1	7	4	
112	*Hippocrepinella hirudinea*												3	3			
113	*Vanhoeffenella* sp.1															1	1
114	*Vanhoeffenella* sp.2															1	
115	*Conqueria* sp.1												1	1			
116	Indeterminate sp.1												3	3			
117	Indeterminate sp.9															1	1
118	Indeterminate sp.10															1	1
119	Indeterminate sp.11															1	
120	Indeterminate sp.14															2	
	Total	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**8**	**8**	**7**	**30**	**6**
	Lituolida: Hormosinacea																
121	*Hormosina dentaliniformis*												3	2	1		
122	*Leptohalysis* sp.1				1	1			3	1							
123	*Reophax* aff. *advenus*	202	94	36													
124	*Reophax horridus*															2	
125	*Reophax scorpiurus*												9	9	41		
126	*Reophax spiculifer*												5	5	1		
127	*Reophax* sp.1									95	10	17	3	2	15		
128	*Reophax* sp.3									16		1	5				
129	*Reophax* sp.4									3		5			1		
130	*Reophax* sp.5									2							
131	*Reophax* sp.6												3	3			
132	*Reophax* sp.7												1	1			
133	*Reophax* sp.9	193	113	48													
134	*Reophax* sp.10	4															
135	*Reophax* sp.11			16	2	1											
136	*Reophax* sp.12															1	1
137	*Reophax* sp.13															5	5
138	*Reophax* sp.14															3	3
139	*Reophax* sp.15								1								
140	*Reophax* sp.16														1		
141	*Reophax* sp.17														2		
142	*Reophax* sp.18	8															
	Total	**407**	**207**	**100**	**3**	**2**	**0**	**0**	**4**	**117**	**10**	**24**	**29**	**22**	**62**	**11**	**9**
143	**Trochamminida: Trochomminacea**	**13**	**13**	**0**	**0**	**0**	**0**	**0**	**0**	**9**	**7**	**0**	**1**	**1**	**0**	**3 (3)**	**0**
	Textulariida: Textulariacea																
144	*Martinottinella communis*															2	1
145	*Martinottinella* sp.2														2		
146	*Textularia pseudogramen*	136	104														
	Total	**136**	**104**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**	**2**	**1**

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
	Other MAF																
147	*Ammoscalaria* sp.1												2	2			
148	*Cribrostomoides wiesneri*				1	1	1	1	5							1	
149	*Evolutinella* sp.1														1		
150	*Haplophragmoides* sp.1				1	1							1	1			
151	*Labrospira* sp.1								1								
152	*Recurvoides* sp.1												1				
153	*Veleroininoides scitulus*											1	1		2		
154	*Veleroninoides* sp.1								1								
	Total	**0**	**0**	**0**	**2**	**2**	**1**	**1**	**7**	**0**	**0**	**1**	**5**	**3**	**3**	**1**	**0**
	Miliolida																
155	Miolida sp.1			4													
156	Miliolida sp.2			4													
157	Miliolida sp.3			4													
158	Miolida sp.4			32													
159	Miliolida sp.5			4													
160	*Pyrgo depressa*												1	1		1	
161	*Pyrgoella* sp.1															1	
162	*Sigmoilopsis* sp.2															1	1
163	*Spiroculina* sp.1	4	4	2													
164	*Triloculina tricarinata*	37	37	8													
	Total	**41**	**41**	**58**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**3**	**1**
	Lagenida																
165	*Amphycoryna* sp.1	9	1	1													
166	*Dentalina* sp.2	1															
167	*Dentalina* sp.3			1	1	1											
168	*Hemirobulina* sp.1															1	
169	*Lenticulina* aff. *iota*	77	73	75	6	6	8	8	23	10	10	7					
170	*Lenticulina* sp.2	9	9	4													
171	*Nodosaria* sp.1	8	8	4													
172	*Saracenaria* sp.1				4	4						1					
	Total	**104**	**92**	**83**	**11**	**11**	**8**	**8**	**23**	**10**	**10**	**8**	**0**	**0**	**0**	**1**	**0**
	Buliminida																
173	*Bolovina albatrossi*	17	17														
174	*Boltvina* aff. *inflata*			1					1	3	1	2					
175	*Boltvina* sp.1											1					
176	*Bolivina seminuda*	16	16	37					1								
177	*Brizalina* sp.1						1	1									
178	*Bulimina aculeata*												9	1			
179	*Globobulimina affinis*				10	10	9	9	10	6	1		3	2			
180	*Globobulimina* aff. *turgida*				21	10	3	2	30	8	2	1	3			4	
181	*Globobulimina turgida*						5	5	2								
182	*Globobulimina* sp.3															4	
183	*Uvigerina* ex gr. *semiornata*	864	812	803	2	2											

	Site	100-m			400-m		700-m			850-m			1250-m			3400-m	
	Station	12708#5		12708#3	12695#5		12682#5		12685#2	12713#3		12711#3	12723#3		12725#3	12687#3	
	Sediment layer	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm	0-1 cm	0-5 cm	0-1 cm
184	*Uvigerina* sp.1									12	11	6					
185	*Uvigerina peregrina*				9	9			1	11	1				1		
186	*Uvigerina* sp.2						1	1					1				
187	*Uvigerina* sp.4														1		
	Total	**897**	**845**	**841**	**42**	**31**	**19**	**18**	**45**	**40**	**16**	**10**	**16**	**3**	**2**	**8**	**0**
	Rotaliida																
188	*Ammonia* sp.1	41	41	6													
189	*Cancris auriculus*	80	68	65	19	19	2	2	1	22	17	11					
190	*Chilostomella oolina*												5				
191	*Chilostomella ovoidea*				1								2	2	1		
192	*Hanzawaia concentrica*	23	23	17									2	2	1		
193	*Hyalinea baltica*												4	4			
194	*Melonis affinis*												1				
195	*Nonionella* sp.1									4			1				
196	*Oridorsalis* sp.1												1	1			
197	*Pullenia* sp.1														1		
198	Calcareous foram			4													
	Total	**144**	**132**	**92**	**20**	**19**	**2**	**2**	**1**	**26**	**17**	**11**	**16**	**9**	**3**	**0**	**0**
	Robertiniida																
199	*Hoeglundina elegans*						23			1							
	Total	**0**			**0**		**23**			**1**			**0**			**0**	
	Grand Total of Specimens	**2858**	**1734**	**1297**	**182**	**160**	**64**	**62 (5)**	**144**	**263**	**87**	**65**	**129**	**77**	**101**	**72**	**25**
		(1)	**(1)**	**(1)**	**(57)**	**(3)**	**(6)**		**(29)**	**(129)**		**(17)**	**(645)**	**(46)**		**(50410)**	**(50168)**

Appendix B

A taxonomic survey of Foraminifera from the Oman margin of the Arabian Sea

1 Introduction

The purpose of this Appendix is to present a brief taxonomic survey of the more abundant macrofaunal (> 300 µm) foraminifera species on the Oman margin. For each species, a reference is given to a representative illustration, if possible from the Arabian Sea. Undescribed species are briefly characterized.

2 Species descriptions

Allogromiid sp.1 – Organic-walled, sausage-shaped test with 2 terminal apertures, one at either end. Two live specimens found at Station 12713#3 (850 m).

Allogromiid sp.2 – Spherical, organic-walled test without obvious aperture. Three live specimens found at Station 12713#3 (850 m).

Allogromiid sp.13 – Oval, thick-walled, organic test with an oral capsule. This species may be a gromiid. Five live specimens found at Station 12723#3 (1250 m).

Allogromiid sp.14 – Spherical, thick-walled, organic test without obvious aparture. This species may be a gromiid. Three live specimens found at Station 12723#3 (1250 m).

Allogromiid sp.21 – Oval thick-walled, organic test with an oral capsule. It differs from Allogromiid sp.13 in having a narrower test near the aperture. This species may be a gromiid. Five live specimens found at Station 12682#5 (700 m).

Micrometula sp.1 – Elongate, cone-shaped, hyaline, organic test with a rounded aperture. It differs from *Micrometula hyalostriata* from the Gullmar Fjord, described by Nyholm (1952), in being more elongated and with constrictions in the proximal parts. Eight live specimens found at Station 12695#5 (400 m).

Nemogullmia longevariabilis Nyholm, 1953 – Very thin, thread-like organic-walled test with 2 apertures, one at either end. The Arabian Sea specimens are essentially similar to *Nemogullmia longevariabilis* as described by Nyholm (1953) from the Gullmar Fjord. Six live specimens found at Station 12713#3 (850 m); three were found inside cysts; three were free living.

Saccamminid sp.1 – Soft-shelled saccamminid with shiny silver test composed of very fine agglutinated particles and with a single aperture. Six live specimens found at Station 12713#3 (850 m), of which 4 were found in a nest.

Saccamminid sp.9 – Oval-shaped, agglutinated test composed of very fine sand grains with very small aperture at one end. Seventy four live tests were found at Station 12708#5 (100 m).

Saccamminid sp.15 – Oval-shaped, agglutinated test composed of very fine sand grains with very small aperture at one end. Very similar to Saccamminid sp.9 but with a thicker more robust test. Two dead tests were found at Station 12687#3 (3400 m).

Lagenammina sp.1 – Single-chambered agglutinated test composed of small, juvenile *Globigerina* tests and drawn out into a tubular apertural extension. Twenty eight live and dead tests found at Station 12713#3 (850 m).

Lagenammina sp.2 – More or less spherical agglutinated test, 300 - 400 µm diameter, composed of very fine sand grains. Very small aperture located on pointed projection. Thirty live and dead tests found at Station 12713#3 (850 m).

Lagenammina sp.3 - More or less spherical agglutinated test, 300 - 400 µm diameter, composed of very fine sand grains. Very small aperture at the end of a tubular extension. Twenty one live and dead tests found at Station 12723#3 (1250 m).

Lagenammina sp.4 – Test 800-1000 µm long and 500-700 µm wide; flask-shaped with short apertural neck; agglutinated wall composed of foraminiferal tests mainly planktonic but some benthic. Seventeen live and dead specimens at Station 12723#3 (1250 m).

Lagenammina sp.6 (Plate 1, Figure 1) – Test 400-800 µm long and 300-500 µm wide; flask-shaped with short apertural neck. Agglutinated wall composed of foraminiferal tests, mainly planktonic but some benthic, and occasional mineral grains. It differs from *Lagenammina* sp.4 in being more robust. Twenty live and dead specimens at Station 12695#5 (400 m).

Psammosphaera fusca Schulze, 1875 – See *P. fusca* var. *testacea* of Flint (1899, Pl. 8, Fig.2). Test between 600 and 1200 µm diameter, nearly spherical and constructed of a single layer of dead planktonic foraminiferal tests. Forty four live and dead specimens were found at Station 12723#3 (1250 m).

Psammosphaera sp.3 – Test spherical, with no obvious aperture. Wall almost transparent, composed of very fine agglutinated particles. The test is very fragile and disintegrates easily. One hundred and twenty two specimens at Station 12708#5 (100 m).

Psammosphaera sp.5 (Plate 1, Figures 2 and 3) – Test more or less spherical, between 300 and 500 µm diameter, with no obvious aperture; wall made entirely of large transparent quartz grains. A large number (5583) of live and dead specimens found at Station 12708#5 (100 m).

Bathysiphon sp.1 – Test up to 3000 µm long and 100 µm wide and composed of finely agglutinated material. It is open at both ends, but unlike typical *Bathysiphon* species, it is parallel sided and does not taper. Three live specimens were found at Station 12713#3 (850 m).

Bathysiphon sp.2 (Plate 2, Figures 2-8) – Tubular test between 420 µm and 1240 µm long, open at both ends, slightly curved, and tapering from about 50 µm at the apertural end to about 15 µm at the proximal end. When dried, it tends to collapse, except near the apertural end. Wall finely agglutinated, smooth, with a reflective sheen. There is a distinct outer layer composed of imbricated, plate-like grains a few microns in size. This species occurs at all stations across the Oman margin between 100 m and 850 m, but with highest abundances (22 per 25.5 cm^3) at Station 12695#5 (400 m). Most specimens are living, as indicated by rose Bengal staining and the presence of detrital material around the aperture.

Bathysiphon sp.3 (Plate 2, Figure 1) – Tubular test between 480 µm and 1000 µm long, more or less straight, and tapering from 60 µm at the apertural end to about 20 µm at the proximal end. Wall is composed of fine material grains and incorporates projecting sponge spicules that are directed backwards, away from the aperture. There is generally less detrital material around the aperture than in the case of *Bathysiphon* sp.2. This species occurs at most stations across the Oman margin between 100 m and 700 m, but with highest abundances (17 per 25.5 cm^3) at Station 12695#5 (400 m).

Rhizammina sp.2 (Plate 1, Figure 4) – Flexible branched test, typically between 50 µm and 100 µm diameter, composed of fine sediment particles and small fragments of planktonic and benthic foraminiferal tests. More than 50,000 test fragments were found at Station 12687#3 (3400 m). Maas (2000) also reported a *Rhizammina* species from 233 m and 902 m on the Pakistan margin.

"*Crithionina*" sp.2 – Test resembling a soft, fine grained mud ball, and containing stained protoplasm and stercomata. This species is not a true *Crithionina* and represents a new genus. Seven live specimens found at Station 12687#3 (3400 m).

Crithionina sp. 3 – Oval test, between 700-1200 µm long and 300-700 µm wide. White wall is composed of fine mineral grains and incorporates projecting sponge spicules that are directed outwards, away from the test wall. There is an inner layer of different composition surrounding stained protoplasm and stercomata. Ten live specimens found at Station 12687#3 (3400 m).

Crithionina sp.4 – Spherical test, between 350 µm and 700 µm diameter. White wall finely agglutinated with a smooth, reflective sheen surface. There is an inner layer of different composition surrounding stained protoplasm and stercomata. Seven live and dead specimens were found at Stations 12723#5 and 12687#3 (1250 m and 3400 m respectively).

Hippocrepinella hirudinea Heron-Allen and Earland, 1932 – See Loeblich and Tappan (1987, Pl. 17, Figs. 1-5). Cylindrical, flexible agglutinated test, about 1300 µm length and 100 µm wide. Wall whitish composed of very fine sediments. Three live specimens were found at Station 12723#3 (1250 m).

Ammodiscus cretaceous Reuss, 1846 – See Maas (2000 Pl. 1, Fig. 2). Three live and dead specimens were found at Stations 12713#3 and 12723#3 (850 m and 1250 m respectively).

Leptohalysis sp.1 – See Loeblich and Tappan (1987, Pl. 44, Fig. 21). Delicate test, uniserial and rectilinear, about 500 µm long and 50 µm wide with flask-like chambers arranged in an almost straight series; wall transparent and flexible, made of very tiny mica grains. Eleven live and dead specimens were found at Stations 12695#5, 12685#2 and 12723#3 (400 m, 700 m and 1250 m respectively).

Reophax aff. *advenus* Cushman, 1919 (Plate 1, Figures 8 and 9) – See Zheng and Fu (2001, Pl. XIII, Figs. 7-9). Test free, 700-1000 µm long and 100-500 µm wide, consisting of 2-3 chambers separated by a slight constriction. Aperture not obvious aperture. Wall transparent, made entirely of large quartz grains. Three thousand, seven hundred and ninety live and dead specimens found at Station 12708#5 (100 m).

Reophax horridus – See Zheng and Fu (2001, Pl. XVII, Fig. 10). Test about 1000 µm long and 90 µm wide, uniserial, composed of fine agglutinated sediment particles and incorporating

projecting sponge spicules that are directed backwards, away from the aperture. Three live and dead specimens were found at Station 12687#3 (3400 m).

Reophax scorpiurus Montfort, 1808 (Plate 1, Figure 5) – See Flint (1899, Pl. 17, Fig. 1). Test 1500-2000 µm long and 500-700 µm wide; slightly curved at the bottom, composed almost entirely of dead planktonic foraminiferal shells. Total of 50 live specimens and 53 dead specimens found at Station 12723#3 (1250 m). Hermelin and Shimmield (1990) reported *Reophax scorpiurus* from 1000 m on the Oman margin, but their species looks different from the present one. *Reophax scorpiurus* was originally described from beach sands in the Adriatic (Brönnimann and Whittaker 1980). It has since been reported very widely from numerous different habitats and is best regarded as a morphotype, rather than a single species.

Reophax spiculifer Brady, 1879 – See Jones (1994, Pl. 31, Figs. 16-17). Test 1500-2000 µm long with elongate almost cylindrical chambers in an almost straight series; wall made of sponge spicules. Six live specimens found at Station 12723#3 (1250 m).

Reophax sp.1 (Plate 1, Figure 6) – Test 1800-2000 µm long and 500-700 µm wide, composed of well-cemented quartz grains and broken *Globigerina* shells. One hundred and twelve live and dead specimens found mostly at Station 12713#3 (850 m), but some at Station 12723#3 (1250 m).

Reophax sp.4 – Test about 350 µm long and 100 µm wide, with constriction in the middle between both chambers, wall composed of minute dead *Globigerina* tests. Fifty eight live and dead specimens found at Stations 12713#3 and 12723#3 (850 m and 1250 m respectively).

Reophax sp.9 (Plate 1, Figure 7) – Test, about 1500-2000 µm long and 500-700 µm wide, composed of a mixture of large and small quartz grains, broken foraminiferal shells and fine sediments. One hundred and ninety three live specimens found at Station 12708#5 (100 m).

Martinottiella communis (d'Orbigny 1846) – See Hermelin and Shimmield (1990, Pl. 1, Figs. 15 and 19). Test elongate, cylindrical, about 1000 µm long. Wall finely agglutinated composed of very fine sediment. Terminal aperture. Three live and dead specimens were found at Station 12687#3 (3400 m).

Textularia pseudogramen Chapman and Parr, 1937 (Plate 1, Figure 10) – See Jones (1994, Pl. 43, Figs. 9-10). Test triangular, biserial throughout, 1100 µm long and 900 µm wide at the apertural end and 200 µm at the opposite end. Wall composed of a mixture of large and small

degraded foraminiferal shells and mineral grains. One hundred and thirty six live specimens were found at Station 12708#5 (100 m).

Tritaxia sp.1 – See Zobel (1973, Pl. 1, Figs 55-56). Test elongate, triserial, and triangular in early stages, about 1000 µm long. Wall composed of very finely agglutinated sediment, relatively thick and solid. Round, central terminal aperture on the inner margin. Hermelin and Shimmield (1990, Pl. 1 Figs. 13-14) also reported a *Tritaxia* sp. between 700 m and 1000 m, but their illustrated specimen looks different from this one. Twenty four dead tests found at Station 12685#2 (700 m).

Cribrostomoides wiesneri (Parr 1950) – See Hermelin and Shimmield (1990, Pl. 1, Figs. 4-5). Test, up to 800 µm diameter, discoid, planispirally coiled. Agglutinated wall composed mainly of very fine quartz grains. Aperture oval to slit-like aerial opening at the base of the apertural face. One hundred live and dead specimens were found between 400 and 3400 m. Live specimens were very rare, 1 each found at 400 m and 3400 m. The majority of tests were dead and found at Station 12685#2 (700 m).

Labrospira sp.1 – See *Labrospira* sp.A1 of Maas (2000, Pl. 1, Fig. 1). Test, up to 500 µm diameter, discoid, planispirally enrolled. Agglutinated wall composed mainly of very fine quartz grains. Aperture oval to slit-like aerial opening slightly above the base of the apertural face. Twenty five dead specimens were found at Station 12685#2 (700 m).

Veleroninoides scitulus Brady, 1878 – See Jones (1994, Pl. 34, Figs.11-13). Test between 500 and 770 µm diameter, planispiral, evolute, with numerous low chambers in about two and a half whorls, periphery broadly rounded, margins slightly lobate, chambers much wider than high. Finely agglutinated wall, surface smoothly finished. Aperture forms a protruding slit, located slightly above the base of the final chamber. Three live and dead specimens were found at 12723#3 (1250 m).

Pyrgo depressa d'Orbigny, 1826 – See Jones (1994, Pl. 2, Figs. 16-17). Smooth compressed, round white porcelaneous test; margin thin and sharp. Aperture a long, narrow slit partly obscured by a narrow lower lip. Twenty two live and dead tests were found at 12723#3 (1250 m).

Triloculina tricarinata sensu Parker, Jones and Brady, 1865 – See Jones (1994, Pl. 3, Fig.17). Test about 700 µm long, distinctly triangular in end view, the three angles thickened and slightly produced or keeled. Two of the angles are formed by the last chamber, the third by the

free margin of the proceeding segment. Aperture triangular, with prominent tooth. Thirty seven live tests were found at Station 12708#5 (100 m).

Lenticulina aff. *iota* (Cushman, 1923) (Plate 3, Figure 1) – See Hermelin and Shimmield (1990, Pl. 2, Figs. 1-2). Test enrolled, planispiral, with relatively broad and low chambers that increase slowly in size as added. Sutures radial, slightly curved. Calcareous, hyaline wall with shiny smooth surface. Slightly produced radiate aperture at the end of last chamber. The slight difference between this species and *Lenticulina iota,* clearly illustrated in Jones (1994, Pl. 70, Figs. 4-6) is the absence of a pronounced keel at the edge of the test. Large number (1436) of live and dead specimens were found between 100 m and 1250 m Most live specimens were found at Station 12708#5 (100 m), while most dead tests were found at Station 12685#2 (700 m).

Saracenaria sp.1 – Test planispiral enrolled in the early stage, later flaring and tending to become rectilinear; triangular in section. Apertural face broad and flat, commonly with carinate margins and dorsal angle. Sutures curved and depressed. Calcareous hyaline wall with shiny smooth surface. Thirty live and dead specimens were found at Station 12695#5 (400 m).

Bolivina aff. *inflata* Heron-Allen and Earland, 1932 – Test ovoid to triangular in outline, slightly compressed. Chambers broad and low biserial throughout. Calcareous hyaline wall. Aperture forms a narrow loop at base of final chamber. Five live and dead specimens were found at Station 12713#3 (850 m).

Bolivina seminuda Cushman 1919 – See Hermelin and Shimmield (1990, Pl. 2, Fig. 8). Test elongate to triangular in outline, compressed. Chambers broad and low biserial throughout. Calcareous hyaline wall. Aperture a narrow loop at base of final chamber. Sixteen live specimens were found at Station 12708#5 (100 m). This species was also reported in very high abundances at 400 m of the Oman margin by Gooday et al. (2000).

Bulimina aculeata d'Orbigny, 1839 (Plate 4, Figures 1 and 2) – See Hermelin and Shimmield (1990, Pl. 2, Figs. 9 and 13). Test short, conical, triserial, slightly compressed on three sides, chambers somewhat inflated, the earlier ones bearing long slender spines, the later ones sometimes smooth, sometimes with short spines or slight protuberances. Calcareous hyaline wall. Aperture a loop extending upwards from the base of the last chamber. Ninety one live specimens were found at 12723#3 (1250 m).

Globobulimina affinis (d'Orbigny 1839) (Plate 4, Figure 3) – See Maas (2000, Pl. 2, Fig. 8). Test between 300-800 µm long and 200-500 µm wide, ovate with short and inflated chambers

and a distinctively pointed proximal end. Calcareous hyaline wall. One thousand, two hundred and fifty five live and dead specimens were found between 400 m and 1250 m, the majority of which were found at Station 12695#5 (400 m).

Globobulimina aff. *turgida* (Bailey 1951) **(**Plate 4, Figure 4) – I follow Maas (2000, Pl. 2, Fig. 7) in naming this species. Test between 300-600 µm long and 200-400 µm wide, ovate very slightly compressed with thin, transparent wall. Overlapping chambers, the final three chambers sometimes enveloping all earlier chambers. Calcareous hyaline wall. One thousand, one hundred and eighty six live and dead specimens were found between 400 m and 1250 m, the majority of which were found at Station 12695#5 (400 m).

Globobulimina turgida (Bailey 1951) (Plate 4, Figures 5 and 6). Test between 300-500 µm long and 200-300 µm wide, very similar to *Globobulimina turgida* Bailey 1951 with one main difference, the presence of spines at the base of test, opposite the aperture. The Arabian Sea specimens are essentially the same as *Globobulimina turgida* illustrated by Höglund (1947, Pl.21, Figs. 4 and 8). Calcareous hyaline wall. Six hundred and forty five live and dead specimens were found between 400 and 3400 m, the majority of which were found at Station 12685#2 (700 m).

Uvigerina peregrina Cushman, 1923 – See Hermelin and Shimmield (1990, Pl. 2, Fig. 12) and Maas (2000, Pl. 2, Fig. 4). Test about 600 µm long and 450 µm wide, elongate rounded in section, triserial, early chambers closely appressed, later ones inflated with keel-like ridges widely distributed. On later chambers, ridges break up into rows of spines. Aperture at end of short neck. Calcareous hyaline wall. Seven hundred and eighty live and dead specimens found across the OMZ (400 to 1250 m), but highest abundance of dead tests found at Station 12685#2 (700 m).

Uvigerina ex gr. *semiornata* d'Orbigny, 1846 (Plate 4, Figures 7 and 8) –The identification of this abundant species follows Maas (2000, Pl. 2 Figs. 1-3). Test between 300-500 long and 700-1000 µm wide, elongate rounded in section. Apertural neck located in depression. Calcareous hyaline wall. Eight hundred and sixty four live specimens and over 50,000 estimated dead tests found at Station 12708#5 (100 m).

Uvigerina sp.1 (Plate 4, Figure 9) – Test about 850 µm long and 550 µm wide, elongate rounded in section, triserial, early chambers closely appressed, later ones with widely-spaced keel-like ridges. Aperture depressed. Calcareous wall which is white when dried. Sixty live and dead specimens were found at Stations 12695#5 and 12713#3 (400 m and 850 m respectively), but most live specimens were found at 850 m.

Ammonia sp.1 – See Zobel (1973, Pl. 1, Figs. 4-5). Test biconvex with low trochospiral coil of 3 to 4 volutions, spiral side evolute, umbilical side involute. Calcareous hyaline test. Forty one live specimens were found at Station 12708#5 (100 m).

Cancris auriculus (Fichtel and Moll 1798) (Plate 4, Figures 2 and 3) – See Maas (2000, Pl. 2 Fig. 9). Test elongate ovate to auriculate in outline, lenticular in section, periphery angled to carinate, chambers increasing rapidly in breadth as added in a flaring trochospiral coil, sutures depressed, arched on the spiral side, nearly radial around the open umbilicus on the opposite side. Calcareous hyaline wall. One hundred and eighty four live and dead specimens found between 100 m and 700 m.

Chilostomella oolina Schwager, 1878 (Plate 3, Figure 4) – See Zobel (1973, Pl. 2, Figs. 36-37). Test about 500 µm long and 300 µm wide, oval, circular in section, planispiral and involute. Finely perforate, calcareous test with smooth surface. Aperture a narrow interiomarginal and equatorial slit. Twenty live and dead specimens were found at Station 12723#3 (1250 m).

Chilostomella ovoidea Reuss, 1850 – See Hermelin and Shimmield (1990, Pl. 3, Fig. 6). Test between 600-700 µm long and 300-500 µm wide, ovoid, circular in section, planispiral and involute. It differs from *Chilostomella oolina* in being fatter. Finely perforate, calcareous test with smooth surface. Aperture a narrow interiomarginal and equatorial slit. Twenty six live and dead specimens were found at Stations 12695#5 and 12723#3 (400 m and 1250 m respectively).

Ehrenbergina sp.1 – See Zobel (1973, Pl. 2, Fig. 23). Test about 600 µm long, biserial and enrolled but evolute, lenticular in section, ventral inner side flattened, lateral margins carinate to spinose. Calcareous, finely perforate wall with smooth surface. Aperture a curved elongate slit perpendicular to the base of the apertural face. Thirty five dead tests were found at Station 12723#3 (1250 m).

Hanzawaia concentrica Cushman, 1918 – See Zobel (1973, Pl.1, Figs. 44-45). Test about 500 µm diameter, trochospiral, planoconvex, whorls enlarging rapidly, chambers numerous, sutures thickened and strongly curved back at the periphery, convex side involute, flattened side partially evolute. Calcareous optically granular wall with moderately large pores. Twenty live specimens were found at Station 12708#5 (100 m) and 8 live and dead specimens were found at Station 12723#3 (1250 m).

Hyalinea baltica (Schroeter 1783) (Plate 3, Figure 5) – See Hermelin and Shimmield (1990, Pl. 2, Fig.15-16). Test about 500 µm diameter, discoidal, very low trochospiral to nearly

planispiral, semievolute on both sides. Calcareous finely perforate wall. Thirty live and dead specimens were found at Station 12723#3 (1250 m).

Hoeglundina elegans (d'Orbigny 1826) (Plate 3, Figures 6 and 7) – See Hermelin and Shimmield (1990, Pl. 2, Figs. 3-4). Test between 450 and 650 µm, trochospiral, close coiled, biconvex, chambers enlarging gradually. Calcareous, aragonitic, finely perforate wall with smooth surface. Full description in Loeblich and Tappan (1987). Four hundred and twenty eight live and dead specimens found between 700 m and 1250 m, but most live specimens were found at Station 12685#2 (700 m).

Plate 1. **1** *Lagenammina* sp.6, **2** and **3** *Psammosphaera* sp.5, **4** *Rhizammina* sp.2, **5** *Reophax scorpiurus*, **6** *Reophax* sp.1, **7** *Reophax* sp.9, **8** *Reophax* aff. *advenus*, **10** *Textularia pseudogramen*.

Plate 2. **1** *Bathysiphon* sp.3, **2-8** *Bathysiphon* sp.2.

Plate 3. **1** *Lenticulina* aff. *iota*, **2** and **3** *Cancris auriculus*, **4** *Chilostomella oolinea*, **5** *Hyalinea baltica*, **6** and **7** *Hoeglundina elegans*.

Plate 4. **1** and **2** *Bulimina aculeata*, **3** *Globobulimina affinis*, **4** *Globobulimina* aff. *turgida*, **5** and **6** *Globobulimina turgida*, **7** and **8** *Uvigerina* ex gr. *semiornata*, **9** *Uvigerina* sp.1.

PLATE 1

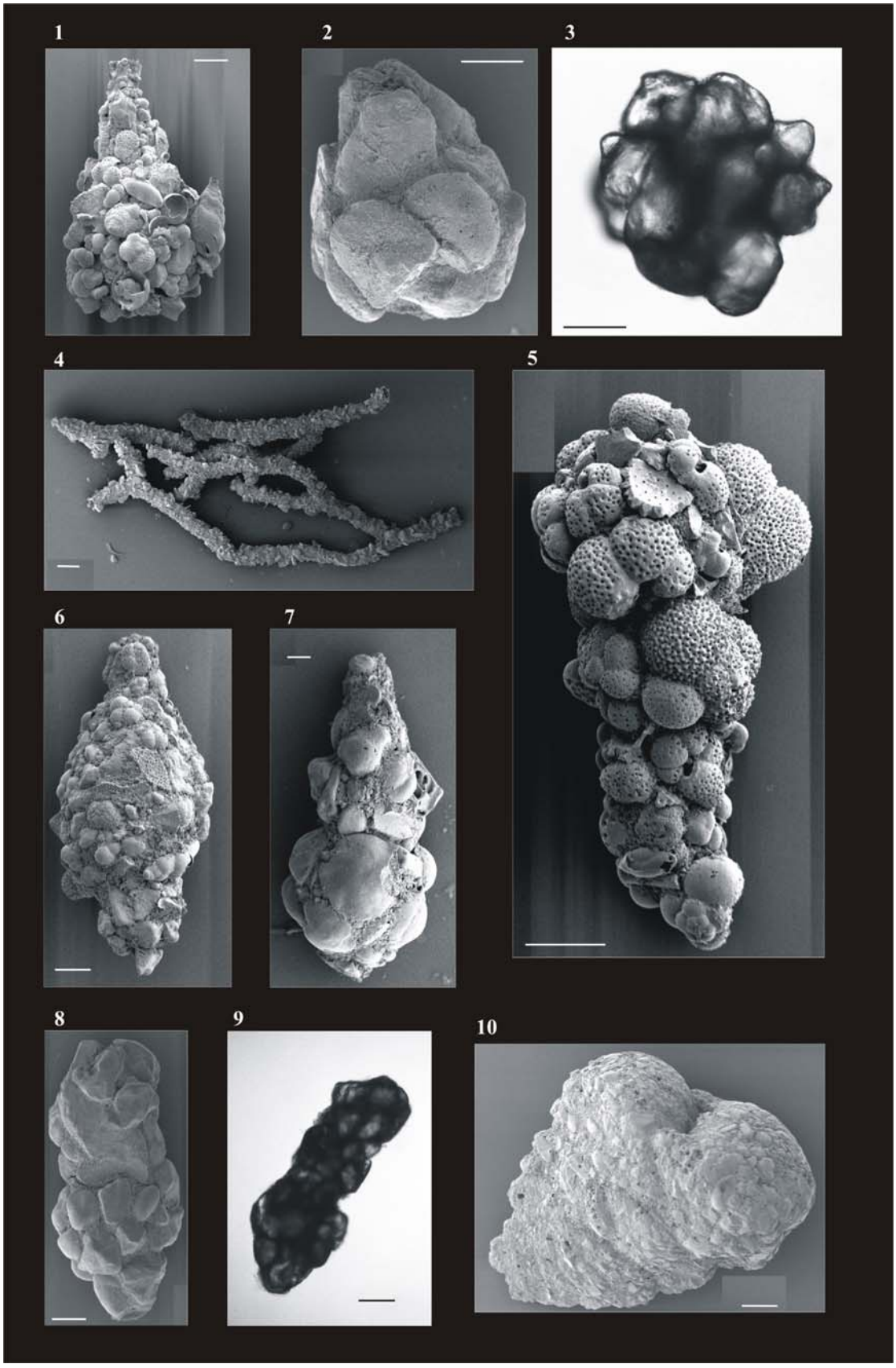

PLATE 2

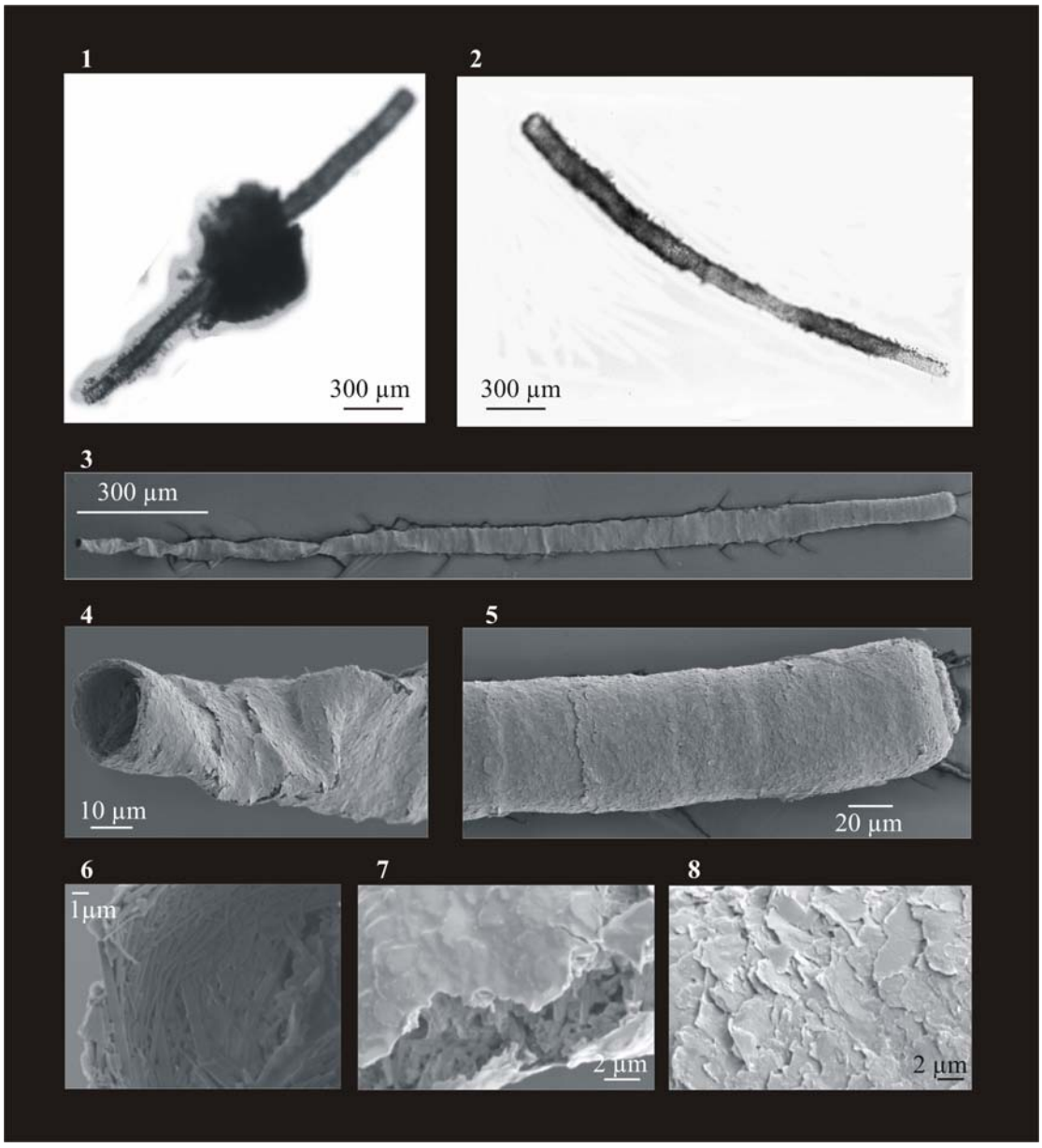

PLATE 3

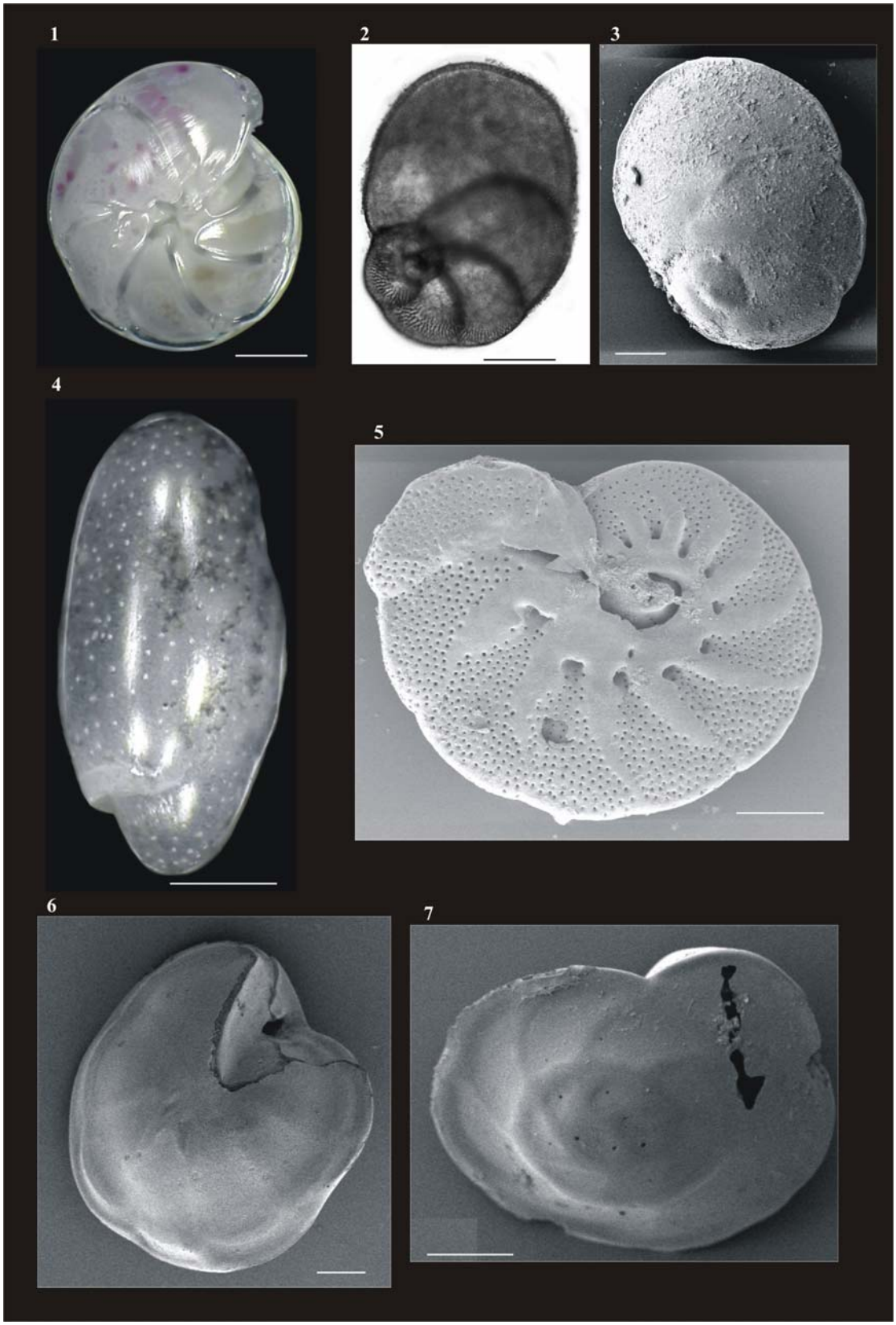

PLATE 4

Appendix C

Live and dead foraminifera (>300 μm) picked from samples collected during D211, from the 0-5 cm sediment layer. () number of fragment individuals.

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
	Allogromiida												
1	Allogromiid sp.1							2					
2	Allogromiid sp.2							3					
3	Allogromiid sp.3							1					
4	Allogromiid sp.4							1					
5	Allogromiid sp.6							1					
6	Allogromiid sp.7							1					
7	Allogromiid sp.8							1					
8	Allogromiid sp.9							1					
9	Allogromiid sp.10							1					
10	Allogromiid sp.13									5			
11	Allogromiid sp.14									3			
12	Allogromiid sp.15									1			
13	Allogromiid sp.16									1			
14	Allogromiid sp.17									1			
15	Allogromiid sp.18									1			
16	Allogromiid sp.19									1			
17	Allogromiid sp.20									(4)			
18	Allogromiid sp.21					5							
19	Allogromiid sp.22					1							
20	Allogromiid sp.23	17 (1)											
21	Allogromiid sp.24	4											
22	Allogromiid sp.25	4											
23	Allogromiid sp.27			2									
24	Allogromiid sp.28			1									
25	Allogromiid sp.29			1									
26	Allogromiid sp.30			1									
27	Allogromiid sp.31			1									
28	Allogromiid sp.32			1									
29	Allogromiid sp.33			1									
30	Allogromiid sp.34			1									
31	Allogromiid sp.35			1									
32	Allogromiid sp.36			1									
33	Allogromiid sp.37											2	
34	Allogromiid sp.38											1	
35	Allogromiid sp.39											1	
36	Allogromiid sp.40											1	
37	Allogromiid sp.41											1	
38	Allogromiid sp.45											1	
39	Allogromiid sp.46												
40	Allogromiid sp.47												
41	Allogromiid sp.48												
42	Allogromiid sp.49												
43	Allogromiid sp.50												

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
44	Allogromiid sp.51												
45	Allogromiid sp.52												
46	Allogromiid sp.53												
47	Allogromiid sp.54												
48	Allogromiid sp.55												
49	Allogromiid sp.56												
50	Allogromiid sp.57												
51	Allogromiid sp.58												
52	Allogromiid sp.59												
53	Allogromiid sp.60												
54	Allogromiid sp.61												
55	Allogromiid sp.62												
56	Allogromiid sp.63	4											
57	Allogromiid sp.64												
58	Allogromiid sp.65												
59	*Micrometula* sp.1			8									
60	*Nemogullmia longevariabilis*							6					
	Total	**29 (1)**		**19**		**6**		**18**		**13 (4)**		**7**	
	Astrorhizida: Astrorhizacea: Saccamminidae: Soft and hard-shelled												
61	Saccamminid sp.1							6					
62	Saccamminid sp.2							1					
63	Saccamminid sp.3							1					
64	Saccamminid sp.4							1					
65	Saccamminid sp.6									1			
66	Saccamminid sp.7									1			
67	Saccamminid sp.8									1			
68	Saccamminid sp.9	74		8	62								
69	Saccamminid sp.12												
70	Saccamminid sp.13												
71	Saccamminid sp.14												
72	Saccamminid sp.15												2
	Total	**74**		**8**	**57**	**0**		**9**		**3**		**0**	**2**
	Astrorhizida: Astrorhizacea: Saccamminidae: Lagenammina												
73	*Lagenammina* sp.1							16	12				
74	*Lagenammina* sp.2							10	20				
75	*Lagenammina* sp.3									9	16		
76	*Lagenammina* sp.4									2	2		
77	*Lagenammina* sp.6			15	5								
	Total			**15**				**26**	**32**	**11**	**18**		
	Astrorhizida: Astrorhizacea: Psammosphaeridae: spheres and domes												
78	*Psammosphaera fusca*									7	37		

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
79	*Psammosphaera* sp.1										1		
80	*Psammosphaera* sp.2									2	9		
81	*Paemmosphaera* sp.3	122											
82	*Psammosphaera* sp.4	4											
83	*Psammosphaera* sp.5	835	4748										
84	Very distinctive sphere											1	
85	Indeterminate sp.4										2		
86	Indeterminate sp. 7 – spheres and domes									13			
87	Indeterminate sp.8	4											
88	Indeterminate sp.12											1	
89	Indeterminate sp.13											1	
	Total	**965**	**4748**	**0**		**0**		**0**		**22**	**49**	**3**	
	Astrorhizida: Astrorhizacea: Bathysiphonidae												
90	*Bathysiphon* sp.1									3			
91	*Bathysiphon* sp.2	26		39		4	2		1				
92	*Bathysiphon* sp.3	22		23		1							
93	*Bathysiphon* sp.4											3	1
	Total	**48**		**62**		**5**	**2**	**0**	**1**	**3**		**3**	**1**
	Astrorhizida: Astrorhizacea: Hippocrepinacea: Hippocreppinidae: Hyperammina												
94	*Hyperammina friabilis*											(1)	
95	*Hyperammina* sp.1									1			
96	*Hyperammina* sp.2											(3)	
	Total	**0**		**0**		**0**		**0**		**1**		**0 (4)**	
	Astrorhizida: Komokiacean-like												
97	Chains sp.1											(17)	
98	*Crambis* sp.1											(1)	
99	Komokiacean									(10)			
100	*Reticulum* sp.1											(113)	
	Total	**0**		**0**		**0**		**0**		**(10)**		**(131)**	
	Other Tubes												
101	?*Pelosina* sp.1												
102	*Pelosina* sp.2					(6)				(9)			
103	*Rhizammina* sp.1											(5)	
104	*Rhizammina* sp.2											(50100)	
105	Tubes sp.1			(57)								(153)	
106	Tubes sp.2												
107	Tubes sp.3											(13)	
108	Indeterminate sp.3									(444)		(1)	
109	Indeterminate sp.5									(178)			
	Total	**0**		**(57)**		**(6)**		**0**		**(631)**		**(50272)**	
	Various Astrorhizida												
110	*Crithionina hispida*											1	
111	*Crithionina* sp.1											**1**	

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
112	"*Crithionina*" sp.2											7	
113	*Crithionina* sp.3											10	
114	*Crithionina* sp.4									1		4	2
115	*Hippocrepinella hirudinea*									3			
116	*Vanhoeffenella* sp.1											1	
117	*Vanhoeffenella* sp.2											1	
118	*Conqueria* sp.1									1			
119	Indeterminate sp.1									3	13		
120	Indeterminate sp.9											1	
121	Indeterminate sp.10											1	
122	Indeterminate sp.11											1	
123	Indeterminate sp.14											2	
	Total	**0**		**0**		**0**		**0**		**8**	**13**	**30**	**2**
	Lituolida: Ammodiscacea: Ammodiscidae												
124	*Ammodiscus cretaceous*								1		2		
	Total								**1**		**2**		
	Lituolida: Hormosinacea												
125	*Hormosina dentaliniformis*									3			
126	*Leptohalysis* sp.1			1				1	2		7		
127	*Reophax* aff. *advenus*	202	3588										
128	*Reophax horridus*											2	1
129	*Reophax scorpiurus*									9	53		
130	*Reophax spiculifer*									5			
131	*Reophax* sp.1							95	7	3	7		
132	*Reophax* sp.2								2				
133	*Reophax* sp.3							16	11	5			
134	*Reophax* sp.4							3	5		50		
135	*Reophax* sp.5							2					
136	*Reophax* sp.6									3	24		
137	*Reophax* sp.7									1	9		
138	*Reophax* sp.9	193											
139	*Reophax* sp.10	4											
140	*Reophax* sp.11			2									
141	*Reophax* sp.12											1	
142	*Reophax* sp.13											5	
143	*Reophax* sp.14											3	
144	*Reophax* sp.15												
145	*Reophax* sp.16												
146	*Reophax* sp.17												
147	*Reophax* sp.18	8											
	Total	**407**	**3588**	**3**		**0**		**117**	**27**	**29**	**150**	**11**	**1**
148	**Trochamminida: Trochomminacea**	**13**		**0**	**13**	**0**		**9**		**1**		**3 (3)**	
	Textulariida: Textulariacea												
149	*Karreriella bradyi*												1

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
150	*Martinottinella communis*											2	1
151	*Martinottinella* sp.2												
152	*Textularia pseudogramen*	136											
153	*Textularia* sp.1						1				9		
154	*Textularia* sp.2						1				3		
155	*Textularia* sp.3						1						
156	*Tritaxia* sp.1						24		1				
	Total	**136**		**0**		**0**	**27**	**0**	**1**	**0**	**12**	**2**	**2**
	Other MAF												
157	*Ammobaculites agglutinans*												2
158	*Ammoscalaria* sp.1				13					2	3		
159	*Cribrostomoides wiesneri*			1		1	118		1			1	
160	*Evolutinella* sp.1												
161	*Haplophragmoides* sp.1			1						1			
162	*Labrospira* sp.1						25				1		
163	*Recurvoides* sp.1									1			
164	*Veleroininoides scitulus*									1	2		
165	*Veleroninoides* sp.1												
166	Indeterminate sp.6										12		
	Total	**0**		**2**		**1**	**143**	**0**	**1**	**5**	**18**	**1**	**2**
	Miliolida												
167	Miliolida sp.1												
168	Miliolida sp.2												
169	Miliolida sp.3												
170	Miliolida sp.4												
171	Miliolida sp.5												
172	*Pyrgo depressa*									1	21	1	
173	*Pyrgo serrata*										2		
174	*Pyrgoella* sp.1											1	
175	*Sigmoilopsis* sp.1										7		
176	*Sigmoilopsis* sp.2											1	
177	*Spiroculina* sp.1	4											
178	*Triloculina tricarinata*	37											
	Total	**41**		**0**		**0**		**0**		**1**	**30**	**3**	
	Lagenida												
179	*Amphicoryna* sp.1	9											
180	*Astaculus crepidulus*						1						
181	*Dentalina* sp.2	1					1						
182	*Dentalina* sp.3			1	5								
183	*Hemirobulina* sp.1											1	
184	Lagenid sp.1										1		
185	Lagenid sp.2												1
186	Lagenid sp.3												1
187	Lagenid sp.4												1

	Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
	Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
	Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
188	*Lenticulina* aff. *iota*	77		6	167	8	813	10	361		2		
189	*Lenticulina* sp.2	9											
190	*Mesolenticulina* sp.1						1						
191	*Nodosaria* sp.1	8											
192	*Saracenaria* sp.1			4	26				1				
	Total	**104**		**11**	**198**	**8**	**816**	**10**	**362**	**0**	**3**	**1**	**3**
	Buliminida												
193	*Bolivina albatrossi*	17											
194	*Bolivina* aff. *inflata*							3	2				
195	*Bolivina* sp.1												
196	*Bolivina seminuda*	16											
197	*Brizalina* sp.1					1							
198	*Bulimina aculeata*									9	83		
199	*Ehrenbergina* sp.1										35		
200	*Globobulimina affinis*			10	996	9	120	6	71	3	30		
221	*Globobulimina* aff. *turgida*			21	847	3	185	8	99	3	6	4	10
222	*Globobulimina turgida*					5	510		125		5		
223	*Globobulimina* sp.1										1		
224	*Globobulimina* sp.2						1						
225	*Globobulimina* sp.3											4	2
226	*Uvigerina peregrina*			9	38		688	11	32		2		
227	*Uvigerina* ex gr. *semiornata*	864	50000	2									
228	*Uvigerina* sp.1				8			12	40				
229	*Uvigerina* sp.2					1	2			1	1		
230	*Uvigerina* sp.3												21
	Total	**897**		**42**	**1889**	**19**	**1506**	**40**	**369**	**16**	**163**	**8**	**33**
	Rotaliida												
231	*Ammonia* sp.1	41											
232	*Cancris auriculus*	80		19	4	2	3	22	54				
233	*Chilostomella oolina*									5	15		
234	*Chilostomella ovoidea*			1	13					2	10		
235	*Cibicidoides* sp.1												1
236	*Gyroidina* sp.1										14		
237	*Hanzawaia concentrica*	23								2	6		
238	*Hyalinea baltica*									4	26		
239	*Melonis affinis*									1	2		
240	*Nonionella* sp.1							4	1	1			
241	*Oridorsalis* sp.1									1	14		
242	*Planulina* sp.1										5		
243	*Pullenia* sp.1										1		
244	Calcareous foram												
	Total	**144**		**20**	**17**	**2**	**3**	**26**	**55**	**16**	**93**	**0**	**1**
	Robertiniida												
245	*Hoeglundina elegans*					23	217	1	184		3		

Site	100-m		400-m		700-m		850-m		1250-m		3400-m	
Station	12708#5		12695#5		12682#5		12713#3		12723#3		12687#3	
Sediment layer	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Total	0		0		23	217	1	184	0	3	0	
Grand Total of Specimens	2858 (1)	58336	182 (57)	2190	64 (6)	2714	263 (129)	1033	129 (645)	554	72 (50410)	47