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Faunal responses to oxygen gradients on the Pakistan margin: A comparison of foraminiferans, macrofauna and megafauna

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ABSTRACT

The Pakistan Margin is characterised by a strong mid-water oxygen minimum zone (OMZ) that intercepts the seabed at bathyal depths (150–1300 m). We investigated whether faunal abundance and diversity trends were similar among protists (foraminiferans and gromiids), metazoan macrofauna and megafauna along a transect (140–1850 m water depth) across the OMZ during the 2003 intermonsoon (March–May) and late/post-monsoon (August–October) seasons. All groups exhibited some drop in abundance in the OMZ core (250–500 m water depth; O_2 : 0.10–0.13 mL L⁻¹ = 4.46–5.80 μM) but to differing degrees. Densities of foraminiferans >63 μm were slightly depressed at 300 m, peaked at 738 m, and were much lower at deeper stations. Foraminiferans >300 μm were the overwhelmingly dominant macrofaunal organisms in the OMZ core. Macrofaunal metazoans reached maximum densities at 140 m depth, with additional peaks at 850, 940 and 1850 m where foraminiferans were less abundant. The polychaete *Linopherus* sp. was responsible for a macrofaunal biomass peak at 950 m. Apart from large swimming animals (fish and natant decapods), metazoan megafauna were absent between 300 and 900 m (O_2 < 0.14–0.15 mL L⁻¹ = 6.25–6.69 μM) but were represented by a huge, ophiuroid-dominated abundance peak at 1000 m (O_2 ~0.15–0.18 mL L⁻¹ = 6.69–8.03 μM). Gromiid protists were confined largely to depths below 1150 m (O_2 > 0.2 mL L⁻¹ = 8.92 μM). The progressively deeper abundance peaks for foraminiferans (>63 μm), *Linopherus* sp. and ophiuroids probably represent lower OMZ boundary edge effects and suggest a link between body size and tolerance of hypoxia. Macro- and megafaunal organisms collected between 800 and 1100 m were dominated by a succession of different taxa, indicating that the lower part of the OMZ is also a region of rapid faunal change. Species diversity was depressed in all groups in the OMZ core, but this was much more pronounced for macrofauna and megafauna than for foraminiferans. Oxygen levels strongly influenced the taxonomic composition of all faunal groups. Calcareous foraminiferans dominated the seasonally and permanently hypoxic sites (136–300 m); agglutinated foraminiferans were relatively more abundant at deeper stations where oxygen concentrations were >0.13 mL L⁻¹ (= 5.80 μM). Polychaetes were the main macrofaunal taxon within the OMZ; calcareous macrofauna and megafauna (molluscs and echinoderms) were rare or absent where oxygen levels were lowest. The rarity of larger animals between 300 and 700 m on the Pakistan Margin, compared with the abundant macrofauna in the OMZ core off Oman, is the most notable contrast between the two sides of the Arabian Sea. This difference probably reflects the slightly higher oxygen levels and better food quality on the western side.

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1. Introduction

The structure and composition of marine benthic communities are influenced by many environmental factors, including temperature, salinity, bottom flow and sediment properties.

The amount of available oxygen and the supply of food to the seafloor are particularly important in the deep sea where other parameters are usually relatively stable (Rowe, 1983; Gage and Tyler, 1991; Levin and Gage, 1998). In deeper water, oxygen minimum zones (OMZs) influence a greater area of seafloor than any other kind of oxygen-deficient environment. These persistent, mid-water features create strong bottom-water oxygen gradients where they impinge on the seafloor along the western rim of the Pacific Ocean, in the SE Atlantic, and in the Arabian Sea and Bay of Bengal (Helly and Levin, 2004). Several recent investigations have described changes in the structure and composition of benthic faunas across OMZs (reviewed by Levin, 2003). Two earlier OMZ studies, on a seamount in the eastern Pacific Ocean (Levin et al., 1991a,b) and on the Peru Margin (Levin et al., 2002), compared patterns among faunal groups. They found that abundances of smaller organisms (bacteria, metazoan and protozoan meiofauna) were relatively unaffected by very low-oxygen concentrations, but that the abundances of larger taxa (macrofauna and megafauna) were depressed. In all groups, distinct changes in taxonomic composition were associated with the OMZ.

In the present paper, we compare trends between different faunal groups across the OMZ on the Pakistan Margin of the Arabian Sea based on two pairs of cruises, one during the intermonsoon period (March–May) and the other during the late-to post-monsoon period (August–October) of 2003. These four cruises formed the centrepiece of a project funded by the UK National Environment Research Council, entitled ‘Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling’. Other papers in this volume and elsewhere provide detailed information on particular faunal size classes and taxa, including foraminiferans (Larkin and Gooday, 2009), large gromiid protists (Aranda da Silva and Gooday, 2009), macrofauna (Hughes et al., 2009; Levin et al., 2009) and megafauna (Murty et al., 2009), across the Pakistan Margin. Here, we address the following questions about patterns in relation to gradients in depth and bottom-water oxygen concentrations in this part of the Arabian Sea. (1) Do metazoans and protists exhibit the same patterns in abundance across the OMZ? (2) Do all groups exhibit the same patterns in diversity? (3) Do calcified and non-calcified taxa exhibit similar patterns? (4) Are OMZ edge effects evident in any groups? (5) Is the turnover rate of species with depth similar or different among taxa? We also ask whether faunal trends and composition are similar or different between the Pakistan and Oman margins of the Arabian Sea and between the Arabian Sea and OMZs in other regions of the world. Our emphasis on protists (foraminiferans and gromiids) reflects the considerable body of data acquired during the Pakistan Margin cruises on these organisms, which are often ignored in studies of deep-sea benthic biology.

2. Study area

The study was conducted in an area centred on 23° 00'N, 66° 25'E, just to the NW of the Indus Canyon, during two pairs of back-to-back cruises aboard the R.R.S. *Charles Darwin*. The first pair, CD145 and 146 (Bett, 2003a; Cowie, 2003a), coincided with the intermonsoon period (March–May 2003) and the second pair, CD150 and 151 (Bett, 2003b; Cowie, 2003b), with the end of the summer (SW) monsoon (August–October 2003; late/post-monsoon). Most of the work was concentrated at five main sites, located at approximately 140, 300, 950, 1200, 1850 m water depths, forming a transect across the OMZ (Table 1; Fig. 1). Additional sites were sampled at a variety of depths between

Table 1
Approximate positions for the main study sites on the Pakistan Margin.

Site (m)	Lat. (°N)	Long. (°E)
140	23°16.70'	66°42.60'
300	23°12.50'	66°34.00'
940	22°55.00'	66°36.50'
1200	23°00.00'	66°24.40'
1850	22°52.40'	66°00'00'

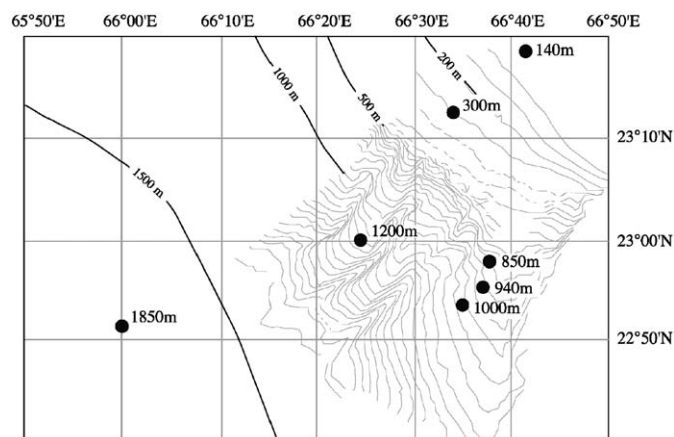


Fig. 1. Location of the main study sites on the Pakistan Margin.

these main stations, and particularly across the lower boundary of the OMZ (Levin et al., 2009).

Environmental data for the main stations and some additional sites during different seasons are summarised in Table 2. At 140-m depth, the bottom-water oxygen values changed dramatically between the two sampling periods, from fully oxic during the intermonsoon to severely dysoxic during the late/post-monsoon season. This change reflected an upward shift in the upper boundary of the OMZ from ~180 to ~80 m over a period of about 5 months (Bett, 2003b; Brand and Griffiths, 2009), presumably driven by monsoonal winds. Based on the depth and the 2003 oxygen profiles, we recognise the following components of the Pakistan Margin OMZ in 2003:

- (1) *Seasonally hypoxic zone*, 130–250 m; O_2 at 140 m = 0.11 (intermonsoon), 2.05 mL L⁻¹ (late/post-monsoon). Interval within which oxygen concentrations fluctuate in response to upward and downward shifts in the upper OMZ boundary. The lower limit is defined by the appearance of laminated sediments. Whether this seasonal fluctuation occurs every year is unknown.
- (2) *OMZ core*, 250–750 m; O_2 = 0.10–0.12 mL L⁻¹ (intermonsoon), 0.12–0.14 mL L⁻¹ (late/post-monsoon). Interval where oxygen concentrations are lowest. Characterised by uninterrupted sediment laminations and the absence of obvious burrows. For convenience, we refer to the ‘upper’ (250–500 m) and ‘lower’ parts (500–750 m) of the OMZ core, but this division is arbitrary and not based on any biological or biogeochemical criteria.
- (3) *Lower OMZ transition zone*, 750–1000 m; O_2 = 0.12–0.15 mL L⁻¹ (intermonsoon), 0.13–0.17 mL L⁻¹ (late/post-monsoon). Interval spanning the progressive change from laminated to fully bioturbated sediments. Characterised by rapid faunal changes with depth.

Table 2
Environmental data (mean values) for Pakistan Margin sites.

Parameter	140 Inter	140 L/P	300 Inter	300 L/P	700 L/P	850 L/P	940 Inter	940 L/P	1000 Inter	1000 L/P	1100 L/P	1200 Inter	1200 L/P	1850 Inter	1850 L/P
T (°C) ^a	22.5	18.2	15.5	14.8	11.2	10.1	9.0	9.3	ND	ND	8.0	7.2	7.3	3.5	3.7
Salinity ^b	36.4	36.0	36.0	35.8	ND	ND	35.5	35.4	ND	ND	ND	35.2	35.4	34.8	34.8
O ₂ (mL L ⁻¹) ^c	2.05	0.11	0.10	0.11	0.13	0.14	0.13	0.15	0.15	0.17	0.23	0.33	0.32	1.78	1.65
O ₂ (μM) ^c	91.47	4.91	4.46	4.91	5.80	6.25	5.80	6.69	6.69	7.59	10.26	14.73	14.28	79.43	73.63
Depth of O ₂ penetration (mm) ^b	3.0	ND	~0	~0	ND	ND	>4.0	>4.0	ND	ND	ND	>5	2.5	16	12
% C _{org} (0–2 cm) ^{d,e}	1.46	1.43	2.36	2.56	2.64	3.14	3.53	3.60	2.69	3.14	3.14	3.42	4.12	1.12	1.00
% TN (0–2 cm) ^e	0.183	0.181	0.268	0.328	0.31	0.36	0.42	0.44	0.33	0.38	0.39	0.42	0.50	0.16	0.16
C/N (0–2 cm) ^e	9.15	8.94	9.97	11.78	9.36	9.38	9.70	9.70	9.45	9.53	9.38	9.63	9.70	8.44	7.65
OM quality (DI) ^f	ND	–0.99	ND	–0.40	ND	ND	ND	0.48	ND	ND	ND	–0.49	ND	ND	–1.17
Sulphate reduction (μM m ⁻² d ⁻¹) ^g	0.23	0.23	0.04	ND	ND	~0	ND	ND	ND	~0	0.03	ND	ND	ND	ND
Denitrification (nitrate flux mmol m ⁻² d ⁻¹) ^h	0.54–1.56	1.56	0.60	2.71	ND	ND	ND	ND	ND	ND	ND	ND	0.10	1.89	–0.23 ⁱ
Total pigments μg (g dry sediment) ^a	7.7	6.2	29.0	40.4	ND	ND	35.5	28.1	ND	ND	ND	8.9	31.1	0.80	1.20
Phaeopigment/chlorophyll α ^a	8.0	7.0	33.0	48.8	37.4	43.2	26.5	29.3	ND	ND	9.9	8.6	30.4	0.81	1.47
Macrofaunal biomass (g(wet) m ⁻²) ^j	6.79	4.26	v. low	v. low	ND	ND	66.5	25.0	ND	ND	ND	0.36	5.27	9.28	1.57
Sediment properties: ^k															
% Clay		34.28		35.75	ND	ND		34.88	ND	ND	ND		35.61		35.81
% Silt		65.6		64.25	ND	ND		65.11	ND	ND	ND		64.39		64.39
% Sand		0.06		0.00	ND	ND		0.01	ND	ND	ND		0.00		0.01
% CaCO ₃ ^e	20.5		21.5	14.1	ND	ND	20.7	20.4	ND	ND	ND	22.6	25	21.2	23.2

Data for some additional sites are given by Levin et al. (2009). ND = no data.

^a Woulds et al. (2007), Woulds and Cowie (2009).

^b Breuer et al. (2009).

^c Levin et al. (2009) and CTD records.

^d Levin et al. (2009).

^e Cowie and Levin (2009).

^f Vandewiele pers commun. (in Woulds and Cowie, 2009).

^g Law et al. (2009).

^h Schwartz et al. (2009).

ⁱ This negative nitrate flux (indicating no denitrification) is contradicted by N₂ production suggesting that denitrification is occurring (Schwartz et al., 2009).

^j Hughes et al. (2009).

^k G. Law (pers. commun.).

(4) *Lower OMZ boundary, 1000–1300 m.* The lowest part of the OMZ characterised by fully bioturbated and oxidised sediments and extending to the depth at which oxygen levels reach 0.5 mL L⁻¹.

A notable feature of the Pakistan Margin OMZ is virtual absence of sulphate reduction (Law et al., 2009).

3. Materials and methods

3.1. Sampling and analysis methods

3.1.1. Foraminiferans and macrofauna

Foraminiferans were sampled using a Barnett-type multicorer (Barnett et al., 1984) equipped with core tubes of 57 mm internal diameter (25.5 cm² cross-sectional area) and a megacorer fitted with tubes of 96 mm diameter (72.4 cm² surface area). At the 140 and 300 m sites (Table 1), four replicate megacores from each season (cruises CD 146 and 151) were processed as follows (Larkin and Gooday, 2009). The upper 1 cm was sliced into two layers, each 0.5 cm thick, below which the core was cut into 1-cm-thick layers to a depth of 5 cm. These sediment slices were fixed in 10% formalin buffered with borax. Single unreplicated multicores from the main sites and some additional sites, collected during the intermonsoon season (CD 145, 146), were processed and fixed in the same way for a micropalaeontological study of benthic foraminiferans (Schumacher et al., 2007).

In the laboratory, fixed sediment slices from the four replicate faunal megacores were washed through a 300-μm screen and stained overnight on the sieve in rose Bengal (Larkin and Gooday, 2009). All stained benthic foraminiferans, both hard- and soft-shelled, were sorted in water in order to study seasonal changes in

larger foraminiferans (>300 μm). The micropalaeontological samples were treated as follows (Schumacher et al., 2007). Each sediment slice was wet sieved over 63, 150 and 300-μm screens and the residues stained for 1 week in ethanol with Rose Bengal. The residues were then washed again, and stained hard-shelled foraminiferans picked in water from three size fractions (63–150, 150–300 and >300 μm), down to 10 cm depth.

Additional megacore sediments were sorted unstained and unfixed on the ship to obtain foraminiferans for biochemical and isotopic studies. They were sieved on a 300-μm screen, the residues placed in a Petrie dish on ice and foraminiferans and metazoans picked as soon as possible after collection. These samples provided semi-quantitative information on larger foraminiferans.

Macrofauna were sampled at the main sites (140, 300, 940, 1200 and 1850 m water depths) during all cruises using a megacorer (see above, Hughes et al., 2009). Additional sites across the lower transition zone were sampled in the same way during cruises CD 146 and 151 (Levin et al., 2009). At least one core per deployment was sliced into the following layers: 0–0.5, 0.5–1.0, 1–2, 2–3, 3–5, 5–10 and 10–20 cm. Other cores were cut into two layers, 0–10 and 10–20 cm. Each slice was kept in 10% buffered formalin for 2–3 days before being washed through a 300-μm screen using filtered seawater. The sieved residues were stored in 10% formalin and then sorted in the laboratory under a dissecting microscope. All taxa were identified to the lowest taxonomic level possible.

Foraminiferal biomass was calculated using the linear regression formulae developed by Altenbach (1985) and later used by Kurbjewit et al. (2000) to estimate biomass in deep Arabian Sea foraminiferans. Since test size was not measured directly, but estimated from sieve sizes used to retain the foraminiferans, the resulting biomass values must be regarded as very approximate.

Wet weight biomass of macrofaunal specimens was measured on a Sartorius top-pan electronic balance after careful blotting on absorbent paper to remove surface liquid (Hughes et al., 2009).

3.1.2. Megafauna

Megafauna, defined as large animals visible in bottom photographs or caught in trawl samples, included the benthopelagic megafauna (swimming animals, mainly fish and decapods) and the invertebrate megabenthos (large benthic animals) (Murty et al., 2009). Large polychaetes and protists (foraminiferans and gromiids) were excluded from the invertebrate megabenthos *sensu strictu*. Megafauna were collected using an Agassiz trawl with a frame 3 m wide and 0.5 m high and a cod-end mesh size of 500 μm . Animals and gromiids were sorted on board ship into main taxonomic groups and preserved in 10% buffered formalin.

Seabed photographic surveys were conducted during the late monsoon season (CD 150) using a wide-angle seabed photography system (WASP) (Murty et al., 2009). This consisted of a tubular steel frame, 3 m in length, on which was mounted a downward-facing camera, continuous video camera, two video lamps, a flash unit and altimeter, operated via an acoustic telemetry system. WASP was towed at ~ 0.5 knots and kept between 2 and 4 m from the seabed by reference to the altimeter. Photographs and video were only recorded within a preset range of 1–10 m from the seabed. WASP was deployed for either 30 or 60 min, and still photographs were recorded every 10 s on 35-mm Kodak Vision 250D colour negative film. The photographs were viewed on a Carl Zeiss Jena DLZ Dokumat film reader and the type and number of visible megafaunal organisms recorded in all photographs suitable for analysis. Organisms were identified to the lowest possible taxonomic level by comparison with specimens collected by the Agassiz trawl. The area of the sea floor visible in each photograph was calculated from the angle of the camera with respect to the seabed and its altitude above the seabed. Total numbers were standardised to a surface area of 1 ha.

3.1.3. Metazoan meiofauna

Metazoan meiofauna were not analysed systematically. During CD151, Ludox floatation followed by centrifugation was used to concentrate meiofaunal organisms at the 300-m site, but the residue yielded remarkably few individuals, almost all of them nematodes. Nematodes and occasional ostracods of macrofaunal size were recorded in the $>300\text{-}\mu\text{m}$ fractions of core samples from the 140 and 300-m sites (Larkin and Gooday, 2009).

3.1.4. Environmental parameters

We include a selection of the physical and biochemical parameters measured during the Pakistan Margin project (Table 2). Bottom-water oxygen concentrations were taken from CTD profiles obtained during CD145 and CD150 (Bett, 2003a,b; Levin et al., 2009). Detailed information about other methods can be found in the papers cited in footnotes to Table 2.

3.1.5. Diversity

We used a small set of diversity measures that are in common use in either the marine biological literature or the foraminiferal literature.

$E(S_{100})$ = expected number of species in a rarefied sample of 100 individuals (Hurlbert, 1971).

H' = Shannon–Wiener diversity index (\log_e) (Shannon and Weaver, 1963).

α = Fisher alpha index (Fisher et al., 1943).

R1D = rank 1 dominance (% abundance of the top-ranked species).

4. Results

This section synthesises the results of a number of studies, either published in the present volume or elsewhere, combined with unpublished data on foraminiferans and on trawl samples. All faunal groups were analysed at the five main sites (140, 300, 940, 1200 and 1850 m), but data for some taxa were also obtained from additional stations located at or around 133, 250, 274, 300, 400, 512, 600, 700, 738, 850, 900, 1000 and 1100 m water depth.

4.1. General trends among main faunal groups

4.1.1. Abundance

The main faunal groups exhibited different patterns of abundance in relation to the OMZ (Fig. 2). Foraminiferans were present across the entire transect. The density of smaller ($>63\text{ }\mu\text{m}$) hard-shelled species in unreplicated multicores peaked (1020 indiv. 10 cm^{-2}) at 738 m in the lower transition zone, was somewhat depressed (257–371 indiv. 10 cm^{-2}) at 150–512 m in the OMZ core, higher at 136 and 598 m (485 and 428 indiv. 10 cm^{-2}), with lowest values (43–200 indiv. 10 cm^{-2}) below 800 m depth (Schumacher et al., 2007). Larger foraminiferans ($>300\text{ }\mu\text{m}$), including soft-shelled species, were the dominant macrofaunal organisms at 140 m and particularly at 300 m where oxygen values were lowest and metazoan macrofauna rare (Larkin and Gooday, 2009). Their abundances in replicate megacorer samples increased during the post-monsoonal season. Gromiids were confined to regions below the lower transition zone (Gooday and Bowser, 2005; Aranda da Silva and Gooday, 2009). They first appeared in megacores at 1000 m and were common in trawl samples from 1174 to 1177 and 1620 to 1852 m (Fig. 3).

Considering only the five main sites, mean metazoan macrofaunal densities in the intermonsoon and post-monsoon periods were highest at 140 m (respectively, 15,909 and 10,945 indiv. m^{-2}), followed by 940 m (5218 and 3691 indiv. m^{-2}) and 1850 m (4582 and 4581 indiv. m^{-2}) (Fig. 2). They were very scarce (127 and 223 indiv. m^{-2}) in cores from 300 m and present in low numbers (955 and 509 indiv. m^{-2}) at 1200 m (Hughes et al., 2009). Sampling for macrofauna at 50-m depth intervals across the lower OMZ boundary revealed very few animals at 700 and 750 m, higher densities at 800 m, at least during the post-monsoon season, and highest densities at 850 and 950 m. Progressively lower numbers of macrofauna were found at deeper sites (1000, 1050 and 1100 m) across this transition zone (Levin et al., 2009).

Twenty-seven Agassiz trawl samples taken during the four cruises provided information on megafauna and larger macrofauna. Invertebrates were present at 134–138 m in the seasonally hypoxic zone during the intermonsoon season but were absent in two trawls taken in the OMZ core (299–341 m) and one trawl from 758 to 777 m. They reappeared at 878–890 m and were present in all deeper catches. Detailed analyses of megafaunal animals in WASP photographs obtained during CD150 revealed a similar pattern (Fig. 2). Invertebrate megabenthos were rare (187 indiv. $\text{ha}^{-1} = 0.019\text{ indiv. m}^2$) at 140 m and absent between 300 and 900 m, where the only strictly benthic organisms visible were bacterial mats at 300, 400, 500 and 600 m depth. However, the most striking feature of this survey was the enormous megafaunal density, almost 280,000 indiv. ha^{-1} ($= 28\text{ indiv. m}^{-2}$), at 1000 m. Densities were much lower at 1100 and 1200 m (5206 and 6983 indiv. $\text{ha}^{-1} = 0.52$ and $0.70\text{ indiv. m}^{-1}$, respectively) and lower still at 1850 m (167 indiv. $\text{ha}^{-1} = 0.017\text{ indiv. m}^{-1}$). Fish and natant decapods (benthopelagic megafauna) were the only live organisms captured in trawl samples at 299–341 and 758–777 m. Undifferentiated natant decapods were abundant in photographs from 1100 m (Murty et al., 2009).

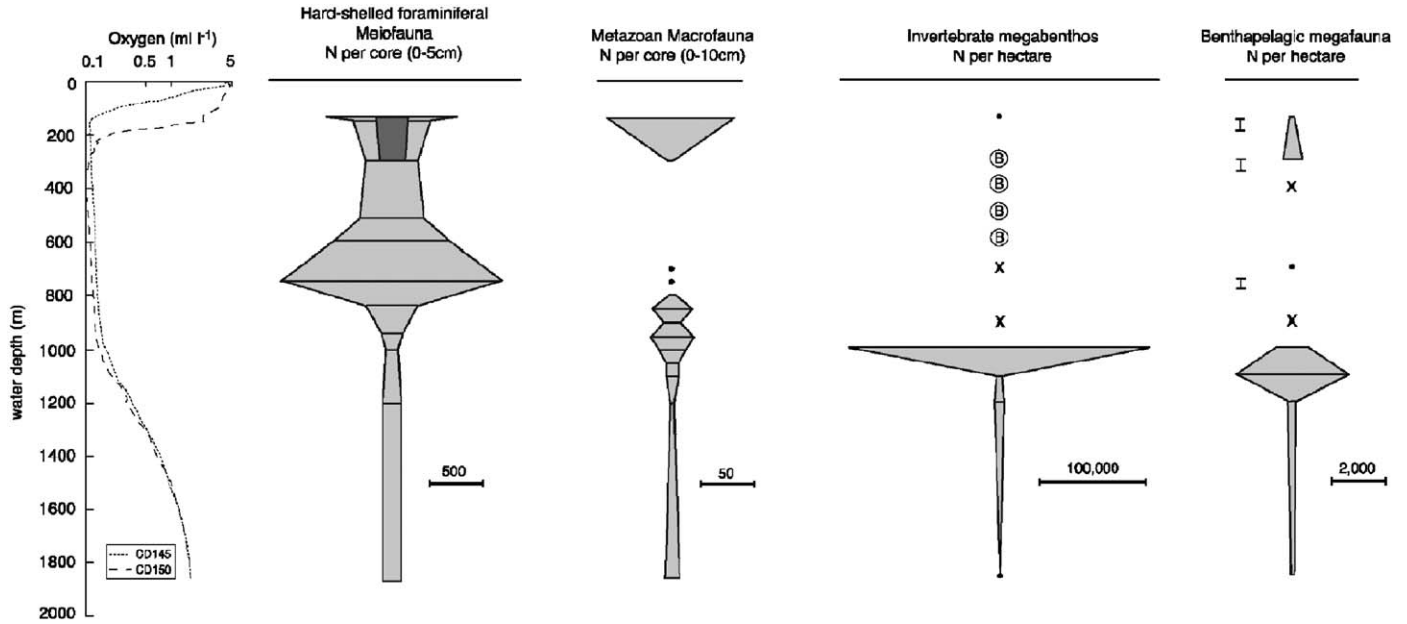


Fig. 2. Bathymetric distribution and abundance of different faunal groups across the Pakistan Margin OMZ. Invertebrate megabenthos and benthopelagic megafauna (fish, natant decapods and octopods) based on WASP photographs (Murty et al., 2009). Metazoan macrofauna based on megacore samples (Hughes et al., 2009; Levin et al., 2009). Hard-shelled foraminifera based on multicorer samples (Schumacher et al., 2007); the superimposed darker trapezoid indicates the abundance of macrofaunal foraminifera in megacorer samples at 140 and 300 m (Larkin and Gooday, 2009). Filled circles indicate numbers that are too small to represent accurately. Crosses indicate absence. For the invertebrate megafauna, 'B' indicates the occurrence of patches of filamentous bacteria. For nekton, the short vertical lines indicate occurrences in trawl samples. Oxygen profiles for the intermonsoon (CD145) and late monsoon (CD 150) seasons are shown on the left-hand side.

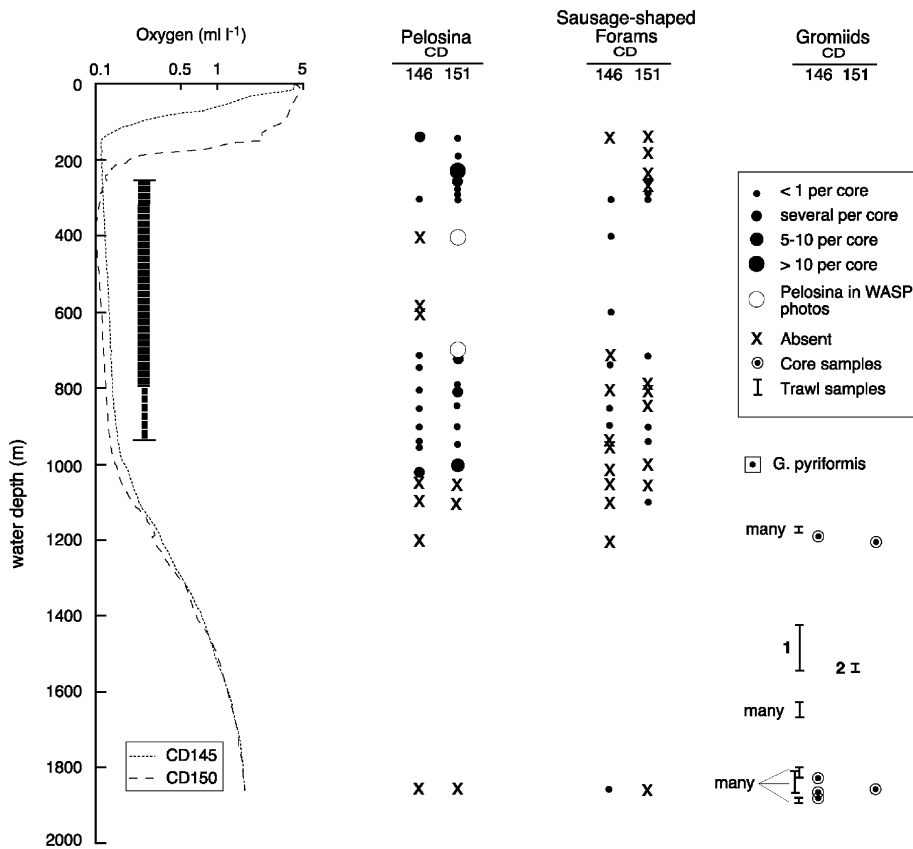


Fig. 3. Distribution of arborescent foraminiferan *Pelosina*, sausage-shaped, monothalamous foraminiferans and gromiids in WASP photographs (*Pelosina*), megacores (*Pelosina* and gromiids), multicores (monothalamous foraminiferans) and trawl samples (gromiids) across the Pakistan Margin OMZ. Records for the intermonsoon (CD146) and late/post monsoon (CD151) seasons are indicated separately. The abundance of gromiids (1, 2 or many) is indicated for the trawl samples. The vertical black bar with the white horizontal lines shows the depth interval across which the sediments are laminated; the laminations progressively disappear between 800 and 940 m (narrower part of bar).

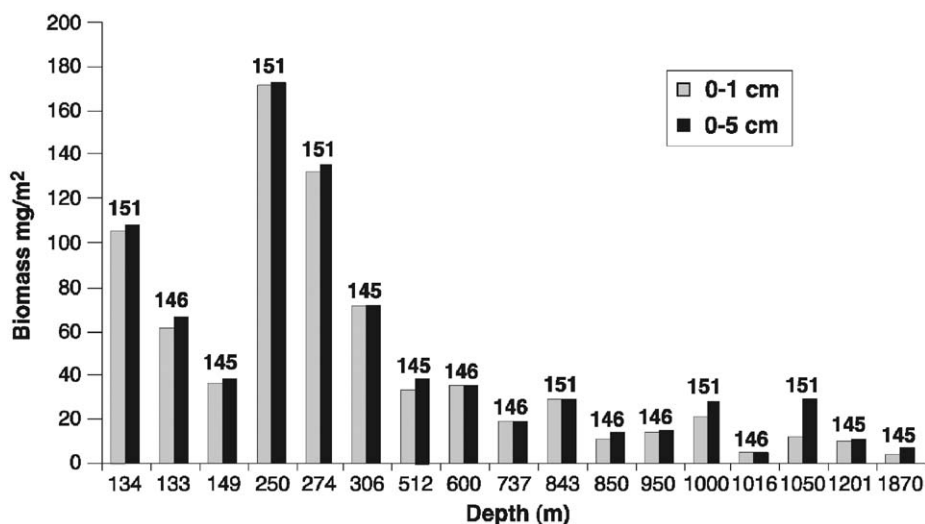


Fig. 4. Biomass of small, hard-shelled foraminiferans (>63 µm fraction) at different depths across the Pakistan Margin OMZ. The data are derived from samples collected during the intermonsoon (CD145, 146) and late/post monsoon (CD 151) seasons.

To summarise, foraminiferal densities (>63 µm fraction) were only slightly depressed within the OMZ core (300–500 m) and exhibited a peak around the upper limit of the lower transition zone (700–800 m) at depths where the macrofauna and invertebrate megabenthos were largely absent. Very few macrofauna were present between 300 and 750 m but densities were maximal at 850–950 m within the lower transition zone. Except for the benthopelagic megafauna, large animals were also excluded from the OMZ core. They peaked in abundance at a slightly greater depth (1000 m) than the macrofauna. In all groups, densities declined sharply at 1200 m and below.

4.1.2. Biomass

Foraminiferal and macrofaunal biomass exhibited different trends with depth. Rough estimates of the biomass of hard-shelled foraminiferans in the >150-µm fraction, derived from samples collected during different cruises, were highest at 250 and 274 m (CD151) and also high at 134 m (CD151), 133 m (CD146) and 306 m (CD145) (Fig. 4) (Schumacher, unpublished). Values were lower below 300 m and tended to decrease with increasing water depth. Wet weight macrofaunal biomass at the main stations reached a distinct maximum at 940 m, particularly during the intermonsoon season. The larger size of macrofaunal animals at this site, compared with those at 140 m, was partly responsible for this peak (Hughes et al., 2009; Levin et al., 2009).

4.1.3. Diversity

Foraminiferal species richness (>63-µm fraction) was highest within the seasonally hypoxic zone and at 738 m, with additional peaks at 1201 and 1870 m, and lower in the OMZ core and lower transition zone (Schumacher et al., 2007) (Table 3). When species richness was normalised to 100 individuals ($E(S_{100})$), the peak at 738 m disappeared; values were highest at 140–150 and 940–1850 m and depressed in the OMZ core. Species diversity measured by the Fisher α index, which emphasises species richness, showed a similar pattern; highest at the two shallowest (136–150 m) and the four deepest (944–1870 m) sites, and depressed between 306 and 844 m, except at 738 m. The Shannon–Wiener index (H'), which takes into account the distribution of specimens amongst species (i.e. evenness), was also highest at the four deepest stations and the 136-m site but lower between 150 and 844 m. Unlike the Fisher index, H' was

lowest at 738 m. Rank 1 dominance fluctuated across the transect; it was maximal at 738 m, coinciding with the highest densities, followed by 150 and 844 m depth. The depression of diversity in the OMZ core (300–598 m) was most evident in the 63–150 µm fraction (Schumacher et al., 2007). For foraminiferans in the >300-µm fraction, rarefied species richness ($E(S_{100})$) and diversity (Fisher α and Shannon–Wiener indices) were generally higher, and dominance lower, in replicate samples from the 140-m site compared to the 300-m site (Larkin and Gooday, 2009).

Polychaete species richness peaked at 140 and 1850 m, was lower at 940 m and lowest at 1200 m where densities were also depressed (Table 3) (Hughes et al., 2009). Values of $E(S_{100})$, the Fisher α and Shannon–Wiener indices were also highest at the shallowest and deepest sites. However, in all cases, these indices were substantially larger at 1850 m than at 140 m, reflecting the much lower polychaete densities at this deep site. Dominance was relatively high (typically 20–30%) at 140, 940 and 1200 m depth and considerably lower at 1850 m (8.1–8.5%). The number of identified polychaetes was too low to calculate diversity parameters at 300 m. It is notable, however, that 4 species were represented amongst the 9 individuals picked from core samples at this site. Across the lower transition zone, macrofaunal diversity and species richness were low between 750 and 850 m, increased steeply between 850 and 900 m to reach a peak at 1000 m before declining at 1050 and 1100 m depth (Levin et al., 2009). Dominance showed the opposite trend, with the amphinomid polychaete *Linopherus* sp. comprising nearly 100% of macrofaunal animals at the 800-m site.

Among the invertebrate megabenthos (excluding polychaetes and protists) in WASP photographs, only natant decapods (undifferentiated species) were visible at 300 m depth in the OMZ core (Murty et al., 2009). Elsewhere, species numbers were maximal at 1100 and 1200 m. $E(S_{100})$ and Shannon–Wiener values were highest at 1100 m, whereas the Fisher α index peaked at 140 m (Table 3). The two diversity indices were lowest, and dominance highest, at the 1000-m site where 99% of animals in the photographs were ophiuroids. Dominance was lowest at 140 and 1850 m.

To summarise, trends in diversity across the OMZ varied between faunal groups. Foraminiferal diversity (>63-µm fraction) was somewhat depressed in the OMZ core and lower transition zone (300–940 m) and highest at the shallowest and deepest stations. Macrofaunal diversity increased steeply across the lower

Table 3
Summary of diversity indices for main faunal groups.

Depth (m)	Hard-shelled foraminifera (> 63 µm)						Polychaetes						Megafauna in WASP photographs					
	N	S	E(S ₁₀₀)	H'	α	R1D	N	S	E(S ₁₀₀)	H'	α	R1D	N	S	E(S ₁₀₀)	H'	α	R1D
140	123	37	19.0	2.38	7.2	32.7	458	54	29.9	3.08	15.9	21.0	285	8	2.20	0.68	4.07	52.6
150	714	34	16.1	2.03	7.3	41.5	299	46	29.3	3.06	15.2	19.1	*	*	*	*	*	*
300	895	24	12.2	1.94	4.5	31.8	4	2	–	–	–	–	183	1	–	–	–	–
400	*	*	*	*	*	*	5	3	–	–	–	–	0	0	0	0	0	0
512	630	20	13.1	2.15	3.9	29.5	*	*	*	*	*	*	*	*	*	*	*	*
598	1108	17	12.9	2.10	2.8	28.2	*	*	*	*	*	*	*	*	*	*	*	*
700	*	*	*	*	*	*	*	*	*	*	*	*	0	0	0	0	0	0
738	2097	38	11.8	1.70	6.1	51.1	*	*	*	*	*	*	*	*	*	*	*	*
844	523	17	11.5	1.86	3.4	40.0	*	*	*	*	*	*	*	*	*	*	*	*
900	*	*	*	*	*	*	*	*	*	*	*	*	0	0	0	0	0	0
940	169	24	18.8	2.36	7.6	27.8	189	14	11.2	2.94	3.49	28.6	*	*	*	*	*	
1000	65	20	20.0	2.39	9.9	35.4	67	15	15.0	2.17	6.00	31.3	280,654	10	1.66	0.05	0.69	99.2
1100	*	*	*	*	*	*	*	*	*	*	*	*	8998	13	8.44	1.58	2.31	74.2
1200	140	28	25.5	2.90	10.5	17.9	11	6	6	1.67	5.40	27.3	7041	13	5.50	0.58	1.47	86.5
1850	157	32	25.4	2.62	12.2	29.9	29	11	11	2.20	6.46	20.7	208	7	1.33	0.33	1.89	63.9
							69	46	46	3.69	60.3	8.53						
							82	48	48	3.62	48.5	6.62						

For the polychaetes, the data are given for the intermonsoon (upper figure) and post-monsoon seasons. The foraminiferal data are based on unreplicated cores from the intermonsoon season (CD145/146). The megafaunal data are based on WASP photographs obtained during the late monsoon (CD150). N = number of individuals; S = number of species; E(S₁₀₀) = species numbers normalised to 100 individuals by rarefaction; H' = Shannon–Wiener diversity index (log_e); α = Fisher alpha index; R1D = rank 1 dominance (% abundance of the top-ranked species); * = no data; dashes mean that numbers were too low to calculate diversity indices.

transition zone from low values at 750–850 to a strong peak at 1000 m depth. Polychaete and megabenthic diversity was either minimal or zero in the OMZ core (250–750 m), reflecting the scarcity of larger animals in this region, and peaked at 1850 m for polychaetes and 1100 m for megafauna.

4.2. Patterns of zonation within main faunal groups

4.2.1. Community trends across the OMZ profile

Obvious trends in the taxonomic composition of different faunal groups were evident across the OMZ.

4.2.1.1. Foraminiferans. Calcareous individuals constituted 80% or more of the smaller, hard-shelled foraminiferans (> 63 µm fraction) at 136–306 m depth compared with < 50% at deeper stations (512–1870 m) where agglutinated species were relatively more important (Schumacher et al., 2007). Buliminids and rotaliids predominated among the calcareous component. Biserial and triserial morphotypes typically made up more than 80% or 90% of live calcareous individuals down to 738 m depth and remained relatively abundant at the 844-m site. At deeper stations, these morphotypes constituted a variable but usually smaller proportion of the much-reduced calcareous foraminiferal standing stock. At the species level, there was a switch at ~500 m depth within the OMZ core from dominance by apparently endemic species, notably *Uvigerina* ex gr. *semiornata* and *Bolivina* aff. *dilatata*, to more cosmopolitan taxa such as *Chilostomella* spp., *Globobulimina* spp., *Praeglobobulimina* spp. and *Uvigerina peregrina* (Schumacher et al., 2007).

Calcareous individuals represented 76–85% of stained foraminiferans > 300 µm at 140 m and 57–68% at 300 m depth (Larkin and Gooday, 2009). There was no major change in assemblage composition between the two seasons at the 140-m site, despite the sharp reduction in oxygen concentrations from 2.0 mL L⁻¹ (intermonsoon) to 0.1 mL L⁻¹ (post-monsoon). The top-ranked species, *Uvigerina* ex gr. *semiornata*, was the same in both cases. However, there was a notable increase in carbon processing by these foraminiferans after the monsoon (Woulds et al., 2007).

Additional data on the relative abundance of different foraminiferal groups were acquired during shipboard sorting of 300-µm residues (Fig. 5). Although unstained, most foraminiferans were probably live based on the presence of visible cytoplasm. These data are not precise, but they do reflect the approximate proportions of different foraminiferal groups at the main stations, except at 1850 m where numbers were low. Calcareous taxa (buliminids and rotaliids) predominated at 140 and 300 m while agglutinated taxa (mainly *Reophax* and *Hormosina*) predominated at 950, 1200 and 1850 m depth. Species of Komokiaceae, a deep-sea taxon currently included in the Foraminifera, were an important faunal element at the deepest stations. Although never common, soft-shelled monothalamous foraminiferans (allogromiids and saccamminids) were distributed across the entire transect in the > 300 µm fraction. The saccamminids included sausage-shaped species with two terminal apertures which spanned most of the OMZ (250–1100 m) (Figs. 3 and 6C–D). A tree-like *Pelosina* species occurred over a similar depth range. It was common in megacores from around 230 and 1000 m, generally uncommon in the OMZ core, but visible in WASP photographs at 400 and 700 m (Figs. 3 and 6A–B). Gromiids were most common below 1150 m where oxygen levels exceeded 0.20 mL L⁻¹ (Aranda da Silva and Gooday, 2009), although a single species occurred around 1000 m (Gooday and Bowser, 2005).

4.2.1.2. Metazoan macrofauna. Different taxa exhibited different patterns of abundance across the OMZ. The absolute abundance of polychaetes, the dominant group, mirrored that of the macrofauna as a whole. Overall, polychaetes represented > 50% of metazoan macrofaunal density and most of the biomass. They accounted for 76–87% of macrofaunal animals at 140 m, 60–79% at 940 m, 42–65% at 1200 m and 52–55% at 1850 m depth (Hughes et al., 2009). The majority (62–83%) of the very sparse macrofauna at 300 m were polychaetes. The amphinomid polychaete *Linopherus* sp. represented > 85% of macrofaunal individuals between 750 and 850 m (Levin et al., 2009). Molluscs were always less abundant than polychaetes. They constituted a lower percentage (0–10%) of the macrofauna at 140 and 300 m, compared to 14–26%

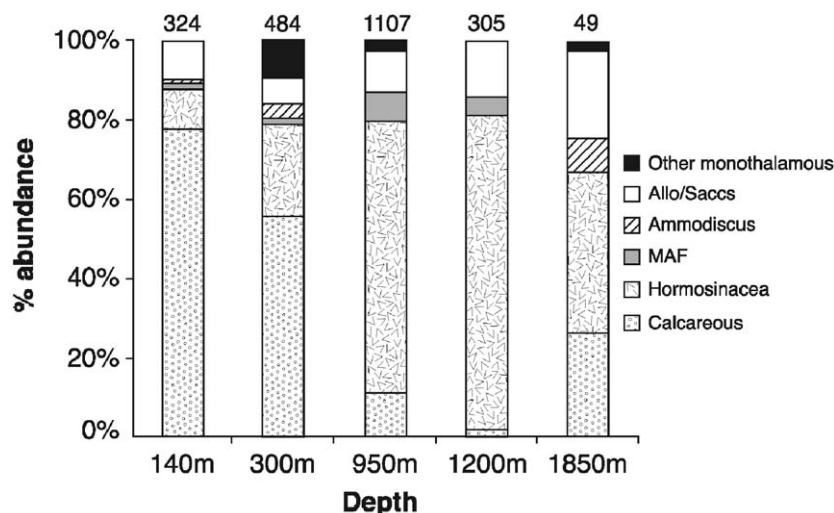


Fig. 5. Relative proportions of different foraminiferal groups at the main study sites, based on shipboard sorting of unstained >300 μm residues. The total numbers of specimens examined are indicated at the tops of the columns. MAF = multichambered agglutinated foraminiferans.

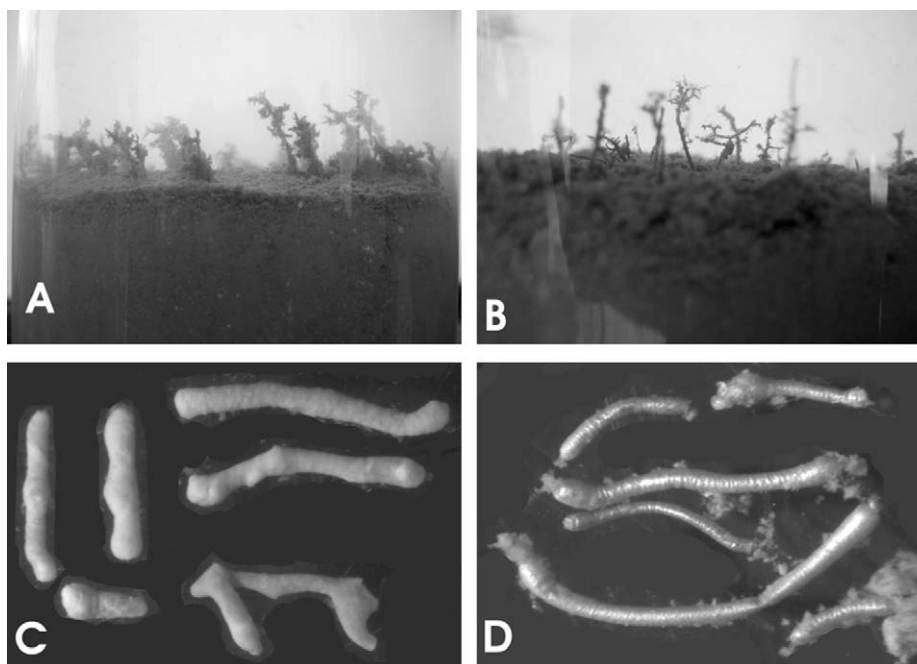


Fig. 6. Foraminiferans from the Pakistan Margin OMZ. (A–B) Tree-like species of *Pelosina* resembling *P. arborescens*: (A) Stn 56109#1, 232 m water depth; (B) 56122#1, 1000 m. The core tubes are 10-cm diameter. (C–D) Sausage-shaped agglutinated monothalamous foraminiferans. (C) White species from Stn 56113, 710 m; (D) brownish species with reflective surface from Stn 56107#2, 300 m.

at the deeper sites (950, 1200 and 1850 m). Crustaceans were fairly common at 950 m (13% during the post-monsoon season), 1200 m (13–14%) and 1850 m (18–30%), but represented <10% of the macrofauna at 140 m and were absent at 300 m (Hughes et al., 2009). Echinoderms always accounted for <10% of the macrofauna and were absent at 300 and 1850 m. With rising oxygen concentrations within the lower transition zone (700–1100 m), molluscs and crustaceans reappeared at 900 m and echinoderms (mainly ophiuroids) at 950 m (Levin et al., 2009). Nemerteans were confined to 300 m (Hughes et al., 2009).

4.2.1.3. Invertebrate megabenthos. Shifts in megabenthic assemblage composition with depth were even more abrupt than those

for foraminiferans and metazoan macrofauna (Murty et al., 2009). Gastropods, asteroids, ophiuroids and crabs were seen in WASP surveys at 140–200 m depth but demersal fish and natant decapods were the only animals visible in the OMZ core (300 and 700 m). Ophiuroids were almost entirely responsible for the massive abundance peak at 1000 m. Densities were still fairly high at 1100 m where the megafauna was most diverse and included pennatulids, crinoids, holothurians, anemones and other cnidarians in addition to ophiuroids. Many small burrow openings were observed on the sediment surface at this site. A diverse suite of ‘normal’ deep-sea animals and burrows was evident at deeper stations with tunicates being particularly numerous. Three Agassiz trawl samples taken in the seasonally hypoxic zone (134–182 m) yielded a diverse assemblage of small invertebrates

that were not visible in photographs. These included molluscs, crustaceans, a few echinoderms, anemones, polychaetes, and at 161–182 m, a large number of fish. Three hauls from the core of the OMZ (299–341 m) and from 758–777 m obtained only fish and natant decapods, consistent with the absence of invertebrate megabenthos in WASP images from this region. Seven trawl samples taken across the lower transition zone (800–1100 m) revealed a succession of different taxa, discussed below. Trawl catches from >1200 m were generally small but diverse with anemones, echinoderms, crustaceans, molluscs and sipunculan worms often much in evidence.

4.2.2. Depth ranges across the OMZ

The metazoan macrofauna underwent rapid, species-level changes with depth across the lower transition zone (Levin et al., 2009). Trawl catches also suggested a strong faunal zonation in this region. Burrowing edwardsiid anemones and polychaetes (*Linopherus* sp. and *Prionospio* sp.) were abundant at 878–890 m; ophiuroids and *Linopherus* sp. were abundant at 889–955 m; edwardsiid anemones, and small holothurians (*Psolus* sp.) were abundant, with subordinate numbers of other invertebrates (including pennatulids, tunicates and asteroids), at 961–1075 m. Many of the species identified by Murty (2005) from trawl samples across the lower transition zone and OMZ boundary (950–1200 m), had limited depth distributions, typically ~200 m or less. Species living below the OMZ, however, tended to have wider bathymetric ranges; for example, the polychaete *Hyalinoecia* sp. (1264–1832 m) and the echinoid *Phormosoma placenta* (1264–1705 m). The WASP photographs generally confirmed that many megabenthic animals had restricted bathymetric ranges in the lower part of the OMZ. Notably, ophiuroids were confined to the 1000 m site, where they were extraordinarily abundant, and the 1100 m site, where they were common. The widest-ranging megafaunal species within the OMZ was a synodontid fish (*Saurida tumbil*), present at the 300 and 700-m sites (Murty et al., 2009).

Foraminiferans appear to have wider depth ranges than the metazoans (Schumacher et al., 2007). *Uvigerina* ex gr. *semiornata* and *Bolivina* aff. *B. dilatata* were the main species in the seasonally hypoxic zone (136 and 150 m) and within the OMZ core (306 m) and both persisted down to 500 m depth. Other examples of foraminiferal species with wide bathymetric ranges included *Bulimina exilis* (300 and 1200 m), *Uvigerina peregrina* (500 and 1050 m), *Ammodiscus tenuis* (300 and 1000 m) and *Pelosina* sp. (140–1100 m).

4.2.3. Trends in lifestyles

Changes in lifestyles and trophic biology occurred in relation to the OMZ. Natural lipid analyses and tracer studies indicated that the abundant calcareous foraminiferans at 140 and 300 m fed on fresh algal material when it was available, whereas some agglutinated foraminiferans (including species of *Reophax* and *Ammodiscus*) had a larger bacterial component to their diet (Larkin, 2006; Woulds et al., 2007). Since agglutinated species, particularly hormosinaceans, become relatively more abundant with depth, we infer that a predominantly algal diet ('herbivory') was more prevalent at shallower sites while deposit feeding was more important at deeper sites. The komokiaceans that were common at 1850 m probably feed on sediment and associated bacteria and organic matter (Gooday et al., 2009). The large tree-like foraminiferan *Pelosina* sp. (Fig. 6C–D), which was a conspicuous feature of some megacores collected between 140 and 1100 m (Fig. 3), is a suspension feeder.

Among the polychaetes, surface feeders constituted the most abundant trophic group at all depths, with carnivores/omnivores

and subsurface deposit feeders generally less common (Hughes et al., 2009). Suspension feeders were usually either rare (1–2%) or absent, except the 1850-m site (~9%). Across the lower transition zone there was a shift from detritus feeding at 700–900 m, mainly by *Linopherus* sp., which constructs a permanent burrow, to surface deposit feeding by mobile burrowers and tube builders at 950–1100 m (Levin et al., 2009). Suspension-feeding bivalves (pectinids and thyasirids) were common between 900 and 950 m.

The megafauna at 140, 300 and 700 m depth were either mobile predators/scavengers (fish and crustaceans at all sites) or deposit feeders (echinoderms and molluscs, at 140 m only) (Murty et al., 2009). The megabenthic peak at 1000 m consisted almost entirely of mobile deposit feeders (ophiuroids). Large, sessile suspension-feeding animals, including pennatulids and other cnidarians, first appeared at 1100 m where they represented about two thirds of the visible megabenthos, the remainder comprising predator/scavengers and deposit feeders. The megabenthos at 1850 m was a similar mix of sessile suspension feeders (33%), mobile deposit feeders (11%) and predator/scavengers (56%). However, at 1200 m, where the tunicate *Asajirus indicus* was very abundant, 94% of the megafauna were sessile suspension feeders.

5. Discussion

5.1. Comparison of benthic faunas on the Pakistan and Oman margins

Oxygen profiles across the Oman and Pakistan margins showed a similar rapid decline within the upper 200 m and a gradual increase between 950 and 1300 m depth. However, oxygen concentrations in the OMZ core were lower (~0.10 mL L⁻¹) off Pakistan than on the Oman Margin (~0.13 mL L⁻¹) (Levin et al., 2000). Similarly, oxygen values in the deeper part of the OMZ were 0.32–0.33 mL L⁻¹ off Pakistan (1250 m) compared to 0.52 mL L⁻¹ off Oman (1200 m) (Table 5). Sediments were bioturbated across the Oman OMZ (Smith et al., 2000) but laminated in the Pakistan OMZ core (Hughes et al., 2009; Levin et al., 2009), reflecting the greater degree of hypoxia on the eastern side of the Arabian Sea. The sediments also contained a relatively high proportion of sand on the Oman Margin compared with the absence of sand on the Pakistan Margin (Table 2). The Oman Margin experiences more intense upwelling than the Pakistan Margin, and hence higher productivity and flux rates to the seafloor (e.g., Banse and McClain, 1986; Nair et al., 1989; Burkill et al., 1993). Although the percentage of organic carbon in the sediment at 1200 m on the Oman Margin is rather lower than at comparable depths off Pakistan, pigment concentrations are much higher (Table 5), suggesting a greater input of fresh organic matter or reduced utilisation in the water column.

Benthic faunas off Oman were studied in 1994 along a transect of the OMZ south of Masirah Island (Discovery Cruise 211; Gage et al., 2000) and further north between Muscat and the headland of Ra's al Hadd (Charles Darwin Cruise; Jacobs, 2003). Table 4 compares the results of these studies with those from the Pakistan Margin. The main points are as follows:

- (1) On both margins, foraminiferans were abundant in the OMZ core where the dominant species > 300 µm was *Uvigerina* ex gr. *semiornata*. Other macrofaunal species common to both margins included *Bolivina* aff. *dilatata*, *Bulimina exilis* and *Cancris auriculata*. However, the sausage-shaped monothalamous species which were a minor but distinctive component of the Pakistan assemblages, were apparently absent on the Oman Margin.

Table 4
Comparison of faunal characteristics on the Pakistan and Oman margins.

Pakistan	Oman: off Masirah Is and between Muscat and Ra's al Hadd	Reference
<i>Foraminiferans</i>		
Macrofaunal forams (>300 µm) common in OMZ. Mean abundance 86 indiv. 10 cm ⁻² (Intermonsoon); 122 indiv. 10 cm ⁻² (SW monsoon)	Macrofaunal forams common in OMZ off Masirah Is; densities = 31 indiv. 10 cm ⁻² and 71 indiv. 10 cm ⁻²	Gooday et al. (2000), Aranda da Silva (2005) and Larkin and Gooday (2009)
<i>Uvigerina</i> ex gr. <i>semiornata</i> dominates >300 µm fraction at 140 and 300 m	<i>Uvigerina</i> ex gr. <i>semiornata</i> dominates >300 µm fraction at 100 m off Masirah Is.	Gooday et al. (2000), Aranda da Silva (2005) and Larkin and Gooday (2009)
<i>Bulimina exilis</i> fairly common at 300–1200 m in finer fractions	<i>Bulimina exilis</i> fairly common in finer fractions at 100 and 400 m	Schumacher et al. (2007)
<i>Bolivina</i> aff. <i>dilatata</i> very common in >150 µm fraction at 140–600 m	<i>Bolivina</i> aff. <i>dilatata</i> common in finer fractions at 400 m	
<i>Cancris auriculus</i> common at 300 m (>300 µm)	<i>Cancris auriculus</i> occurs at 300 m (>300 µm fraction)	
Sausage-shaped saccamminids distributed throughout OMZ (250–1000 m)	Sausage-shaped saccamminids not present in either area of Oman margin.	Gooday and Larkin (unpublished)
<i>Pelosina</i> occurs across OMZ; most abundant at 230–250 m and around 1000 m.	Off Masirah Is., <i>Pelosina</i> first appears at 746 m; less common at 822–857 m. Also present at 792 and 800 m between Muscat and Ra's al Hadd	Gage (1995), Jacobs (2003) and Gooday and Larkin (unpublished)
<i>Gromiids</i>		
<i>Gromia pyriformis</i> at 1000 m. Various other species between 1174 and 1868 m; uncommon in cores (max 2 per core at 1192 m) but abundant in trawls from 1174–1177 and 1620–1852 m. <i>Gromia spherica</i> occurs between 1620 and 1852 m	Various species occur between 1093 and 2128 m between Muscat and Ra's al Hadd; abundant in cores from 1390 to 1698 m (up to 34 indiv. per megacore) and in trawl from 1260 m in same area. Off Masirah Is, <i>Gromia spherica</i> occurs between 1194 and 1633 m and grape and sausage-shaped species between 1252 and 1624 m	Gooday et al. (2000), Aranda da Silva and Gooday (2009) and Gooday and Bowser (2005)
<i>Macrofaunal metazoans</i>		
Macrofauna very scarce in OMZ core; mean density at 300 m = 223 indiv. m ⁻² (intermonsoon) and 127 indiv. m ⁻² (post-monsoon). Very low densities in OMZ core lead to much lower overall densities than on Oman Margin	Large, low-diversity populations in OMZ core off Masirah Is.; density = 12,362 indiv. m ⁻² at 400 m. Polychaete <i>Prionospio</i> (<i>Minuspio</i>) sp. dominant. Overall densities associated with OMZ much higher than on Pakistan Margin	Levin et al. (1997, 2000) and Hughes et al. (2009)
Abundance maximum at 950 m	Abundance maximum at 700–850 m	Levin et al. (2000) and Hughes et al. (2009)
Amphinomid polychaete <i>Linopherus</i> sp. dominant at 950 m	<i>Linopherus</i> sp. not present (only one amphinomid listed in Levin et al., 2000, Table 3)	Levin et al. (2000) and Levin et al. (2009)
Cirratulid mudballs present at 1850 m	Cirratulid mudballs common at 820–900 m; probably a different species	Levin and Edessa (1997) and Hughes et al. (2009)
Ampeliscid amphipods common at 900–1000 m	Ampeliscids occur at 700–850 m but are less common	Gage (1995), Levin et al. (2000) and Hughes et al. (2009)
<i>Megafaunal metazoans</i>		
Megafauna rare or absent in the OMZ core	Megafauna dominated by bivalve <i>Amygdalum anoxicolum</i> ; gastropods, ascidians and juvenile spider crabs (<i>Encephaloides armstrongi</i>) also present	Gage (1995) and Oliver (2001)
Gastropod <i>Tibia delicatula</i> uncommon (12 live, 6 dead) in trawls taken at 133–134 m during late monsoon; not seen in WASP photographs	Live individuals of <i>T. delicatula</i> common in trawl sample from OMZ core (400–500 m) between Muscat and Ra's al Hadd; large numbers seen in SHRIMP survey (300–450 m)	Ramirez-Llodra and Olabarria (2005)
Few spider crabs observed. Indeterminate ophiuroids very abundant at 1000 m	High density patches of spider crab <i>Encephaloides armstrongi</i> and ophiuroid <i>Ophiolimna antarctica</i> around 1000 m off Masirah Is.	Smallwood et al. (1999) and Murty (2005)

- (2) Gromiid densities were generally much higher on the Oman Margin than off Pakistan. Two species, one of them *Gromia sphaerica*, were common on both sides of the Arabian Sea but other species were apparently confined to one margin.
- (3) Overall, macrofaunal densities were considerably higher on the Oman than on the Pakistan Margin. Macrofauna were abundant in the core of the Oman OMZ but scarce on the equivalent part of the OMZ off Pakistan. The dominant species at 400 m off Oman, the spionid polychaete *Prionospio* (*Minuspio*) sp., was represented by occasional individuals on the Pakistan Margin.
- (4) Ampeliscid amphipods were fairly common at 700 and 850 m on the Oman Margin but were much less common off Pakistan, although some occurred at 900–1000 m.
- (5) There were similarities and contrasts among the megafauna. Ophiuroids were abundant around 1000 m on both margins. Molluscs were rare or absent in the core of the Pakistan OMZ (300 m) whereas bivalves and gastropods were fairly common at equivalent depths (300–450 m) on the Oman transects. Mudball-building cirratulids were present on both margins, but they appear to be different species and occur at different depths (800 vs 1850 m) (Levin and Edessa, 1997; Hughes et al., 2009). The spider crab *Encephaloides armstrongi* was the dominant megafaunal organism on the Oman Margin, and reached enormous densities (>100 indiv. m⁻²) within a 50-m wide depth band centred on 985 m (Smallwood et al., 1999), but was uncommon off Pakistan.

Table 5

Environmental characteristics in the OMZ core on the Oman and Pakistan margins of the Arabian Sea. Inter = intermonsoon; L/P = late/post-monsoon.

	Oman ^a 400 m	Pakistan 300 m			Oman ^a 1250 m	Pakistan 1200 m	
			Inter	L/P		Inter	L/P
Temperature (°C) ^a	13.3	15.5	14.8		6.7	7.2	7.3
Oxygen (ml/l) ^b	0.13	0.10	0.11		0.52	0.33	0.32
% C _{org} ^c	4.99±0.44	2.3±0.1	2.5±0.1		2.67±0.07	3.27	3.27
Pigments (µg/g dry sediment) ^a	770	29.0±6.2	40.4±17.8		68±26	8.6	
% CaCO ₃ ^c	55.1	14.5	14.1		66.1	20.7	20.4
% Sand (0–1 cm) ^d	22.3	0	0		56.8	0	0
Macrofaunal biomass (wet wt g m ⁻²) ^e	14.2±5.8	0.02±0.02	0.01±0.02		~3.6	0.36±0.81	5.27±8.13
Macrofaunal density (indiv. m ⁻²) ^e	12,362	159±122	486±817		2485	1018±422	987±433
Sediment laminations	Absent	Present	Present			Absent	Absent

^a Levin et al. (2000); sediment laminations from Smith et al. (2000).^b CTD records.^c Cowie and Levin (2009).^d G. Law, pers. commun.^e Hughes et al. (2009).

(6) Lower boundary edge effects were evident on both margins. Macrofaunal abundance maxima comprising mainly polychaetes were located at different depths (700–850 m on the Oman Margin, 850–950 m on the Pakistan Margin) but similar oxygen levels (0.16–0.17 mL L⁻¹). Off Oman, spionid, ampharetid, paraonid and cirratulid polychaetes were common in this zone. Off Pakistan, a single species of the amphinomid polychaete genus *Linopherus* dominated at 850 m with other polychaete taxa (acrocirrids, ampharetids and cossurids) important at 950 m.

Differences in oxygen and food availability probably explain why metazoan macrofauna were considerably more abundant in the Oman OMZ core (400 m) than on the Pakistan (300 m) margin. Environmental parameters at these two sites are summarised in Table 5. Compared to values off Pakistan, the bottom-water oxygen concentrations and the percentage of organic carbon were both slightly higher in the upper part of the Oman OMZ (400 m) while the pigment concentrations were much higher. It is presumably the slightly higher oxygen availability, combined with food-rich sediments, that allows the development of an abundant macrofauna at this site (Levin et al., 1997). However, the extremely low diversity of this assemblage, which consists largely (90%) of two polychaete species, suggests that very few macrofaunal species can tolerate bottom-water oxygen concentrations of 0.13 mL L⁻¹. Support for this suggestion comes from whole-community ¹³C-tracing experiments on the Pakistan Margin, which identify a threshold oxygen concentration between 0.11 and 0.13 mL L⁻¹. Above this threshold, metazoan macrofauna functioned efficiently and took up the algal food source, while below it they were out-performed by the foraminiferans (Woulds et al., 2007). On the Pakistan Margin, the low-oxygen concentrations, possibly in combination with lower OM inputs, serve to eliminate most macrofaunal animals. Comparison of these two margins generally supports the hypothesis that in hypoxic environments, oxygen depletion exerts a strong influence on species richness while food availability influences the abundance and dominance of particular species (Levin and Gage, 1998; Levin et al., 2009).

Other differences between faunas on the two sides of the Arabian Sea, particularly the presence or absence of certain taxa, are more difficult to explain. Similar contrasts in the taxonomic composition of macrofauna have been observed between the Peru (11°S) and Chilean (36°S) margins; oligochaetes are abundant in the former but absent in the latter (Levin et al.,

2002; Gallardo et al., 2004). In addition to environmental factors, these differences may reflect undersampling, seasonal fluctuations in population sizes or biogeographic patterns. OMZs are believed to promote speciation by creating barriers to gene flow between populations and by favouring traits that increase tolerance to hypoxia (Rogers, 2000). Such processes could lead to the development of species with restricted distributions.

5.2. Comparison with other deep-water hypoxic systems

Levin (2003) reviews the characteristics of benthic faunas inhabiting OMZs. At the community level, typical features include: (1) generally high densities of foraminifera and metazoans; (2) a dominance of smaller organisms (foraminiferal and metazoan meiofauna) where oxygen concentrations are lowest; (3) faunal aggregations above and below the OMZ core (edge effects); (4) depressed species richness and diversity combined with high dominance among most faunal groups; (5) a dominance of certain groups, notably rotaliids and buliminids among the foraminiferans, nematodes among the meiofauna and annelids among the macrofauna, where hypoxia is severe (<~0.15 mL L⁻¹). The faunal patterns observed off Pakistan were generally consistent with these trends. Foraminiferans were dominant in the OMZ core. The macrofauna and invertebrate megabenthos were very scarce or absent with peak abundances located in the lower transition zone.

Sanders (1969), working off Walvis Bay in the SE Atlantic, was the first to examine community-level trends in faunas impacted by OMZs. However, these features are most extensively developed in the eastern Pacific (Helly and Levin, 2004), where several studies have compared trends between different faunal groups in relation to bottom-water oxygen gradients. Therefore, we focus our comparison on data from this area, particularly the studies of Wishner et al. (1990, 1995) and Levin et al. (1991a,b) across the summit and flanks of the Volcano 7 seamount which penetrates the OMZ to the west of Mexico (see also Levin, 2002), and of Levin et al. (2002) across the OMZ off Peru during the 1997–1998 El Niño.

5.2.1. Protists (foraminiferans and gromiids)

Field and experimental evidence suggests that foraminiferans and metazoan meiofauna generally tolerate hypoxia better than larger metazoans (Josefson and Widbom, 1988; Moodley et al.,

1997). Foraminiferans were the overwhelmingly dominant eukaryotic group among those analysed in the core of the Pakistan Margin OMZ. As in other oxygen-deficient environments (reviewed by Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999), assemblages in the core were largely calcareous, with species belonging to the Buliminida predominating. However, agglutinated species were also fairly common at 300 m (Fig. 5; Larkin and Gooday, 2009) and elongate monothalamous foraminiferans occurred between 250 and 1000 m (Fig. 6C–D). Species of *Reophax* and some other multilocular agglutinated genera (Bernhard and Sen Gupta, 1999), as well as monothalamous forms (e.g., Bernhard et al., 2006), are known from other hypoxic settings. Numerous agglutinated foraminiferans are reported to encrust phosphatic hardgrounds within the OMZ at $\sim 11^\circ\text{S}$ on the Peru Margin (Resig and Glenn, 1997). These assemblages exhibited much higher dominance (82–96%) than those at 300 m on the Pakistan Margin (40–58% during intermonsoon; 49–73% during the SW monsoon) (Larkin and Gooday, 2009).

Levin et al. (2002) reported a high density of sediment-dwelling foraminiferans in the OMZ core on the Peru Margin ($\sim 12^\circ 30'\text{S}$). At their severely hypoxic Stn A (305 m water depth; $\text{O}_2 = 0.02 \text{ mL L}^{-1}$), foraminiferans ($> 150 \mu\text{m}$ fraction, 0–1 cm layer) were 28–36 times more abundant than at three deeper stations where oxygen levels were higher (0.26, 0.84 and 1.78 mL L^{-1} at 563, 831 and 1210 m depth, respectively). The proportion of calcareous foraminiferans was also very high (91%) at 305 m, decreasing to 89%, 63% and 11% at 563, 831 and 1210 m, respectively. On the Pakistan Margin, there was a similar decrease in the proportion of calcareous taxa with increasing oxygen levels in the $> 150 \mu\text{m}$ (Schumacher et al., 2007) and $> 300 \mu\text{m}$ fractions (Fig. 5). However, foraminiferal densities ($> 150 \mu\text{m}$ fraction) at 300 m off Pakistan were $< 3\%$ of the very high standing crops at a similar depth in the core of the Peru OMZ.

Nienstedt and Arnold (1988) described foraminiferans (0–2 cm, $> 63 \mu\text{m}$, unstained) from three seamounts, including Volcano 7, on the East Pacific Rise. The lowest Shannon–Wiener diversity values were from sandy sediments collected between 788 and 1058 m depth. Dominance was $> 50\%$ at 788 m on the summit of Volcano 7, similar to values (40–73%) in the upper part of the OMZ core off Pakistan. The East Pacific Rise OMZ community dominants, however, were members of the family Cassidulinidae (*Ehrenbergina* and *Cassidulina*) rather than the species of *Bolivina* and *Uvigerina* prevalent on the Pakistan Margin.

Arborescent *Pelosina* species, often referred to *Pelosina arborescens*, are fairly widespread in oxygen-deficient settings. Their tree-like tests, which project well above the sediment surface and have pseudopodia deployed from the ends of the branches, probably facilitate oxygen uptake as well as the collection of suspended food. On the Pakistan Margin, *Pelosina* spans a depth range from 130 to 1100 m and oxygen concentrations from 0.10 to 0.23 mL L^{-1} . Similar species occur where oxygen levels are between 0.2 and 0.5 mL L^{-1} off Oman and Peru (Gooday et al., 2000) and in the San Diego Trough (Thistle, 1979) and Santa Catalina Basin (0.4 mL L^{-1}) (Levin et al., 1991c) on the California Borderland. *P. arborescens* is reported from 'anoxic bottoms' off the Swedish west coast and can tolerate anoxic conditions for 10 days in the laboratory (Cedhagen, 1993). The presence of these large protists is contrary to the reduced test size of many foraminiferans in OMZ settings (Bernhard and Sen Gupta, 1999).

The frequent occurrence of gromiids in well-oxygenated, shallow-water habitats (Arnold, 1972; Bowser et al., 1996) is consistent with their main occurrence below the Pakistan Margin OMZ. Gromiids appear to prefer areas where hypoxia is not too severe but food availability is relatively high. Their sack-like tests contain voluminous masses of stercomata, suggesting that they

are deposit feeders ingesting sediment and associated detritus and bacteria (Aranda da Silva, 2005).

5.2.2. Macrofauna

Macrofauna typically exhibit low species richness, high dominance and a predominance of polychaetes in OMZ settings (Levin, 2003; Gallardo et al., 2004). Although densities are often depressed where oxygen levels are lowest (Levin, 2003), the Pakistan Margin appears unique in having a very low macrofaunal density within the OMZ core (Hughes et al., 2009). At our 300-m site, the sparse macrofauna comprised polychaetes and nemerteans. A polychaete-dominated macrofauna was well developed on the Chilean shelf, where oxygen dropped to levels ($\sim 0.1 \text{ mL L}^{-1}$) comparable to those on the Pakistan Margin (Gallardo et al., 2004). Further north off Peru, metazoan macrofauna were most abundant at even lower oxygen concentrations (0.02 mL L^{-1} ; Station A). Here, the dominant species (85%) was *Olavius crassitunicatus*, a small gutless oligochaete with subcuticular symbiotic bacteria (Giere and Krieger, 2001; Levin et al., 2003). On Volcano 7, average macrofaunal densities on the lower summit (770–850 m; $\text{O}_2 = 0.13 \text{ mL L}^{-1}$) were ~ 4 times higher than on the upper summit (0.09 mL L^{-1}), flank (0.81 mL L^{-1}) and base (2.55 mL L^{-1}) of the seamount (Levin et al., 1991a,b). More than 70% of the macrofauna on the lower summit were polychaetes and 21% were represented by a burrowing anemone. The oxygen values on the lower summit of Volcano 7 were similar to those at the 400-m site on the Oman Margin where polychaetes were also common, although diversity was much lower (Levin et al., 1997, 2000). At similar oxygen levels on the Pakistan Margin (940 m), macrofaunal densities were again fairly high and polychaetes comprised 80% of the fauna (Hughes et al., 2009). The upper summit foraminiferal sands of Volcano 7 yielded a sparse macrofauna dominated (almost 50%) by a species of aplacophoran mollusc. This assemblage had no equivalent on the Pakistan Margin.

The rarity of macrofauna in the Pakistan Margin OMZ above 700 m suggests that oxygen levels were below a critical threshold (Woulds et al., 2007, 2009; Levin et al., 2009). On the Peru Margin (Levin et al., 2002) and Volcano 7 (Levin et al., 1991a), oligochaetes and aplacophorans replace polychaetes at oxygen levels $< 0.10 \text{ mL L}^{-1}$. These taxa were rare in our study area, where oxygen values never dip below this level. Oligochaetes and aplacophorans are both known to harbour symbiotic chemotrophic bacteria (Giere and Krieger, 2001; Katz et al., 2006) and so the fact that sulphidic conditions were not developed on the Pakistan Margin (Law et al., 2009) may explain their absence. The coarser, sandier sediment on Volcano 7, and corresponding differences in sediment chemistry, are other possible factors responsible for faunal differences between the two areas.

5.2.3. Megafauna

The absence of megafauna, other than demersal fish and natant decapods, in the core of the Pakistan OMZ is consistent with the patterns generally observed within oxygen-deficient environments. For example, Mullins et al. (1985) reported that larger organisms, including crustaceans, molluscs and echinoderms, were absent or rare within the OMZ off central California. There are some parallels between megafaunal patterns off Pakistan and those seen on Volcano 7. In both cases, fish occurred where oxygen concentrations were lowest (Wishner et al., 1990; Levin et al., 1991a; Levin, 2002). Fish often enter OMZs, probably in order to feed or to avoid predators (Levin, 2003), and so their presence in the OMZ core off Pakistan is not surprising. However, scavenging amphipods, another group known to exhibit 'eat and run' behaviour, seem to be absent (Murty et al., 2009).

The Volcano 7 megafauna exhibited highest abundances on the lower summit (780–1000 m); huge numbers of animals were observed during submersible dives at 800–810 m (Wishner et al., 1990; Levin, 2002). The distribution of organisms was strongly patterned by depth with narrow bands of galatheid crabs, natant decapods, ophiuroids and anemones succeeding each other between 750 and 800 m (Wishner et al., 1995; Levin, 2002). On the Pakistan Margin, trawl samples indicate that the megafauna changed rapidly with depth across the lower transition zone of the OMZ. However, the rate of change was not as extreme as that seen on the steep slopes of Volcano 7 and some groups, for example galatheid decapods, were much less common. The rock outcrops that provided attachment substrates for solitary coelenterates and sponges on the summit of Volcano 7 were not available for sessile organisms in our study area.

5.3. Foraminiferan–metazoan interactions

Although foraminiferans are an important component of the meio- and macrofauna in deep-sea and hypoxic settings, their interactions with metazoans are rarely examined (Gooday et al., 2001 and references therein). Unlike the metazoan macrofauna, foraminiferans occur across the OMZ on both Arabian Sea margins. Phleger and Soutar (1973) and Bernhard (1992) suggested release from macrofaunal predation pressure as one factor promoting the development of large foraminiferal populations in OMZs. In the Arabian Sea, however, foraminiferal densities were high in the upper OMZ core, irrespective of whether the macrofauna were abundant (400 m off Oman) or scarce (300 m off Pakistan). Thus, the presence of macrofauna does not seem to limit foraminiferal populations in these regions, possibly because there is enough food to sustain both faunal components. However, Woulds et al. (2007, 2009) observed a change from domination of carbon processing by metazoan macrofauna to domination by the foraminiferal macrofauna at 140 m on the Pakistan Margin between the inter- and post-monsoon seasons, corresponding to a 10-fold decline in bottom-water oxygen concentrations. This shift suggests the possibility of metazoan–protozoan competition for food mediated by oxygen levels.

Only a few metazoans, notably scaphopods and certain isopods, are known to be specialist predators on foraminiferans (Lipps, 1983; Svavarsson et al., 1993; Gudmundsson et al., 2000, 2003). Occasional scaphopods, which were usually dead, occurred at 140, 1405–1530 and 1850 m depth; isopods were common only at 1850 m (Murty, 2005; Hughes et al., 2009). Thus active macrofaunal predation on foraminiferans is unlikely to be widespread in our study area.

5.4. Edge effects

Mullins et al. (1985) coined the term edge effects for narrow zones with elevated benthic metazoan and foraminiferal abundances at the upper (500 m) and lower (1000 m) boundaries of the central Californian OMZ. Similar density peaks have been reported from other OMZs (Levin, 2003), including the lower summit of Volcano 7 (Wishner et al., 1990; Levin et al., 1991a,b). Dense concentrations of two polychaete species occur at the border between the oxygenated and anoxic/sulphidic parts of the Black Sea (Zaika et al., 1999). These narrow, densely populated bands reflect an abundant food supply combined with a release from oxygen limitation (Levin, 2003) and appear to be associated with enhanced biological and biogeochemical activity (Wishner et al., 1995). Woulds et al. (2007) documented enhanced rates of carbon processing at the upper and lower transition zones of the Pakistan Margin. These benthic edge effects have parallels in the water

column, where zooplankton aggregate and microbial activity is elevated in narrow zones (Wishner et al., 1995, 2000).

Other papers in this volume note the existence of edge effects among macrofauna (Levin et al., 2009) and megafauna (Murty et al., 2009) off Pakistan. A notable feature of these patterns is that abundance peaks are located at progressively greater depths with increasing organism size (Fig. 2); ~750 m for foraminiferans, 850–950 m for macrofauna, and ~1000 m for megafauna (ophiuroids) (Fig. 2). Previous studies have reported that abundance peaks coincide with lower oxygen concentrations for macrofauna than for megafauna (Thompson et al., 1985; Wishner et al., 1995; Levin, 2002). Such patterns are consistent with the generally greater tolerance to hypoxia of foraminiferans than metazoan macrofauna, which in turn are more tolerant than megafauna (Josefson and Widbom, 1988; Moodley et al., 1997; Levin, 2003).

The rapid changes in megafaunal community composition across the lower transition zone, noted above, are probably another expression of an edge effect. Some macrofaunal species also had narrow ranges on the Pakistan and Oman margins, for example, the polychaete *Linopherus* sp. between 750 and 950 m (Levin et al., 2009), the thyasirid *Leptaxinus indusarium* between 800 and 1000 m (Oliver and Levin, 2006), and the gromiid *Gromia pyriformis* around 1000 m depth (Gooday and Bowser, 2005). Interestingly, burrowing anemones were common within a narrow zone on the lower summit of Volcano 7 (Levin et al., 1991a) and in one of the trawl samples taken in the lower part of the Pakistan Margin OMZ (878–890 m). Many foraminiferal species, however, had much broader bathymetric ranges across the OMZ on the Pakistan Margin. For example, *Bulimina exilis* occurs between 500 and 1200 m, *Uvigerina peregrina* between 500 and 1050 m, and *Ammodiscus tenuis* between 300 and 1000 m (Schumacher et al., 2007).

6. Concluding remarks

To a greater or lesser extent, all groups exhibited depressed species diversity within the OMZ core (250–750 m). Abundance trends across the OMZ, however, differed among faunal groups and there were also differences in the turnover rate of species with depth. Macrofaunal and megafaunal animals showed a rapid change in species composition across the lower part of the OMZ whereas some foraminiferans had fairly broad depth ranges. Based on these observations, we propose the following zonation scheme to characterise cross-margin biological trends off Pakistan.

- (1) *Seasonally hypoxic region* (140–250 m; O_2 fluctuating from 0.11 to 2.05 mL L⁻¹). The fauna comprised diverse, predominantly calcareous foraminiferans, metazoan macrofauna and megafauna. The activity levels of foraminiferans and metazoan macrofauna switched seasonally.
- (2) *OMZ core* (250–750 m; $O_2 = 0.10$ – 0.14 mL L⁻¹). Fauna dominated by foraminiferans, with macrofaunal metazoans present but rare. Calcareous foraminiferans, some of which may be endemic, abundant in the upper part (250–500 m); agglutinated foraminiferans become relatively more important in the lower part (500–750 m).
- (3) *OMZ transition zone* (750–1000 m; $O_2 = 0.12$ – 0.17 mL L⁻¹). Each faunal group showing successively deeper abundance maxima as a function of size, and with diversity gradually increasing. Sediments shift from fully laminated to fully bioturbated. Macrofauna change from being extremely rare at the base of the zone to forming an abundant, low-diversity assemblage followed by a high diversity assemblage. Between ~800 and 1100 m, the megafauna undergo similar transitions, with narrow bands of high abundance.

- (4) *OMZ boundary* (1000–1300 m; $O_2 = 0.15\text{--}0.50\text{ mL L}^{-1}$). Sediments fully oxidised and bioturbated. Macrofaunal abundance and diversity decline from peaks at 950 and 1000 m, respectively.
- (5) *Beneath the OMZ* (1300–1850 m; $O_2 > 0.50\text{ mL L}^{-1}$). Agglutinated species dominate protozoan assemblage, gromids fairly common, and all metazoan groups exhibit enhanced diversity but reduced abundances relative to the lower part of the OMZ.

Important differences exist between this zonation and the pattern seen on the Oman Margin, notably that metazoan macrofauna were abundant in the core of the Oman, key metazoan species were different and the depth of abundance maxima for each group differed. Many features of the Pakistan OMZ resemble those observed across OMZs in other part of the world, despite important taxonomic differences. However, the extreme rarity off Pakistan of macrofauna between 300 and 700 m, and of megafauna between 300 and 900 m, may be a characteristic of very thick, intense OMZs. We predict that similar patterns may occur off Mexico and in the Bay of Bengal where 1000 m thick OMZs impinge on the continental margin.

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