Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas

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Abstract

Previous work has shown that some foraminiferal species thrive in organically enriched, oxygen-depleted environments. Here, we compare 'live' (stained) faunas in multicorer samples (0–1 cm layer) obtained at two sites on the Oman margin, one located at 412 m within the oxygen minimum zone (OMZ) ($O_2 = 0.13 \, \text{ml} \, l^{-1}$), the other located at 3350 m, well below the main OMZ ($O_2 \sim 3.00 \, \text{ml} \, l^{-1}$). While earlier studies have focused on the hard-shelled (predominantly calcareous) foraminifera, we consider complete stained assemblages, including poorly known, soft-shelled, monothalamous forms. Densities at the 412-m site were much higher (16,107 individuals.10 cm^{-2} in the > 63-µm fraction) than at the 3350-m site (625 indiv.10 cm^{-2}). Species richness (E(S$_{100}$)), diversity (H′, Fishers Alpha index) and evenness (J′) were much lower, and dominance (R1D) was higher, at 412 m compared with 3350 m. At 412 m, small calcareous foraminifera predominated and soft-shelled allogromiids and sacamminids were a minor faunal element. At 3350 m, calcareous individuals were much less common and allogromiids and sacamminids formed a substantial component of the fauna. There were also strong contrasts between the foraminiferal macrofauna (> 300-µm fraction) at these two sites; relatively small species of *Bathysiphon*, *Globobulimina* and *Lagenammina* dominated at 412 m, very large, tubular, agglutinated species of *Bathysiphon*, *Hyperammina*, *Rhabdammina* and *Saccorhiza* were important at 3350 m. Our observations suggest that, because they contain

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fewer soft-shelled and agglutinated foraminifera, a smaller proportion of bathyal, low-oxygen faunas is lost during fossilization compared to faunas from well-oxygenated environments. Trends among foraminifera (> 63 μm fraction) in the Santa Barbara Basin (590 and 610 m depth; $O_2 = 0.05$ and 0.15 ml l^{-1} respectively), and macrofaunal foraminifera (> 300 μm) on the Peru margin (300–1250 m depth; $O_2 = 0.02$–1.60 ml l^{-1}), matched those observed on the Oman margin. In particular, soft-shelled monothalamous taxa were rare and large agglutinated taxa were absent in the most oxygen-depleted (< 0.20 ml l^{-1}) stations.

Foraminifera often outnumber metazoans (both meiofaunal and macrofaunal) in bathyal oxygen-depleted settings. However, although phylogenetically distant, foraminifera and metazoans exhibit similar population responses to oxygen depletion; species diversity decreases, dominance increases, and the relative abundance of the major taxa changes. The foraminiferal macrofauna (> 300 μm) were 5 times more abundant than the metazoan macrofauna at 412 m on the Oman margin but 16 times more abundant at the 3350 m site. Among the meiofauna (63–300 μm), the trend was reversed; foraminifera were 17 times more abundant than metazoan taxa at 412 m but only 1.4 times more abundant at 3350 m. An abundance of food combined with oxygen levels which are not depressed sufficiently to eliminate the more tolerant taxa, probably explains why foraminifera and macrofaunal metazoans flourished at the 412-m site, perhaps to the detriment of the metazoan meiofauna.

1. Introduction

Persistent oxygen depletion of bottom water and sediment pore water occurs in certain regions, mainly associated with areas of upwelling or restricted circulation (Diaz and Rosenberg, 1995). Oxygen minimum zones (OMZs) are long-term oceanographic features that lead to the development of strong oxygen gradients where they impinge on the seafloor. Water in silled basins and fjords also may become depleted in oxygen over long time periods due to poor circulation and enrichment with organic matter derived from natural sources or pollution (Alve, 1995a,b; Phleger and Soutar, 1973). Other basins are periodically flushed, sometimes seasonally, with oxygenated water leading to a cycle of oxygen depletion and renewal (e.g. Bernhard and Reimers, 1991). River inputs of fine-grained sediments rich in organic matter also may lead to the periodic development of low-oxygen or anoxic conditions on continental shelves (Murrell and Fleeger, 1989), although the distribution of these regions is strongly influenced by hydrographic and other conditions (van der Zwaan and Jorissen, 1991).

The importance of foraminifera in oxygen-deficient benthic communities has prompted reviews by Sen Gupta and Machain-Castillo (1993), Bernhard (1996) and Bernhard and Sen Gupta (2000). Studies on low-oxygen foraminifera have focused mainly on the following topics: taxonomic composition of assemblages, adaptive morphology, life-history strategies ('opportunism') and cellular ultrastructure, and experimental studies involving foraminiferal responses to oxygen depletion, anoxia and hydrogen sulphide. Most of these studies have concerned the fossilizable (calcareous and multilocular agglutinated) component of the fauna. With the exception of some recent experimental work (Bernhard and Alve, 1996; Moodley et al., 1997,1998), little is known about the response of morphologically simple foraminifera

(monothalamous allogromiids and saccamminids and tubular agglutinated taxa) to oxygen depletion. Moreover, very few studies specifically address the structure and diversity of complete (i.e. including all taxonomic components) rose Bengal-stained ('live') assemblages, or compare foraminiferal and metazoan abundance and diversity.

We focus here on these rarely addressed aspects of benthic foraminiferal faunas in low-oxygen habitats. We consider data from two contrasting sites on the Oman margin. One site is located at 412 m depth in the core of the OMZ and is permanently dysoxic. The other is located below the main OMZ at a depth of 3350 m and is reasonably well oxygenated. Our principle aim is to provide a detailed description of the structure of complete stained foraminiferal assemblages at the two sites. We then use these faunal data (1) to compare and contrast trends with respect to oxygen and organic enrichment gradients among foraminifera and metazoans (both meiofauna and macrofauna) and (2) to compare the diversity and taxonomic composition of the Oman margin assemblages with those of faunas from the Santa Barbara Basin on the California Borderland, where oxygen concentrations fluctuate according to the hydrographic conditions (Bernhard and Reimers, 1989).

Aspects of the metazoan macrofauna from the shallower Oman margin site were described by Levin et al. (1997). Metazoan macrofauna from both sites are treated by Levin et al. (2000) and nematode abundances by Cook et al. (2000). Herring et al. (1998) described the hydrography and midwater biology of the area on the basis of observations made during August 1994. Gooday et al. (1997,1998) presented some preliminary data on large agglutinated foraminifera and species diversity from the deepest site (around 3400 m) sampled during *Discovery* Cruise 211. The only other previous studies of modern benthic foraminifera from the Oman margin are those of Stubbings (1939) and Hermelin and Shimmield (1990). Burmistrova (1969,1976,1977), Zobel (1973), Gupta (1994), Jannink et al. (1998) and den Dulk et al. (1998) provide accounts of Recent or Holocene foraminifera in other parts of the Arabian Sea.

2. Materials and methods

2.1. Sampling

The Oman margin samples were collected during R.R.S. *Discovery* Cruise 211 (October 9 to November 11 1994) using a Barnett–Watson multiple corer equipped with core tubes of 25.5 cm^2 cross-sectional area. As soon as possible after recovery, the cores were taken to a cold room adjusted to the ambient bottom-water temperature (Table 1). A small amount of the 'topmost' sediment (< 1 ml) was removed using a plastic pipette in order to sample the fauna living at the sediment-water interface. The core was then sliced into 1 cm thick layers down to 10 cm depth. All samples were preserved in 10% formalin ($= 4$% formaldehyde solution) buffered with sodium borate (borax). The top 1 cm and 'topmost' sediment material from one core taken at each site were examined for this study.

In the laboratory, the sediment was sieved on 300-, 125- and 63-μm screens, stained on the sieve for several hours using Rose Bengal, and sorted in water under a

Table 1
Environmental data for the Oman margin study sites, summarised from Levin et al. (2000)

Property	Station 12692	Station 12687
Depth (m)	412 m	3350
Temperature (°C)	13–14	1.7
Oxygen (ml l^{-1})	0.13	~ 3.00
%TOC	4.9	2.71
C : N ratio	8.5	9.4
Mean grain size	42.2	42.8
%CaCO$_3$	55.0	39.5
Surface (0–0.5 cm) pigments (μg g^{-1})	770	185

binocular microscope for stained benthic foraminifera. In the case of the 63–125-μm fraction, the residue was split using a plankton splitter and a 1/16th subsample sorted completely for foraminifera. Some well-stained specimens were mounted dry on micropaleontological slides to provide taxonomic reference material. However, most were placed in glycerol in a glass cavity slide to enable the stained contents to be examined in detail under a compound microscope. Species differed in their staining characteristics. Some consistently stained brightly while others included both brightly stained and less well-stained specimens. In all cases, only the brightly stained tests were regarded as 'live'. Metazoan meiofauna also were removed from the sieve residues and counted. Data for metazoan macrofauna were obtained from boxcore samples collected nearby. Details of metazoan macrofaunal sampling and sample processing methods are given in Levin et al. (2000).

Samples were taken in the Santa Barbara Basin (SBB) using a Soutar-type box corer which was subsampled using a cut-off syringe, either 1.9 cm (Station SBB298E) or 2.6 cm (Station SBB298S) diameter. The top 1 cm of each subcore was removed and fixed in 3% glutaraldehyde in 0.1 M sodium cacodylate buffer. The sample was placed in a graduated cylinder, agitated, and a subsample drawn off with a plastic pipette. Both the subsample and the original sample were allowed to settle in graduated cylinders for 1 h and their volumes recorded. The subsample was stained in Rose Bengal for 12 h, sieved over a 63-μm screen, and sorted wet for all stained benthic foraminifera. The volume of material sorted was 1.215 cm^3 (out of an original volume of 2.84 cm^3) from Station SBB298E and 1.99 cm^3 (out of an original volume of 5.3 cm^3) from Station SBB298S. A subsample from Station SBB298S was also sieved over a 125-μm screen.

Rarefaction curves and diversity indices (H' log$_{10}$, J' log$_{10}$, Fisher alpha) were calculated using the 'BioDiversity' programme (© Natural History Museum, London/Scottish Association of Marine Sciences).

2.2. Study sites

The 412-m site (*Discovery* Station 12692 # 4; 19°22.07′N, 58°15.43′E) was situated close to the core of the OMZ. The 3350-m site (*Discovery* Station 12687 # 8;

18°59.33′N, 58°59.09′E) was situated well below the lower OMZ boundary, located at approximately 1000 m (Levin et al., 2000). The horizontal distance between the two sites was about 87 km.

Environmental data for these localities are summarised in Table 1. The sediment at 412 m was a soupy mud rich in organic matter, with little evidence of bioturbation although without obvious laminations (Smith et al., 2000). Oxygen concentrations were much lower at depths around 400 m (0.13 ml l^{-1}) than at 3350 m ($\sim 3.00 \text{ ml l}^{-1}$) (Levin et al., 2000). The C : N ratios and mean sediment grain size were similar between sites. A surface layer of phytodetritus was present on multicorer samples from the deeper station. Percent TOC and surface pigment concentrations were all higher at 412 m than at 3350 m, suggesting more enriched conditions at the shallower site. However, considering the bathymetric depth, both %TOC and pigment concentrations were surprisingly high at 3350 m (Gooday et al., 1998, Table 1 therein). This probably reflects the fact that phytoplankton pigment concentrations in the upper water column are broadly similar above the two sites (Banse and McClain, 1986, Fig. 4). Thus, the greater bathymetric depth and distance from land of the deeper site (Lee et al., 1998), rather than contrasts in surface primary productivity, seem to be responsible for the differences in TOC and pigment concentrations shown in Table 1.

Cores from the central SBB (Station 298E; 34°13.48′N; 120°02.93′W; 590 m depth) consisted of fine-grained mud with well preserved laminations and organic carbon values of 5–8% (Reimers et al., 1990). Bottom-water oxygen concentrations were approximately 0.05 ml l^{-1} and samples were devoid of animals larger than about 1 cm. Station 298S off Palos Verde (33°46.69′N; 118°32.49′W; 610 m depth) was characterised by rather coarser-grained sediments (silty mud), bottom-water oxygen concentrations of 0.15 ml l^{-1}, and occasional ophiuroids. Oxygen concentrations were measured using microwinkler analysis (Broenkow and Cline, 1969) in water collected in Niskin bottles attached to the frame of the corer.

2.3. Terminology and taxonomic notes

There is no consistent, universally accepted terminology for bottom-water oxygen concentrations (Tyson and Pearson, 1991). Here, we employ the terms oxic ($> 1.00 \text{ ml O}_2 \text{ l}^{-1}$), dysoxic ($0.10$–$1.00 \text{ ml O}_2 \text{ l}^{-1}$) and microxic ($< 0.10 \text{ ml O}_2 \text{ l}^{-1}$; with or without reducing conditions) (Bernhard and Sen Gupta, 2000). Oxygen depletion is used as a general term for concentrations $< 1.00 \text{ ml l}^{-1}$. Most macroinfaunal animals have some direct contact with the overlying bottom water. However, we recognise that oxygen concentrations within the sediments will be lower than bottom-water values and may also fluctuate spatially and temporally. The amount of oxygen available to meiofaunal organisms living below the sediment/water interface is therefore very difficult to measure accurately and, in any case, will change as the organisms move around within the sediments (Moodley et al., 1998). Hence, we use the above-mentioned terms to characterise benthic habitats and not the microenvironments in which individual foraminifers reside.

The two most abundant species at 412 m are problematic. The top-ranked species is a slender form resembling *Bolivina seminuda* Cushman 1911 (see Barmawidjaja et al.,

1992, p. 2, Figs. 1–4). The second-ranked species, while closely similar, has more inflated later chambers and resembles *Bolivina inflata* Heron-Allen and Earland 1913 (see Todd and Brönnimann, 1957, p. 8, Fig. 32–34). We recognise that *B. seminuda* exhibits a continuous range of variation with *B. dilatata* Reuss. However, the form that we identify as *B. inflata* has more clearly inflated chambers than illustrations of *B. dilatata* given by Barmawidjaja et al. (1992) and Jannink et al. (1998, p. 1, Fig. 1). We regard *B. inflata* and *B. seminuda* as distinct species in our material, although their taxonomic status merits further study.

Species are classified into higher taxa according to the system of Loeblich and Tappan (1987). The sub-order Rotaliina includes buliminid and bolivinid genera.

3. Results

3.1. Abundance

Stained foraminiferal densities in the upper 1 cm of sediment were different at the two sites. In the > 300-μm fraction (i.e. the macrofauna), foraminifera were 1.5 times more numerous at the 412-m site (80 individuals.$10\,cm^{-2}$) compared to the 3350-m site (52 indiv.$10\,cm^{-2}$). The differential increased when finer sieve fractions were considered. In the > 125-μm fraction (125–300 plus > 300 μm), foraminifera were 7.5 times more numerous at 412 m (2457 indiv. $10\,cm^{-2}$) than at 3350 m (342 indiv. $10\,cm^{-2}$), while in the > 63-μm fraction (63–125 plus 125–300 plus > 300 μm), densities were about 25 times higher at the 412-m site (16,107 indiv. $10\,cm^{-2}$; estimated from a 1/16th split) than at the 3350-m site (625 indiv. $10\,cm^{-2}$) (Table 2).

These density values include foraminifera extracted from the 'topmost sediment' and associated phytodetrital aggregates. The topmost sediment (volume 0.65 ml) from the 412-m core was extremely rich in stained specimens. Compared to the remainder of the 0–1 cm layer, it yielded 2.9 times (> 125 μm) and about 3.7 times (> 63 μm) more foraminifera, when numbers were normalised to the same volume (Table 2). At 3350 m, there was no clear concentration of stained foraminifera in the > 125-μm fraction of topmost sediment, but smaller specimens (those in the > 63-μm fraction) were about 1.7 times more abundant in the surface material than in the 0–1 cm layer. Phytodetrital aggregates present in the 412-m core contained 33 stained individuals ($= 13$ indiv. $10\,cm^2$). Only three individuals were directly associated with the phytodetritus present in the 3350-m core. In both cases the amount of phytodetritus present was very small (< 0.1 ml).

3.2. Taxonomic composition

Hyaline calcareous foraminifera (rotaliids) dominated the stained fauna at 412 m. Their dominance was particularly evident in the > 63-μm fraction where 85% of specimens were rotaliids compared to about 70% in the > 125-μm fraction (Table 3). The only other taxa (all but one non-calcareous) representing $> 1\%$ of the assemblage (> 125- and > 63-μm fractions) were allogromiids, bathysiphonids

Table 2
Abundance of stained foraminifera (individual per 10 cm²) in macrofaunal (> 300 μm) and meiofaunal (63–125 μm + 125–300 μm) size ranges and in different parts of the sample. Numbers are indiv.10 cm⁻², calculated from numbers per core (25.5 cm²).

	Station 12695 (412m)				Station 12687 (3350m)			
	0–1 cm	Topmost sediment	Phytodetritus	Total	0–1 cm	Topmost sediment	Phytodet.	Total
Volume	24.35 cm³	0.65 cm³	v. small	25.0 cm³	25.75 cm³	~ 1 ml	v. small	26.75 cm²
Foraminifera								
Attached	0	0		0	13 (2.2%)	0		13 (2.1%)
Total >300 μm	**65 (0.45%)**	**600 (1.09%)**		**80 (0.5%)**	**49 (8.4%)**	**90 (9.1%)**		**52 (8.3%)**
125–300 μm	5836 (15.9%)	6460 (11.7%)		2453 (15.2%)	269 (45.9%)	220 (22.2%)		277 (44.3%)
Total >125 μm	**2465**	**7059**		**2533**	**330**	**310**		**342**
63–125 μm	12,235 (83.9%)[a]	47,908 (87.2%)		13,457 (83.5%)	256 (43.7%)	680 (68.6%)		283 (45.3%)
Total >63 μm	**14,700**	**54,967**	**13**	**16,107**	**586**	**990**	**1**	**625**
Metazoans								
Total >300 μm	**3 (0.32%)**	**16 (3.5%)**		**4 (0.42%)**	**11 (2.2%)**	**2 (6.5%)**		**13 (2.5%)**
125–300 μm	368 (39.6%)	16 (3.5%)		368 (39.1%)	218 (44.1%)	11 (35.5%)		229 (43.7%)
Total >125 μm	**371**	**32**		**372**	**228**	**13**		**241**
63–125 μm	558 (60.1%)[a]	428 (92.6%)		569 (60.5%)	265 (53.6%)	18 (58.1%)		283 (54.0%)
Total > 63 μm	**929**	**462**	**0**	**940**	**494**	**31**	**0**	**524**

[a]Estimate based on complete sort of 1/16th of 63–125 μm fraction.

Table 3
Percentage abundance of major groups at the two Oman margin stations and Santa Barabara Basin (SBB). TS = 'topmost sediment'; MAF = multilocular agglutinated foraminifera. The > 63 µm (i.e. 63–125 µm + > 125 µm fractions) data from Station 12692 (0–1 cm layer) are based on a 1/16th split of the 63–125 µm fraction.

Station	12687 Oman margin 3350 m − 3.00		12692 Oman margin 412 m 0.13				298E SBB 590 m 0.05	298S SBB 610 m 0.15	
Bathymetric depth O$_2$ (ml.l^{-1})									
Size fraction	> 63 µm	> 125 µm	0–1 cm > 63 µm	0–1 cm > 125 µm	TS > 63 µm	TS > 125 µm	> 63 µm	> 63 µm	> 125 µm
Allogromiina	22.6	16.1	0.88	2.77	0.39	1.69	0	1.18	6.22
Astrorhizacea:									
Saccamminidae:									
Soft-shelled	23.2	18.9	0.09	0.23	0.22	0	1.39	0.29	0.96
Lagenammina	5.93	5.48	0.09	3.79	0.48	3.59	0	0	0
Psammosphaeridae:									
Spheres and domes	7.12	11.8	0.01	0.08	0.03	0.21	0	0.59	0
Bathysiphonidae	1.06	1.97	1.09	5.55	1.96	10.8	0	0	0
Other tubes	2.12	3.95		0	0	0	0	0	0
Hyperamminacea	4.81	4.90	0.30	0.05	0.11	0	0	0	0
Komokiacean-like	1.31	2.57	<0.01	0.03	0	0	0	0	0
Ammodiscacea	0.50	0	0.15	0.05	0	0	0	0	0
Agglutinated chains	1.12	1.98	0	0	0	0	0	0	0
Hormosinacea	16.4	22.4	0.01	3.59	3.11	2.11	0	18.0	21.1
Trochamminacea	3.50	2.22	6.00	11.1	12.4	30.9	0	1.77	2.39
Spiroplectamminacea	0.06	0	1.87	0.86	4.71	0.63	6.69	0	0
Textulariacea	0.31	0	1.94	1.01	0.52	0.63	0	3.53	13.9
Other MAF	0.06	0.21	0	0.01	0	1.48	0	3.83	2.39
Miliolina	1.87	1.17	0	0	0	0.63	0	0.29	0.48
Lagenina	0.69	0.35	0	0	0.03	0.21	0	0.29	0
Rotaliina	4.18	1.17	84.9	70.7	76.4	49.0	91.9	70.2	52.6
Other taxa	2.29	3.97	0	0	0	0	0	0	0
Total specimens	1604	861	33,057	6487	3566	473	866	339	209

(*Bathysiphon* spp.), rigid saccamminids (*Lagenammina* spp.), hormosinaceans (almost entirely *Leptohalysis* spp.), trochamminaceans, spiroplectamminaceans, textularia-ceans and lagenids (mainly *Lenticulina*). The topmost sediment at this site yielded a disproportionately large number of trochamminaceans and bathysiphonids com-pared to the 0–1 cm layer (Table 3).

In contrast, hyaline calcareous foraminifera (lagenids and rotaliids), trocham-minaceans and spiroplectamminaceans were rare in the 125- and > 63-μm frac-tions at the 3350-m site while all other taxa were more abundant than at 412 m. Allogromiids, soft-shelled saccamminids and hormosinaceans (mainly *Reophax* spp.) were most frequent and rigid agglutinated spheres and domes, bathysiphonid and other agglutinated tubes, rigid saccamminids (*Lagenammina* spp.) and hippo-crepinaceans (tiny *Hyperammina* spp.) were also common, again in both size fractions.

At the 412-m site, more than half of the 10 most abundant species in both the > 63-and > 125-μm fractions (total sample, i.e. 0–1 cm layer and topmost sediment combined) were rotaliids (Table 4). The top-ranked species was *Bolivina seminuda*. Species abundances in the topmost sediment (> 63 μm) were rather different from those in the total sample, suggesting that some species are concentrated close to the sediment–water interface. In particular, *Bolivina inflata* was ranked first in the top-most sediment and a tiny agglutinated species, *Morulaeplecta* sp., was substantially more abundant (3.89%) in this layer than in the 0–1 cm layer as a whole (0.93%). At the 3350-m site, only one calcareous species (*Epistominella exigua*) appeared among the top ten (> 63-μm fraction only) (Table 4). Most of the remaining species belonged to a variety of agglutinated taxa. A species of the hormosinacean genus *Leptohalysis* sp. was ranked first in both residues.

3.3. Diversity and dominance

Sixty-four unfragmented species were recognised in the > 125-μm fraction at 412 m. About 5000 specimens removed from the 63–125-μm fraction (topmost sedi-ment and 1/16th split of 0–1 cm sample) yielded only six additional species. The 3400-m site was more speciose with 158 unfragmented species recognised in the > 125-μm fraction and 208 in the > 63-μm fraction. Species richness measured by rarefaction ($E(S_{100})$) was 23.9 at 412 m and 58.7 at 3350 m (> 125-μm fraction). Rarefaction curves (Fig. 1) confirm these strong differences. Dominance (R1D) was substantially higher at 412 m (27.0%) compared to 3350 m (6.8%). It is even higher (44.1%) in the > 63-μm fraction of the topmost sediment from the shallower site.

The 412-m assemblage (> 125-μm fraction; 0–1 cm layer) yielded a Shannon–Wiener Information index (H') of 1.228, Fisher alpha index of 9.28, and Shannon evenness measure (J') of 0.69 (Table 5). We have not incorporated data from the 63–125-μm residue of this sample into diversity calculation since only a subsample was sorted. However, diversity measures for the > 63-μm fraction of the topmost sediment were consistently lower than for the 0–1 cm layer (Table 5). Corresponding values for the 3350-m assemblage (> 125-μm fraction) were as follows: $H' = 1.939$; Fisher Alpha index $= 60.97$; $J' = 0.87$.

Table 4
Percentage abundance of top ten species in different size fraction at two sites on the Oman margin. "Total" refers to 0–1 cm layer and topmost sediment combined. TS = topmost sediment, SWS = Soft-walled saccamminid. Major taxa are identified as follows: A = Allogromiida; He = Hemisphaeramminidae; Ho = Hormosinacea; L = Lageniina; P = Psammosphaeridae; R = Rotaliina; Sp = Spiroplectamminacea; Sr = Saccamminidae rigid-walled; Ss = Saccamminidae soft-walled; Te = Textulariacea; Tr = Trochamminiacea. *Trochammina* sp. 1 (412-m site) may be conspecific with *Trochammina pacifica* Cushman of Bernhard et al. (1997) and *Trochammina* sp. of Kaminski et al. (1995).

12695 # 2 (412 m)

TS > 63 µm			Total > 125 µm			Total > 63 µm		
B. inflata	R	38.1	*Bolivina seminuda*	R.	24.2	*Bolivina seminuda*	R	43.8
Bolivina seminuda	R	18.4	*B. inflata*	R	8.47	*B. inflata*	R	20.6
Trochammina sp. 1	Tr	9.27	*Trochammina* sp. 1	Tr	7.96	*Bulimina* sp.	R	7.36
?Morulaeplecta sp.	Sp	3.89	*Bulimina* sp.	R	5.22	*Trochammina* sp. 1	Tr	4.79
Bulimina sp.	R	3.83	*Suggrunda* sp.	R	5.22	*?Fursenkoina* sp.	R	4.51
Leptohalysis sp. 1	Ho	2.66	*Nonionella* sp.	R	5.08	*Chilost. ovoidea*	R	2.52
?Fursenkoina sp.	R	2.44	*Bolivina* sp. 1	R	4.14	*Nonionella* sp.	R	1.57
Lenticulina	N	2.03	*Leptohalysis* sp. 1	Ho	3.02	*?Textularia*	Te	1.57
Suggrunda sp.	R	1.95	*Bathysiphon* sp. 2	A	2.94	*Leptohalysis* sp. 1	Ho	1.06
Uvigerina peregrina	R	1.84	*Chilostomella ovoidea*	R	2.47	*Spiroplectammina*	Sp	0.88

12687 # 8 (3350 m)

Total > 125 µm			Total > 63 µm		
Leptohalysis sp. 2	Ho	6.79	*Leptohalysis* sp. 2	Ho	5.30
Lagenammina sp. 1	Sl	4.70	*Lagenammina* sp. 1	Sl	4.34
Reophax sp. 2	Ho	3.52	SWS sp. 1	Ss	4.27
SWS sp. 1	Ss	3.26	Allogromiid sp. 1	A	4.27
Indet. psammosph.	P	3.00	'*Nodellum*' sp.	A	2.72
Agglut. tube	Indet.	2.74	*Reophax* sp.1	Ho	2.28
R. aff. *scorpiurus*	Ho	2.74	*Reophax* sp.2	Ho	1.99
Reophax sp. 3	Ho	2.61	Allogromiid sp. 2	A	1.99
Crithionina sp.	He	2.48	*Epistominella exigua*	R	1.84
R. aff. *pilulifera*	Ho	2.09	*R.* aff. *scorpiurus*	Ho	1.77

3.4. Population size structure

The foraminiferal macrofauna (> 300 µm) made up a smaller proportion of all foraminifera at 412 m than at 3350 m. Only 0.5% of the total fauna (> 63 µm) was retained on a 300-µm sieve at 412 m compared with 8.3% at the 3350-m site (Table 2). Maximum test dimensions confirm this shift (Fig. 2). Although tests had a similar size range at the two sites, 92.9% were < 500 µm at 412 m compared with 66.3% at the deeper site. On the other hand, maximum dimensions peaked around 120 µm at 3350 m but around 160 µm at 412 m, reflecting the more elongate test morphologies of many foraminifera within the OMZ.
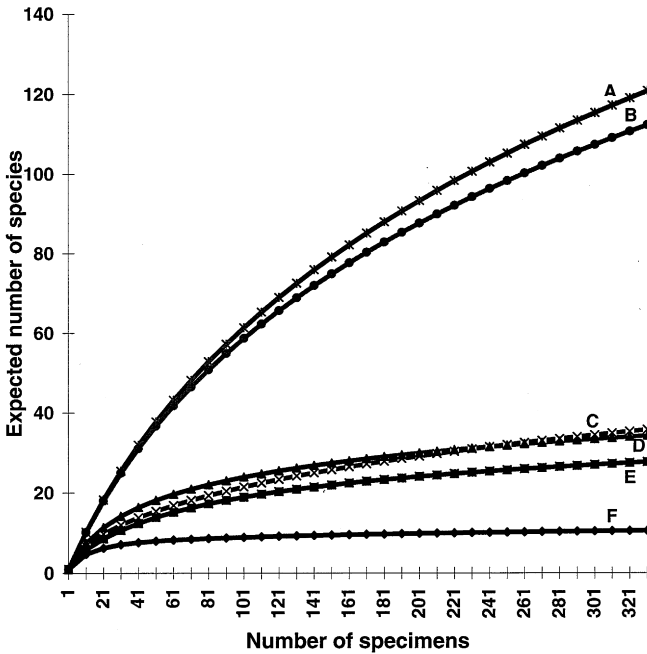
Fig. 1. Rarefaction curves for foraminifera from the Oman margin and Santa Barbara Basin (SBB). Curves are identified as follows: (A) Oman margin 3350 m, > 63-μm fraction, $O_2 \sim 3.00$ ml l^{-1}; (B) same sample, > 125-μm fraction; (C) SBB Station 298S, 590 m, > 63-μm fraction, $O_2 = 0.15$ ml l^{-1}; (D) Oman margin 412 m, 0–1 cm layer, > 125-μm fraction, $O_2 \sim 0.13$ ml l^{-1}; (E) same sample, topmost sediment, > 63-μm fraction; (F) SBB Station 298E, 590 m, $O_2 = 0.05$ ml l^{-1}, > 63-μm fraction.

Stained foraminifera were extremely abundant in the 63–125-μm fraction of the 'topmost sediment' at the 412-m site. This finest fraction yielded 87.2% of all stained specimens in the topmost sediment compared to 11.7% in the 125–300-μm fraction and 1.1% in the > 300-μm fraction (Table 2). Maximum dimensions of most (87.3%) specimens were < 300 μm and almost all (97.9%) were < 500 μm (Fig. 2B).
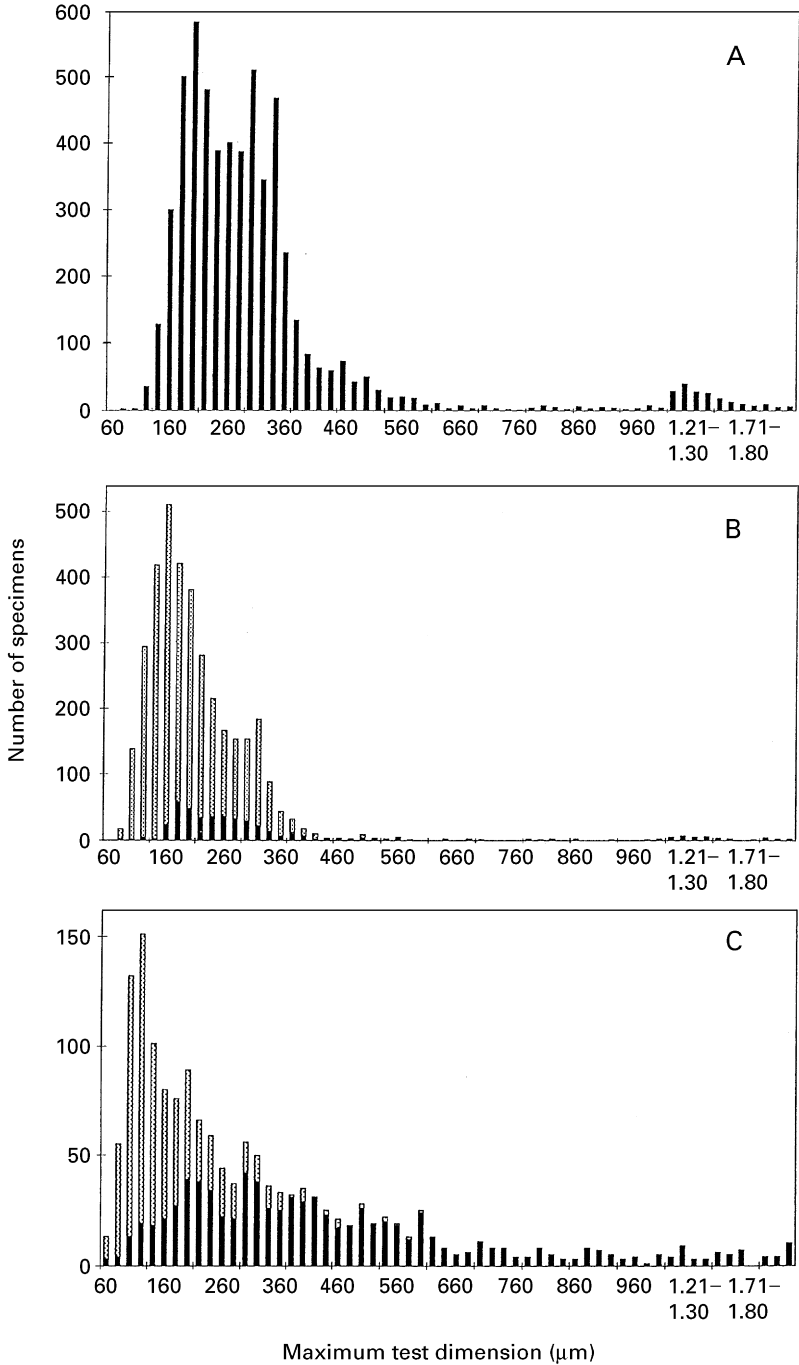
The only foraminifera which consistently exceeded 500 μm at 412 m were two small *Bathysiphon* species, tubular forms which were typically 1–2 mm long. At the 3350-m site, however, several very large, tubular, agglutinated species (*Bathysiphon filiformis, Hyperammina crassatina, Rhabdammina parabyssorum* and *Saccorhiza ramosa*) reached lengths of up to 9 cm (Gooday et al., 1997; Gooday and Smart, 2000). These taxa could not be adequately sampled using a multicorer and are too large to be included in Fig. 2.

3.5. Relation to metazoan faunas

Dense foraminiferal and metazoan macrofaunal (> 300-μm fractions) populations coexisted within the Oman margin OMZ. The macrofauna, particularly the metazoan

Table 5
Diversity data for stained foraminiferal faunas from low-oxygen environments, and from the Florida slope. ND = no data; TS = 'topmost sediment'

Locality and depth	O_2 (ml l^{-1})	Specimens	Species number	$E(S_{100})$	Fisher Alpha	H' (log$_{10}$)	J' (log$_{10}$)	R1D	Reference
Florida slope 185 m	~5.00	2680	30	ND	ND	1.92	ND	52.7%	Sen Gupta et al. (1981), Sen Gupta and Strickert (1982); > 63 μm fraction, 0–3 cm
		32	23	ND	ND	1.88	ND	39.6%	
		3274	20	ND	ND	1.34	ND	62.7%	
		6542	30	ND	ND	1.90	ND	53.2%	
Santa Barbara Basin:									
339 m	0.51	31	7	7.0	2.816	0.742	0.879	25.8%	Bernhard et al. (1997); > 63 μm, 0–1 cm
431 m	0.35	255	11	9.7	2.342	0.783	0.752	37.6%	
522 m	0.08	470	10	8.4	1.797	0.776	0.776	25.5%	
537 m	0.04	323	12	10.3	2.458	0.798	0.740	32.7%	
551 m	ND	575	9	7.5	1.516	0.599	0.628	56.0%	
563 m	ND	393	6	5.5	1.006	0.310	0.398	82.2%	
578 m	0.03	838	10	7.8	1.598	0.780	0.780	32.3%	
580 m	ND	146	6	6	1.261	0.517	0.664	63.0%	
591 m	0.06	450	9	6.7	1.596	0.539	0.564	59.6%	
Santa Barbara Basin:									
590 m	0.05	866	12	8.9	1.974	0.716	0.664	49.3%	This study. > 63 μm, 0–1 cm
610 m	0.15	339	36	21.4	10.19	1.105	0.710	25.4%	

								3 species:	
Santa Barbara Basin:									Phleger and Soutar (1973). > 62 μm, surface sediment
575 m	0.10	2350	~13	ND	ND	ND	ND	86%	
590 m	0.10	2100	ND	ND	ND	ND	ND	80%	
Soledad Basin									
530 m	~0.10	4300	~12	ND	ND	ND	ND	71%	As above
OffPeru									
180 m	ND	1200	~11	ND	ND	ND	ND	95%	As above
Santa Monica Basin									
529 m	<0.20	325	43	29.5	13.62	1.307	0.822	21.1%	Mackensen and Douglas (1989); > 125 μm, 0–1 cm
Santa Catalina Basin									
893 m	0.20–0.50	1319	28	18.2	7.563	0.913	0.574	45.6%	Mackensen and Douglas (1989); > 125 μm, 0–1 cm
897 m	0.20–0.50	730	25	20.0	6.052	1.092	0.747	48.7%	
Oman margin									
412 m, 0–1 cm, > 125 μm	0.13	6188	64	23.9	9.267	1.228	0.692	27.0%	This study
412 m, TS > 63 μm	0.13	3647	49	18.6	8.433	0.985	0.577	44.1%	
3350 m, 0–1 cm, >125 μm	~3.00	893	158	58.7	60.97	1.939	0.881	6.8%	
3350 m, 0–1 cm, > 63 μm	~3.00	1282	208	61.4	67.10	2.017	0.872	5.3%	

Maximum test dimension (μm)

component, was much sparser at the deep site. Foraminiferal densities were 4.8 times greater than values for the metazoan macrofauna at 412 m, but 16.4 times greater at 3350 m (Table 6). In both cases, the foraminifera were sorted from the 0–1 cm layer and the metazoans from the 0–15 cm layer. If the metazoan data are confined to specimens from the 0–2 cm layer, the foraminifera:metazoan (F : Macro) ratio increased to 10.2 at 412 m and to 24.8 at 3350 m (Table 6). However, when the macrofauna is dominated by polychaetes, as at the 412 m site, densities based on 2-cm thick layers are probably not representative since individuals may migrate > 2cm down their tubes during sectioning.

For the meiofauna, our limited data suggest the reverse trend. Foraminifera were 7 times (125–300 μm fraction) and 17 times (63–300-μm fraction) more abundant than metazoan meiofauna at 412 m, within the OMZ, but only 1.4 times (125–300-μm fraction) and 1.2 times (63–300-μm fraction) more abundant at 3350 m, below the OMZ (Table 6). At 412 m, the metazoan meiofauna consisted almost entirely (> 99%) of nematodes, while at 3350 m the 125–300-μm fraction included harpacticoid copepods (13.5%), nauplii (2.1%), kinorhynchs (2.7%), ostracods (2.7%), polychaetes (1.9%), bivalves (1.0%) and loricifera (0.5%), in addition to nematodes (76.6%).

Metazoan macrofaunal diversity was extremely low, and dominance was very high, at the 412-m site. Only 11 species were present, all but two of them polychaetes. The top-ranked metazoan species accounted for 62.8% and the second-ranked species for 27.4% of the fauna (Levin et al., 1997). The diversity of the foraminiferal macrofauna at this site was comparable or rather higher (13 and 19 species in two cores) but dominance values were substantially lower. In two samples, the top ranked foraminiferal species accounted for 22.3% (*Globobulimina* sp.) and 27.5% (*Bathysiphon* sp.) and the second-ranked species for 16.4% (*Bathysiphon* sp.) and 20.4% (*Globobulimina* sp.) of the fauna. No comparable diversity data are currently available for metazoan meiofauna.

3.6. Comparison with Santa Barbara Basin (SBB)

In the central SBB (Station 298E, 590 m depth, $O_2 = 0.05$ ml l^{-1}), calcareous foraminifera constituted > 90% of the stained assemblage (> 63-μm fraction) with saccamminids (1.4%) and spiroplectamminaceans (6.7%) the only other major groups present (Table 3). At a second, better-oxygenated SBB site (Station 298S, 610m depth, $O_2 = 0.15$ ml l^{-1}), calcareous foraminifera were less abundant (70.2% in > 63-μm fraction; 52.6% in > 125-μm fraction) while hormosinaceans (18% in > 63-μm fraction; 21% in > 125-μm fraction) and multilocular agglutinated taxa (7.4% in the > 63-μm fraction; 16.3% in > 125-μm fraction) were fairly common. Soft-shelled

Fig. 2. Distribution of maximum foraminiferal test dimensions at the two Oman margin sites. (A) 412 m, 0–1 cm layer, > 125-μm fraction. (B) 412 m, topmost sediment, > 63-μm fraction. (C) 3350 m, 0–1 cm layer, > 63-μm fraction. Black sections of bars based on data from > 125-μm fraction; stippled sections based on data from 63–125-μm fraction.

Table 6

Abundances of foraminifera compared to abundance of metazoans on the Oman margin. The series numbers refer to deployments of the multiple-corer at each of the two stations. Thus, data on meiofauna are from one core, data on foraminiferal macrofauna are from two cores. Metazoan macrofaunal data are means values derived from 4 box-cores from 401–418 m (Station 12692) and 5 cores from 3360–3400 m (Station 12687) and do not include meiofaunal taxa such as nematodes, copepods and ostracods

	Station 12692			Station 12687		
	series 1	series 4	mean	series 5	series 8	mean
Meiofauna (63–300 µm; indiv. 25.5 cm^{-2})						
Foraminifera (F)						
125–300 µm	ND	6494[a]	6494[a]	ND	872[b]	872[b]
63–300 µm	ND	40,571[a]	40,571[a]	ND	1593[b]	1593[b]
Metazoa (Meio)						
125–300 µm	ND	941	941	ND	584	584
63–300 µm	ND	2393	2393	ND	1305	1305
F : Meio ratio:						
125–300 µm	ND	6.90	6.90	ND	1.49	1.49
63–300 µm	ND	16.95	16.95	ND	1.22	1.22
Macrofauna (>300 µm; indiv. m^{-2})						
Foraminifera (F)	38,039	80,392	59,215	40,000	64,706	52,353
Metazoa (Macro):			12,362 (0–20 cm)			3200 (0–20 cm)
			5810 (0–2 cm)			2112 (0–2 cm)
						1471 (0–1 cm)
F : Macro ratio			4.79 (0–20 cm)			16.4 (0–20 cm)
			10.2 (0–2 cm)			24.8 (0–2 cm)
						35.6 (0–1 cm)

[a]Includes 33 specimens (= 12941 per m^2) in phytodetritus.

[b]Excludes 32 attached specimens.

a and b: both values include specimens in 'topmost' sediment.

monothalamous foraminifera (allogromiids and saccamminids) were again scarce at Station 298S (1.5% in the > 63-μm fraction; 7.2% in the > 125-μm fraction).

Diversity data for complete faunas from the two SBB sites are given in Table 5 and rarefaction curves in Fig. 1. The microxic Station 298E yielded much lower values for all diversity measures than our 412-m Oman margin site. Diversity was higher at the dysoxic Station 298S, but still less than at 412 m on the Oman margin.

The SBB samples (> 63-μm fraction) provided further evidence that foraminifera dominate the meiofauna in oxygen-depleted settings. A small volume (1.21 cm³) of surface sediment from Station 298E yielded 89 nematodes, 8 polychaetes, 14 gastrotrichs and 866 foraminifera. At Station 298S, 1.99 cm² of surface sediment yielded 38 nematodes, 16 crustaceans (harpacticoids and nauplii), 8 polychaetes and 5 other worms (possibly nemertines). The F : Meio ratios of 7.8 at Station 298E and 5.1 at Station 298S compared with the estimated ratio of 16.9 at our 412-m Oman margin site (> 63-μm fraction).

4. Discussion

4.1. Limitations of the study

An important bias arises from the fact that our analysis was restricted to the 0–1 cm layers. The depth to which foraminifera penetrate sediments is controlled largely by food inputs and oxygen profiles (Corliss and Emerson, 1990; Jorissen et al., 1995). Therefore, a much larger proportion of the fauna almost certainly resided > 1 cm depth at 3350 m, leading to a greater underestimation of population density at this site compared to the dysoxic 412-m site. Ignoring deeper sediment layers will also bias our estimates of faunal composition and diversity more strongly at 3350 m than at 412 m. At bathyal and abyssal sites in the NE Atlantic, the relative proportions of most major taxa change somewhat with depth (Gooday, 1986; Gooday, unpublished). On the other hand, the effect of excluding deeper sediment layers on diversity measures is relatively slight (Gooday et al., 1998). Metazoan and foraminiferal densities show similar rates of decline with depth into the sediment at NE Atlantic sites (Gooday, unpublished). Hence the relative abundance of these faunal components in the 0–1cm layer should be fairly representative of the entire inhabited sediment profile.

Because the analysis of abundant and diverse deep-sea foraminiferal populations is extremely time–consuming, we could examine only two Oman margin samples for this study (although these yielded > 11,000 stained individuals and almost 300 species). The faunal differences between these two very different sites are so marked, however, that we believe a detailed comparison of the 0–1 cm layers of single samples can yield important conclusions.

4.2. Comparison with previous studies

Published density data for stained foraminifera from other low-oxygen ($O_2 \leqslant 1.00 \, \text{ml} \, l^{-1}$) and/or organically enriched localities are summarised in Table 7.

Table 7
Density data for stained foraminiferal faunas from deep-sea low-oxygen environments, and from the Florida slope

Locality and depth	Bottom water O_2 (ml l^{-1})	Stained specimens per 10 cm^2	Reference; horizon and sieve fraction examined
Florida slope: 185 m	~ 5.00	320–65,420	Sen Gupta et al. (1981), Sen Gupta and Strickert (1982): > 63 μm, 0–3 cm
Santa Barbara Basin:			
339 m	0.51	133	Bernhard et al. (1997):
431 m	0.35	1176	> 63 μm fraction, 0–1 cm
522 m	0.08	1886	
537 m	0.04	1270	
578 m	0.03	3459	
591 m	0.06	3958	
Santa Barbara Basin:			
486 m slope (Feb. 1988)	~ 0.11	532	Bernhard (1990):
550 m slope (June 1998)	< 0.10	6901	7.5 cm diameter subcores of
550 m centre (Feb. 1988)	< 0.10	4340	box cores; > 63 μm, 0–1 cm
550 m centre ((June 1988)	< 0.10	9557	
550 m centre (Oct. 1988)	0.01	9626	
550 m centre (July 1989)	Anoxic	27	
Santa Barbara Basin:			
575 m	~ 0.10	1175	Phleger and Soutar (1973):
590 m	~ 0.10	1050	box core, > 62 μm, surface sediment
Soledad Basin:			
530 m	0.10	2150	Phleger and Soutar (1973): box core, > 63 μm, surface sediment
Santa Monica Basin:			
529 m	< 0.20	23	Mackensen and Douglas (1989): > 125 μm, 0–1 cm, abundance per cc.
Santa Catalina Basin:			
893 m (slope)	0.20 − 0.50	52	Mackensen and Douglas (1989):
897 m (slope)	0.20 − 0.50	45	> 125 μm, 0–1 cm, abundance per cc
Sagami Bay, Japan:			
1450 m (spring)	1.00	1500–2000	Ohga and Kitazato (1997):
1450 m (summer)	1.00	200–500	> 63 μm or > 28 μm, 0–15 cm
Oman margin:			
412 m	0.13	16,107	This study:
3350 m	~ 3.00	586	> 63 μm, 0–1 cm
412 m	0.13	2533	This study.
3350 m	~ 3.00	342	> 125 m, 0–1 cm

Although depth horizons and sieve fractions vary, making comparisons difficult, it is apparent that densities in the 0–1 cm layer (> 63-μm fraction) at 412 m on the Oman margin were among the highest reported from an oxygen-poor setting. The closest values are from the centre of the SBB (550 m) during October 1988, when oxygen concentrations were < 0.10 ml l^{-1} (Bernhard, 1990). Note that the very high densities (up to 2176 cm^{-3} in the 0–0.25 cm layer) reported by Bernhard and Reimers (1991) from the SBB reflect the concentration of foraminifera near the sediment–water interface and should not be compared to densities in the 0–1 cm layer. However, the Oman margin densities do not approach the extraordinarily high values (up to $> 65,000$ indiv. 10 cm^2 in 0–3 cm layer) reported by Sen Gupta et al. (1981) from a well-oxygenated site on the Florida margin (185 m depth).

According to Sen Gupta and Machain-Castillo (1993), up to about ten hard-shelled foraminiferal species typically live in oxygen-poor areas with two or three species constituting as much as 80% of the fauna. Published diversity data from low-oxygen ($O_2 \leqslant 0.50$ ml l^{-1}) sites are summarised in Table 5. Our Oman margin data (> 63- and > 125-μm fraction) are best compared with the data of Bernhard et al. (1997) from the SBB (> 63 μm fraction). Although Bernhard et al. (1997) omitted soft-shelled foraminifera, their observations are consistent with ours in suggesting that diversity in the microxic central SBB was much lower than at the dysoxic Oman margin site (412 m). On the other hand, reported diversity in the dysoxic Santa Monica ($O_2 \leqslant 0.20$ ml l^{-1}) and Santa Catalina Basins ($O_2 = 0.20$–0.50 ml l^{-1}) (Mackensen and Douglas, 1989), also on the California Borderland, was broadly comparable to that of the 412-m Oman margin fauna. Thus, foraminiferal diversity typically seems to be much lower in microxic ($O_2 < 0.10$ ml l^{-1}) than in dysoxic ($O_2 = 0.10$–1.00 m l^{-1}) settings, and consistently higher in oxic environments. Analysis of bathyal OMZ data suggest a negative correlation also exists between metazoan macrofaunal species richness and bottom-water oxygen concentrations at values $\leqslant 0.50$ ml l^{-1} (Levin and Gage, 1998; Levin et al., 2000).

The total number (70) of stained species recognised at 412 m within the Oman margin OMZ is higher than numbers reported from other dysoxic sites (Table 6). We believe that this reflects the large number (11,760) of specimens examined and the inclusion of all faunal components, both soft- and hard-shelled.

4.3. Environmental influences on foraminiferal faunas

Foraminiferal abundance and biomass are closely related to food availability (Altenbach, 1988; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991). Foraminifera flourish where food is plentiful, but in order to gain access to food they must endure the oxygen depletion that often accompanies an abundance of organic matter. Oxygen concentrations in the sediment pore water become a limiting ecological factor in these environments and foraminiferal assemblages are composed largely of low-oxygen tolerant species (Sen Gupta and Machain-Castillo, 1993). Since the ability of foraminifera to withstand oxygen deficiency varies among major taxa and species (e.g. Bernhard et al., 1997), reduced oxygen concentrations will influence both the taxonomic composition and species diversity of foraminiferal assemblages by

eliminating the less tolerant species, generally those which exhibit epifaunal adaptations (de Stigter, 1996). For species able to survive on little oxygen, food availability is probably the main factor limiting population size. At a dysoxic site ($O_2 = 0.41$–0.47ml l^{-1}) in the Southern California Borderland (1000 m depth), foraminiferal densities increase substantially following seasonal inputs of organic matter (Rathburn, 1998). Moreover, where food is plentiful, low-diversity assemblages dominated by a few, low-oxygen tolerant species may develop, even if the bottom water is well oxygenated. Such assemblages occur on the outer Florida shelf (185 m; $O_2 \sim 5.00$ ml l^{-1}) (Sen Gupta et al., 1981; Sen Gupta and Strickert, 1982) and on the upper slope off Cape Hatteras (680 m; $O_2 \sim 4.10$ ml l^{-1}) (Goodday et al., in prep.). These considerations suggest that foraminiferal densities at 412 m on the Oman margin reflect an abundance of food, as indicated by high (and highly seasonal) surface primary production (Banse and McClain, 1986), high organic carbon fluxes to the seafloor (Lee et al., 1998), high sediment TOC values and pigment concentrations (Table 1), at a site where oxygen depletion is not extreme.

For metazoan macrofauna, and probably also foraminifera, oxygen availability becomes limiting only when concentrations fall well below 1.00 ml l^{-1} (probably < 0.45 ml l^{-1}) (Levin and Gage, 1998). The values of almost 3.00 ml l^{-1} measured at 3350 m were certainly too high to have any perceptible impact on foraminiferal assemblage parameters. The high species diversity at this site was comparable to that found in well-oxygenated areas of the NE Atlantic which experience relatively low organic fluxes compared to eutrophic continental margins (Goodday et al., 1998). Foraminiferal densities, on the other hand, were considerably lower at 3350 m, reflecting the reduced organic matter flux to the seafloor at this deep locality (Lee et al., 1998).

Although the two sites are almost 3000 m apart bathymetrically, depth itself is probably not responsible for either the high species diversity or the abundance of soft-shelled foraminifera at 3350 m. Similar faunas occur elsewhere in shallower water; for example, at 1340 m in the Porcupine Seabight (Goodday, 1986) and 28 m in Explorers Cove, Antarctica (Goodday et al., 1996). Bathymetric depth, however, is strongly linked to parameters such as carbonate undersaturation and temperature which are more likely to influence foraminiferal faunas. The Carbonate Compensation Depth is situated at 5000–5500 km in the Arabian Sea (Berger and Winterer, 1974; Barron and Whitman, 1981; Gupta, 1994) and, according to Belyaeva and Burministrova (1985), the planktonic foraminiferal lysocline is located between 2400 and 2800 m. Stubbings (1939) observed a change from *Globigerina* ooze to 'transitional *Globigerina* ooze-red clay' at around 3700–3800 m depth close to our study area. This may correspond to the deeper, carbonate lysocline of Belyaeva and Burministrova (1985). These observations suggest that carbonate dissolution could possibly have some impact on the abundance of calcareous benthic foraminifera at 3350 m. The influence of temperature is difficult to assess. However, we note that soft-shelled monothalamous taxa are abundant in temperate, shallow-water and intertidal settings (e.g., Arnold, 1982; Ellison, 1984) where water temperatures are likely to be comparable to those at our 412-m site (13–14°C), at least during part of the year.

In summary, differences in stained foraminiferal abundance and assemblage structure on the Oman margin probably reflect the much lower bottom-water oxygen concentration and higher food input at the 412-m site compared to the 3350-m site, possibly combined with the effects of carbonate-undersaturated bottom water at the deeper site.

4.4. *Taxonomic trends in relation to food and oxygen availability*: *meiofaunal foraminifera.*

Calcareous (rotaliid) foraminiferal species, many with small, thin-walled tests, are typical of organically enriched/low-oxygen conditions (Phleger and Soutar, 1973; Koutsoukos et al., 1990; Sen Gupta and Machain-Castillo, 1993; Kaiho, 1994). Small agglutinated taxa (e.g., *Spiroplectammina, Trochammina, Textularia)* are common in some modern (Kaminski et al., 1995; Bernhard et al., 1997) and ancient (Koutsoukos et al., 1990) oxygen-depleted settings, and the small *Leptohalysis* and *Bathysiphon* species at our 412-m site have counterparts in the fauna of organic-rich muds in the Gullmar Fjord, Sweden (Höglund, 1947). These taxa are rarely dominant, however. Agglutinated and allogromiid species (e.g. *Ammodiscus? gullmarensis* and *Allogromia cystallifera*) sometimes constitute a large proportion of live faunas in parts of estuaries recovering from prolonged, organic pollution-induced anoxia (Cato et al., 1980; Alve, 1995a,b). However, foraminiferal distributions in these complex, disturbed systems probably reflect numerous factors, including preferences for particular temperature, salinity and organic-matter input regimes, tolerance of pollutants, and the ability to disperse into unoccupied habitats (Schafer, 1982; Alve, 1995b). Where oxygen data are reported, live assemblages dominated by agglutinated species are confined to oxic areas; for example, 1–4 ml l^{-1} in the case of *A.? gullmarensis* from the Drammensfjord, Norway (Alve, 1995b). The calcareous species *Stainforthia fusiformis*, on the other hand, rapidly recolonises the most oxygen-poor parts of fjords recovering from pollution (Alve, 1994).

Much less is known about the distribution of small, soft-shelled foraminifera (allogromiids and saccamminids) in relation to gradients of food and oxygen availability (Bernhard and Sen Gupta, 2000). Our new data from the bathyal Oman margin and the SBB suggest that they are present under dysoxic and microxic conditions but constitute a much smaller proportion (a few percent) of the fauna in these settings than at well-oxygenated oligotrophic deep-sea sites where they are typically more abundant and diverse than rotaliids (Gooday, 1996; Gooday et al., 1998). Similarly, soft-shelled species are more sensitive to anoxia in experimental systems than some hyaline calcareous and multilocular agglutinated foraminifera (Moodley et al., 1998). Why this should be so is unclear since carbonate shells and skeletons (both metazoan and protozoan) are considered to be difficult to maintain in low-oxygen environments where pH is low (Rhodes and Morse, 1971; Thompson et al., 1985; Kaiho, 1994). Tolerance of oxygen depletion in foraminifera is most likely linked to physiological and cellular adaptations (Bernhard and Alve, 1996; Bernhard, 1996; Bernhard and Sen Gupta, 2000) associated with particular phylogenetic lineages which happen to secrete calcareous tests. In addition, the well-developed test pores present in many hyaline

species possibly facilitate oxygen exchange between the cell and the surrounding medium (Berthold, 1976; Leutenegger and Hansen, 1979; Corliss, 1985; Moodley and Hess, 1992). Miliolids, which lack pores, are generally absent in oxygen-depleted environments.

4.5. *Taxonomic trends in relation to food and oxygen availability*: *macrofaunal foraminifera*.

At 412 m in the core of the Arabian Sea OMZ, *Globobulimina* sp. (calcareous), two *Lagenammina* species and two small *Bathysiphon* species (agglutinated) were among the few foraminifera present in the macrofaunal fraction. None was large enough to be easily visible to the unaided eye on core surfaces. At the 3350-m site, however, some very large tubular foraminifera were readily visible on box-core surfaces in a life-position which suggested that they were suspension or surface-deposit feeders on freshly deposited phytodetritus (Gooday et al., 1997). In the San Pedro and Santa Catalina Basins in the California Borderland (oxygen concentrations $\sim 0.40 \, \mathrm{ml \, l^{-1}}$), Kaminski et al. (1995) described a fauna which also included some large agglutinated species (*Bathysiphon filiformis, Saccorhiza* sp., and *Marsipella* sp.) which project into the water column and have relatively coarse-grained ('arenaceous') tests. These taxa can clearly tolerate moderate dysoxia but not the more extreme conditions found within some OMZs and low-oxygen basins.

Large foraminifera with walls composed mainly of mud particles seem to be more tolerant of oxygen depletion than large arenaceous taxa. On the Oman margin, *Pelosina arborescens* and an undescribed star-shaped, mud-walled astrorhiziid occur-red between 746 and 822–857 m (Gooday and Levin, unpublished observations) where oxygen concentrations were 0.16–$0.20 \, \mathrm{ml \, l^{-1}}$. Levin et al. (1991a) described a similar mud-walled foraminiferal macrofauna from the Santa Catalina Basin (1200–1350 m water depth) on the California Borderland ($O_2 \sim 0.4 \, \mathrm{ml \, l^{-1}}$). Here, arborescent tests of *P. arborescens* projected 1–4 cm from the sediment surface and were easily visible to the unaided eye from a submersible. Cedhagen (1993) reported that *P. arborescens* occurs in periodically anoxic habitats and can survive experi-mental anoxia for at least ten days. Finally, large spherical and sausage-shaped protists with organic tests reaching several centimetres in diameter occur between about 1200 and 1600 m in the Arabian Sea (Gooday et al., 2000).

Preliminary, semi-quantitative observations reveal similar trends among macro-faunal foraminifera ($> 300 \, \mu\mathrm{m}$) across the Peru margin OMZ (Levin et al., unpub-lished results). A partially laminated basin at 305 m ($O_2 = 0.02 \, \mathrm{ml \, l^{-1}}$) yielded cal-careous foraminifera but no large agglutinated taxa. Only data for agglutinated and allogromiid foraminifera are available from the other sites. An arborescent *Pelosina* species and star-shaped, mud-walled astrorhiziids were present at a deeper station (562m; $O_2 = 0.26 \, \mathrm{ml \, l^{-1}}$). The diversity of agglutinated forms increased downslope with many agglutinated, mainly multilocular taxa at 828m; ($O_2 = 0.84 \, \mathrm{ml \, l^{-1}}$). A station at 1210 m ($O_2 = 1.66 \, \mathrm{ml \, l^{-1}}$) was characterised by large, tubular, agglutinated species (*Rhabdammina abyssorum, Bathysiphon* sp., *Hyperammina friabilis, Marsipella cylindrica*), a few star-shaped astrorhiziids, spherical tests of *Psammosphaera fusca*,

various multilocular agglutinated taxa, and *Rupertina stabilis*, a sessile suspension-feeding rotaliid often associated with strong currents (Lutze and Altenbach, 1988).

These observations suggest that large agglutinated foraminifera are associated with a fairly wide range of oxygen concentrations, but apparently cannot tolerate levels below about 0.20 ml l^{-1}. These conspicuous taxa also clearly require a relatively high organic matter flux to sustain their protoplasmic bodies (Gooday et al., 1997).

4.6. Metazoans and foraminifera

Metazoan taxa display differing degrees of tolerance to oxygen deficiency. In general, meiofauna are more tolerant than macrofauna (Josefson and Widbom, 1988; Luth and Luth, 1997) and nematodes are more tolerant than other meiofaunal taxa (Wishner et al., 1990; Levin et al., 1991b; Giere, 1993; Moodley et al., 1997; Cook et al., 2000). This is probably one reason why nematodes were the only metazoan meiofaunal taxon at our dysoxic 412-m site within the Oman margin OMZ, while the oxic 3350-m site yielded a diversity of metazoan taxa. Although foraminifera, as a whole, display a wide range of responses, some species can tolerate oxygen deficiency better than most metazoans (Josefson and Widbom, 1988; Alve and Bernhard, 1995; Moodley et al., 1997). Metazoan meiofaunal densities in our Oman margin samples decreased from 941 specimens per core (412-m site) to 584 specimens per core (3350-m site), but the foraminifer:metazoan (F : Meio) ratio decreased from 6.9 (412 m) to 1.4 (3350 m). In other words, metazoans made up a lower proportion of the total meiofauna within the OMZ than they did at the deep site below the OMZ. Differences between the F : Meio ratios at the two sites were even greater in the 63–300-μm fraction (Table 6). The opposite trend, however, was apparent among the macrofauna where the F : Macro ratio was 4.8 at 412 m compared to 16.4 at 3350 m. This observation is unexpected since, as indicated above, meiofauna are generally more tolerant of dysoxia than macrofauna. However, the ratios were probably strongly influenced by two factors; first, the fact that macrofaunal densities decrease more rapidly with depth than those of the meiofauna, and second, the negative effect of high macrofaunal densities on the metazoan meiofauna.

Foraminifera and metazoans are phylogentically distant and have very different body structures (unicellular vs multicellular). Yet, at the assemblage level, both groups respond to organic enrichment/oxygen–depletion in similar ways. Foraminifera (Sen Gupta et al., 1981; Verhallen, 1987; Sen Gupta and Machain-Castillo, 1993; Alve, 1995a; den Dulk et al., 1998), metazoan macrofauna (Pearson and Rosenberg, 1978), meiofaunal harpacticoid copepods (Murrell and Fleeger, 1989), and nematodes (Keller, 1986), all show an increase in population density and dominance, a decrease in species richness, and a change in the relative abundance of major taxa. Small body size is another feature common to foraminifera and metazoans in oxygen-depleted areas (Levin et al., 1991b).

Although foraminifera typically outnumber metazoans in the deep sea (Coull et al., 1977; Snider et al., 1984; Vincx et al., 1994; Gooday 1986, 1996), higher numbers may not always reflect higher biomass. For example, most foraminifera in the > 300-μm fraction from within the Oman margin OMZ (412-m site) are much smaller,

particularly when protoplasmic volume is considered, than the polychaetes that dominate the metazoan macrofauna (Levin, unpublished observations). Thus, at some low-oxygen sites (although not the microxic central SBB; Buck and Bernhard, unpublished), metazoan biomass is likely to exceed foraminiferal biomass in sieve fractions > 300 μm. Both polychaetes and foraminifera include species which are effective food-gathers and exhibit rapid reproduction, enabling them to exploit the abundant food supplies present in organically enriched areas. Comparisons of foraminiferal life-history strategies with those of the main co-occurring metazoan taxa (polychaetes and nematodes), and investigations that address direct interactions between foraminifera and metazoans (e.g. Chandler, 1989), may be instructive, particularly in deep-sea and dysoxic setting where these groups are abundant.

4.7. Geological implications

Sediments deposited in oxygen-deficient palaeoenvironments attract considerable geological interest, partly because they are the source for much of the world's oil (Tyson and Pearson, 1991). Degrees of oxygen depletion in ancient sediments have been recognised on the basis of various criteria; for example, the degree to which laminations are developed, the presence of macro- and microfossils, and the nature of trace fossil assemblages (Savrda and Bottjer, 1991). Foraminifera often occur in sediments devoid of macrofossils and are therefore important for reconstructing ancient low-oxygen environments (Koutsoukos et al., 1990; Kaiho, 1994), particularly OMZs (Anderson and Garner, 1989; Hermelin, 1992). Our results from the 412-m Oman margin site suggest that a smaller proportion of bathyal low-oxygen faunas is lost during fossilisation compared to deep-water assemblages from well-oxygenated environments. This is because low-oxygen assemblages are dominated by hard-shelled, mainly calcareous foraminifera which are more likely to be preserved than the soft-shelled species which predominate at higher oxygen concentrations. This conclusion assumes an absence of dissolution bias. There is evidence that carbonate dissolution is minimal within some OMZs, although it may be enhanced at edges of these zones (Berelson et al., 1996).

5. Conclusions

(1) Oxygen and food availability strongly influence the structure of 'live' benthic foraminiferal assemblages. At a bathyal (412 m), permanently dysoxic $(O_2 = 0.13 \, \text{ml} \, l^{-1})$ site within the Oman margin OMZ, foraminifera were more abundant, and assemblages exhibited higher dominance, lower species richness (70 species) and lower diversity, than at a deeper (3350 m), well-oxygenated $(O_2 \sim 3.00 \, \text{ml} \, l^{-1})$ locality below the OMZ where 208 species were recognised. A microxic $(O_2 = 0.05 \, \text{ml} \, l^{-1})$ site in the bathyal (590 m) Santa Barbara Basin (SBB), yielded only 12 species.

(2) Within the Oman margin OMZ and in the central SBB, hyaline calcareous taxa were dominant, trochamminaceans, spiroplectamminaceans, and small *Bathysiphon* species were common, but soft-shelled monothalamous foraminifera (allogromiids and saccamminids) were uncommon. However, below the OMZ, calcareous foraminifera were uncommon, and the fauna was dominated instead by hormosinaceans, allogromiids, and soft-shelled saccamminids. These differences suggest that a greater proportion of the foraminiferal fauna is likely to be fossilised at organically enriched/oxygen-depleted sites than in oxic settings.

(3) The distribution of very large foraminifera on the Oman margin, the Peru margin and within California Borderland basins suggests that tubular agglutinated species with coarse-grained walls (e.g. *Bathysiphon, Rhabdammina*) can withstand moderate dysoxia (down to about $0.50 \, \mathrm{ml \, l^{-1}}$), while arborescent, spherical or stellate mud-walled morphotypes (e.g. *Pelosina*) can tolerate rather lower oxygen concentrations (~ 0.20–$0.30 \, \mathrm{ml \, l^{-1}}$) and therefore occur closer to the centres of OMZs and dysoxic basins. These macroscopic taxa are absent in severely oxygen-depleted areas, and also in oligotrophic areas where there is insufficient food to sustain their considerable protoplasmic biomass.

(4) Foraminifera are more abundant than metazoan meio- and macrofauna in many low-oxygen settings. Despite representing different kingdoms, foraminifera and metazoans display similar assemblage responses to organic enrichment and oxygen depletion; abundance increases, species diversity decreases, and there is a change in the relative abundance of major taxa.

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