Oxygen and organic matter thresholds for benthic faunal activity on the Pakistan margin oxygen minimum zone (700–1100 m)

Lisa A. Levin [a,*], Christine R. Whitcraft [a,1], Guillermo F. Mendoza [a], Jennifer P. Gonzalez [a], Greg Cowie [b]

[a] Integrative Oceanography Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0218, USA
[b] School of GeoSciences, The University of Edinburgh, Edinburgh EH9 3JW, Scotland, UK

ARTICLE INFO

ABSTRACT

A transition from fully laminated to highly bioturbated sediments on continental margins is thought to derive from increased animal activity associated with increasing bottom-water oxygen concentration. We examined faunal community responses to oxygen and organic matter gradients across the lower oxygen minimum zone (OMZ) on the bathyal Pakistan margin, where sediments grade from fully laminated sediment at 700 m ($0.12\,mL\,L^{-1}$ O_2 [5 μM]) to highly bioturbated sediment at 1100 m ($0.23\,mL\,L^{-1}$ O_2 [10 μM]). High-resolution sampling of the seafloor (every 50 m water depth) was conducted along a single transect during inter- and post-monsoon periods in 2003 to address (a) the existence of oxygen thresholds regulating macrofaunal abundance, composition, diversity and lifestyles, (b) the interactive effects of organic matter quantity and quality, (c) associated community effects on sediment structure, and (d) potential seasonality in these processes. Macrofaunal biomass and bioturbation depth were positively correlated with organic matter availability, which peaked at 850–950 m (3.39–3.53% Org. C). In contrast, macrofaunal diversity (H′), dominance (R1D), and burrow number exhibited threshold responses at oxygen concentrations of $0.12–0.20\,mL\,L^{-1}$ [5–9 μM]), with few animals and highly laminated sediments present below this concentration and most taxa present in fully bioturbated sediments above it. The highly mobile, burrowing amphinomid polychaete *Linopherus* sp. exhibited almost complete dominance and high density at 750–850 m ($0.12–0.14\,mL\,L^{-1}$ O_2 [5–6 μM]), but despite its activity, sediment laminae remained faintly visible. Formation of permanent burrows and detritivory were dominant macrofaunal lifestyles within the OMZ, allowing laminae to persist at surprisingly high animal density and biomass. Results reflect a shift from organic matter to oxygen regulation of body size and biogenic structures following the monsoon. This study suggests that for assemblages evolving under permanent severe hypoxia, food availability remains a significant determinant of animal abundance and biogenic structure depth. Oxygen influences patterns of diversity and dominance and interacts with organic matter to generate abrupt faunal transitions on the Pakistan margin.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Among the many environmental parameters that vary across continental margins, bottom-water oxygen concentrations and organic matter fluxes to the seabed exhibit some of the steepest gradients, especially beneath areas of upwelling (Cowie, 2005). Oxygen and organic matter availability are understood to greatly influence the distribution and abundance of macrobenthos, and consequently bioturbation, in estuaries and coastal regions (Pearson and Rosenberg, 1978; Rabalais et al., 2001a, b), in fjords (Nilsson and Rosenberg, 2000; Rosenberg et al., 2001, 2002), and

on continental margins (Rowe, 1983; Levin and Gage, 1998; Levin et al., 2001). Strong gradients in both parameters are typically found where permanent oxygen minima persist (Helly and Levin, 2004). Such settings provide ideal environments in which to study how oxygen affects the abundance and structure of benthic communities and to examine the consequences of altered animal communities for the sediment matrix. Information about benthic responses to modern oxygen gradients, and the existence of thresholds for benthic activity, is valuable for interpreting the paleo-oxygen of ancient environments from ichnofacies data, for understanding fates of deposited material under different oxygen regimes, and for predicting how biological and organic matter cycling will respond to changing oxygen regimes in the future.

Previous sampling of open-ocean oxygen minimum zone (OMZ) benthos has suggested a strong lower-boundary effect, with high densities of hypoxia-tolerant faunas aggregating in the lower parts of OMZs (Thompson et al., 1985; reviewed in Levin,

2003). This so-called 'edge effect' has been observed for both macrofaunal and megafaunal invertebrates, typically at oxygen concentrations between 0.15 and 0.40 mL L^{-1} (6 and 18 μM). Manifestations include aggregations of sponges, ophiuroids and shrimp at 800–1000 m in the eastern Pacific off Mexico (Wishner et al., 1995), aggregations of spider crabs at 1000 m on the Oman margin (Smallwood et al., 1999), and elevated macrofaunal densities at varying depths corresponding to the lower OMZ off Oman, West Africa, California and Peru (Levin, 2003). Current understanding predicts the existence of oxygen thresholds, below which most taxa are excluded through physiological intolerance to hypoxia, and above which selected taxa are able to take advantage of an abundant food supply. Notably, meiofauna do not appear to exhibit these responses and often persist at high densities throughout OMZs (Cook et al., 2000; Neira et al., 2001a, b).

Most OMZ biological data have been generated from margin transects in which sampling stations are spaced at depth intervals of several hundred meters or more, and only a few environmental parameters are measured. As a result, the fine-scale responses of benthic organisms to oxygen thresholds, or their interaction with changes in sediment organic properties within the OMZ, have been difficult to detect. We predict that if thresholds occur, very small changes in bottom-water oxygen concentration should yield abrupt (state) changes in benthic community abundance, biomass, composition and diversity, but that these may be modulated by variations in organic matter quantity or quality.

Oxygen biofacies models have been developed that predict increases in diversity, body size and dwelling depth with increasing bottom-water oxygen concentration (reviewed in Savrda and Bottjer, 1991). However, controversy exists regarding which infaunal lifestyles (if any) should be most tolerant of hypoxia, with evidence presented for burrowing deposit feeders (Ekdale and Mason, 1988) and tube builders (Wheatcroft, 1989). This question is of central importance for interpreting paleoenvironments from ichnological (trace) data and for predicting how low oxygen will influence carbon burial and cycling. A detailed examination of infaunal communities and the biogenic structures they construct over a range of very low oxygen concentrations, as well as their response to changing conditions over time, can help address these questions.

This study examines the changes in organic matter properties, macrofaunal communities and sediment structure that occur across the lower oxygen minimum zone on the Pakistan margin. We chose to study the lower OMZ because the oxygen concentration gradient at the upper OMZ boundary is sharp (over a narrow depth range) and its position fluctuates dramatically with season (Brand and Griffiths, 2008; Fig. 1). In contrast the lower OMZ involves gradual oxygen gradients that are more stable in time (Fig. 1), offering a better system to study oxygen thresholds. We focused on the region between 700 and 1100 m where bottom-water oxygen concentrations increase from approximately 0.12 to 0.23 mL L^{-1} (5.3–10.3 μM) (Fig. 1). Sediments and their associated biota were sampled at 50-m depth intervals to address the following questions: (a) Are there changes in organic matter quantity and quality across the lower OMZ and are these associated with community or sediment structure? (b) Are there threshold oxygen concentrations that determine the density, biomass, composition or diversity of macrobenthos? If so, are these thresholds similar for all major taxa? (c) What lifestyles and feeding modes are prevalent, do these change with oxygen level, and are these changes reflected in the distribution of biogenic structures and laminae within sediments? We compared community composition and sediment structure between monsoons (May 2003; termed inter monsoon) and after the Fall monsoon (October 2003; termed post monsoon) to assess whether there
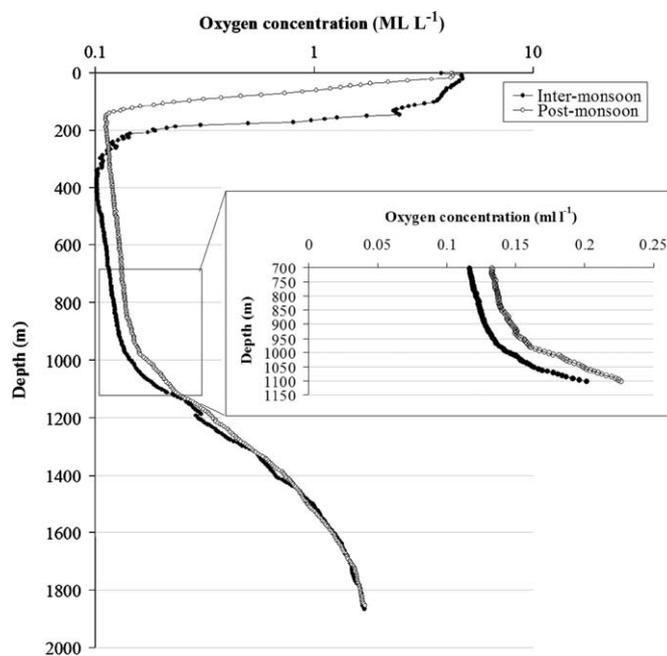
Fig. 1. Oxygen profiles for the Pakistan margin during March/April 2003 (CD 145) and August/September 2003 (CD 150). Inset highlights the lower OMZ zone (700–1100 m), the focus of this paper.

was evidence of monsoon-related variation for any of the phenomena associated with questions a–c. Monsoon-associated variability is of interest in driving potential changes in food supply to the benthos, as well as changing oxygen regimes (Woulds et al., 2007).

2. Methods

2.1. Oxygen

Water-column oxygen profile data were obtained from CTD (Seabird 911 with SBE 43 dissolved oxygen sensor) casts undertaken during RRS Charles Darwin (CD) cruises 145 and 150 (Fig. 2). Oxygen data from each cruise were amalgamated for all Pakistan margin deployments (inter monsoon: CD 145 6 casts, water depths 150–1850 m; late monsoon: CD 150, 16 casts, water depths 100–1850 m; see Bett (2004a, b) for full station details) and averaged in 5-m depth intervals to produce summary profiles for each cruise (CD 145 March/April, 2003; CD 150 August/September, 2003) (Fig. 1). Data were extracted from 50-m depth intervals within the lower OMZ (700–1100 m) for this study.

2.2. Sediment and faunal sampling

Sediment sampling was conducted on the Pakistan margin at 50-m depth intervals along a transect between 700 and 1100 m during CD 146 (inter monsoon, 7–22 May 2003) and CD 151 (post monsoon, 2–17 October 2003) (Fig. 2). The transect is located near the Indus Canyon, and thus this site probably receives organic and mineral inputs during flood or mass transport events. Sediments and associated infauna were sampled with a megacorer containing 8 tubes, each 9.6 cm inside diameter × 30 cm length. One or two megacore drops were made at each depth station during each cruise. Megacore tubes were subsampled for X-radiography, and for quantification of macrofauna (Table 1). Geochemical parameters represent averages from different numbers of replicate analyses on cores from different gear deployments (mega or multicores) from respective sites.
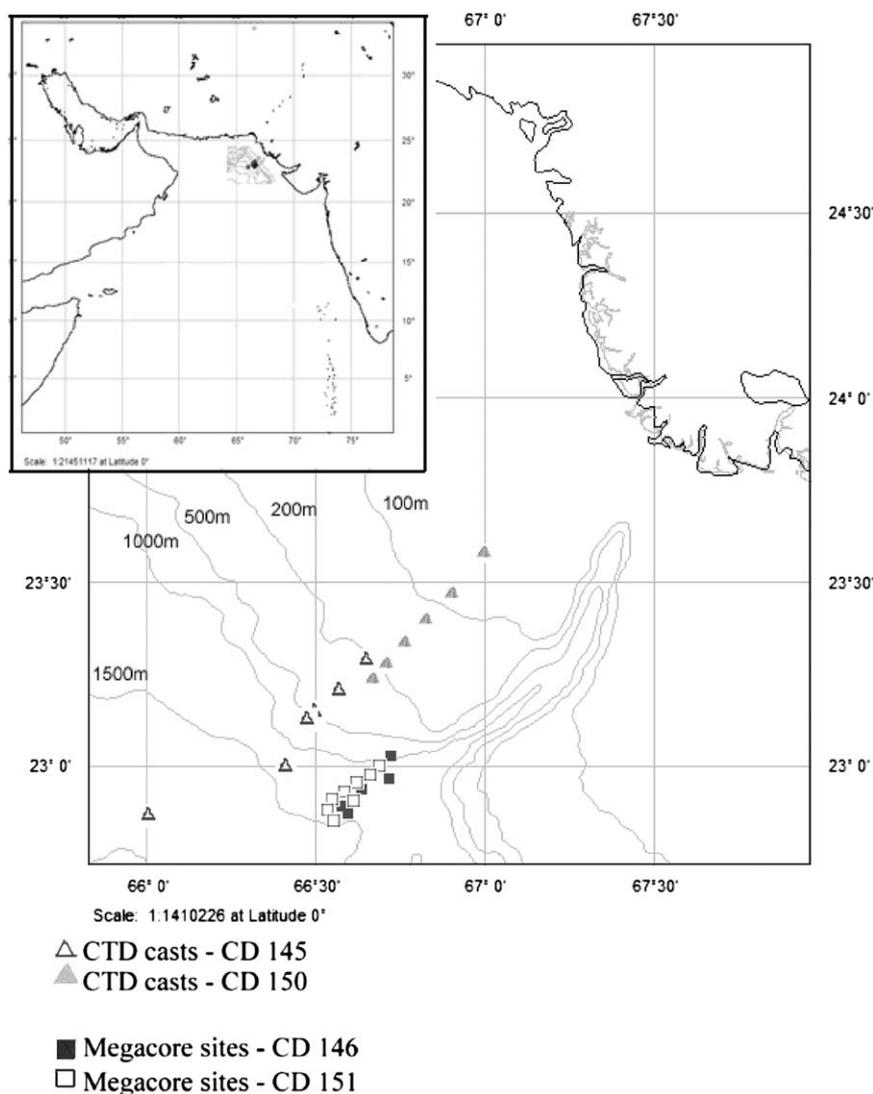
Fig. 2. Map showing locations of the CTD casts generating water-column oxygen data and the lower OMZ transect (700–1100 m) sampled by megacorer on the Pakistan Margin during May 2003 and October 2003. Note transect position near the Indus canyon. Latitude °N, Longitude °E.

2.3. Granulometry and sediment organic matter analyses

Organic carbon content (C_{org}), total nitrogen content (TN) and stable isotopic composition were determined on freeze-dried and homogenized sediment samples using a CE Instruments NA2500 Elemental Analyzer connected to a VG Isogas Prism III isotope ratio mass spectrometer. The elemental compositions are calibrated against acetanilide (Sigma), and a sediment standard (air [$\delta^{15}N$] and PDB standard [$\delta^{13}C$]) is used to calibrate isotopic analysis. Samples were decalcified in silver weighing boats by overnight exposure to an HCl atmosphere (in a dessicator) followed by 2–3 drops of double-distilled 6 N HCl. Precision for replicate analyses ($n = 2$–5) was typically <1% and <2% relative standard deviation (RSD) for % C_{org} and % TN values, except for samples with lowest organic contents (ca. <0.8 wt% C_{org}). Standard deviations for $\delta^{13}C$ and $\delta^{15}N$ values were <0.2 per mil for samples exceeding ca. 0.8% C_{org}.

Amino acid-associated parameters used in the following discussion (total C_{org}-normalized yields [TH AA]; percentage of N as total amino acids [%AA-N]; percentage of total amino acids as β-alanine and γ-amino butyric acid [% (BALA+GABA)]) were determined by reverse-phase high performance liquid chromatography (HPLC) of their orthophthaldialdehyde derivatives follow-ing extraction by acid hydrolysis and addition of charge-matched recovery standards, following the methods of Cowie and Hedges (1992a). Associated parameters used in the following discussion (total C_{org}-normalized yields [THAA]; percentage of N as total amino acids [%AA-N]; percentage of total amino acids as β-alanine and γ-amino butyric acid [% (BALA+GABA)]) are as defined by Cowie and Hedges (1992b, 1994). Degradation indices (DI) were determined using the coefficients of Dauwe and Middelburg (1998), derived from multivariate analysis of amino acid data from a wide range of natural marine samples. Precision for individual amino acid yields for replicate sample analyses ($n = 2$–3) is <8% RSD, and <5% RSD for total yields.

Grain size determinations were made on a LS100 Beckmann Coulter size analyzer, following suspension in distilled water, addition of sodium hexametaphosphate as a disaggregation agent, and filtration through a 1-mm sieve. Replicate analyses give precisions of <10% RSD for mean grain size.

2.4. Macrobenthos processing

Sediment cores were sectioned on board ship at 0–1, 1–2, 2–5, and 5–10 cm vertical intervals. The uppermost 5 cm were

Table 1
Depth and location of mega cores used for analysis of sediment, macrofauna and X-rays.

Date (2003)	Water depth (m)	Station and deployment	Latitude (°N)	Longitude (°E)	Core used for analysis	
					Macrofauna	X-ray
CD 146						
20 May	700	55919#1	22 59.96	66 41.20	X	X
21 May	750	55922#2	22 57.57	66 41.63	X	X
13 May	800	55916#2	23 01.65	66 42.97		
13 May	800	55915#1	22 58.27	66 38.61	X	X
13 May	850	55914#1	22 57.47	66 37.69	X	
13 May	850	55914#3	22 57.47	66 37.69	X	
21 May	850	55921#1	22 57.61	66 37.66		X
07 May	900	55909#1	22 56.80	66 37.01	X	
07 May	900	55909#1	22 56.80	66 37.01	X	X
06 May	938	55908#1	22 55.90	66 36.10		
06 May	950	55908#1	22 55.90	66 36.10		
14 May	950	55913#1	22 55.89	66 36.17		
14 May	950	55929#1	22 55.89	66 36.17	X	
18 May	950	55918#5	22 55.89	66 36.17		X
18 May	950	55918#10	22 53.48	66 36.68		X
22 May	950	55929#1	22 53.56	66 36.71		
07 May	1000	55907#1	22 54.73	66 34.93	X	
07 May	1000	55920#1	22 54.73	66 34.93	X	X
20 May	1050	55906#2	22 54.67	66 34.90	X	X
07 May	1050	55906#1	22 53.60	66 34.90		
07 May	1100	55905#2	22 52.80	66 34.90	X	X
CD151						
02 Oct	700	56113#1	22 59.995	66 41.180	X	X
02 Oct	700	56113#2	22 59.995	66 41.180		
08 Oct	800	56123#1	22 58.312	66 38.915	X	X
08 Oct	800	56123#2	22 58.312	66 38.915		
03 Oct	850	56114#1	22 57.460	66 37.700		
03 Oct	850	56114#5	22 57.492	66 37.688	X	X
09 Oct	850	56127#1	22 57.507	66 37.710		
07 Oct	900	56121#2	22 56.793	66 37.047	X	X
05 Oct	940	56116#4	22 53.490	66 36.650	X	X
05 Oct	940	56116#6	22 53.520	66 36.660		X
12 Oct	940	56136#1	22 53.631	66 36.699	X	
07 Oct	1000	56119#3	22 54.707	66 34.987	X	X
08 Oct	1000	56122#1	22 54.621	66 35.024	X	
17 Oct	1050	56142#1	22 53.604	66 34.987	X	X
17 Oct	1050	56142#2	22 53.604	66 34.029	X	
07 Oct	1100	56120#1	22 53.770	66 34.987		X

preserved unsieved in 8% buffered formalin. The 5–10 cm fraction was sieved on a 0.3 mm mesh sieve prior to preservation. In the laboratory, all samples were washed through a 0.3 mm mesh, and retained invertebrates were sorted in fresh water under a dissecting microscope. Specimens were identified to the lowest taxon possible, with putative species designated for diversity calculations. Biomass (wet weight) of major taxa was determined by blotting formalin-preserved specimens for a standard period (45 s) and weighing them on an analytical balance. Average macrofaunal body size (wet weight) was estimated for each water depth in each season by dividing average biomass by average density.

2.5. X-radiography

Transparent plexiglass slabs were inserted into 9.6-cm diameter megacore tubes. Slabs were either short (6.9 × 0.9 × 14.5 cm) or long and thin (8 × 1.2 × 24 cm; 7 × 1.0 × 20 cm). One core tube was sampled from each of one or two megacore drops at each water depth (Table 1). Sampling was conducted soon after core recovery, and X-ray slabs were stored in the cold room at 6–10 °C until X-rays were taken (within 24 h) on board ship. A portable X-ray unit, ACONA Model PX-20N, was used to generate images. The machine was placed 90 cm from the slab, with settings of 14 Ma and 70 KVF. X-ray film (Kodak AA400) was exposed for 6.3–16.3 s, depending on the slab thickness and sediment texture. The films were developed on board ship.

Preliminary observations on X-radiographs were made using sunlight coming through a circular porthole in the ship as the best transmitted light source. To quantify features within the X-radiographs, digital images, generated using a Nikon Coolpix 995 (3.3 MP), were enlarged and contrast was enhanced using Adobe Photoshop software. Images were then printed for analysis. We recorded the following: presence or absence and thickness of laminae, depth of a visual mixed layer (major bioturbation), depth of a distinctive X-ray-dense turbidite layer, numbers of burrows, tubes, shells, void spaces, types of biogenic structures, and primary burrow dimensions. Tubes were distinguished from burrows by the presence of a high-density wall. A total of 12 X-radiographs were examined from the inter-monsoon period (May 2003) and eight from the post-monsoon period (October 2003). Because each slab was of slightly different size, and some megacores were short, we normalized data to a 10 cm² surface area and limited counts to a depth of 10 cm downcore. Observations are given for sediments below this depth where appropriate.

2.6. Statistical testing

In this study we opted to enhance resolution across the oxygen and organic matter gradients by increasing spatial coverage (with more stations) at the expense of replication. This was necessary because a very limited amount of time was available for this portion of the much larger Pakistan margin study. As a result, statistical analysis was limited by the absence or low number of replicate samples at each depth station and time. Paired *t*-tests were used to examine transition zone-wide changes in sediment and biological parameters between inter- and post-monsoon periods, using the depth stations as replicates. All data were tested for normality using goodness-of-fit tests in JMP, and log transformed when necessary. All percentages (% C_{org}, % clay, % (BALA+GABA), % AA-N, % TN) were arcsine transformed (arcsine of the square root of the proportion). When transformation did not achieve a normal distribution, the appropriate non-parametric test was employed (e.g., Wilcoxon Rank Sum Test). The association between sediment parameters (% C_{org}, % TN, % clay, % AA-N, % (BALA+GABA), THAA, $\delta^{13}C$, $\delta^{15}N$ and DI), bottom-water oxygen concentration and macrofaunal variables (density, biomass, body size, species richness, J' H', rank 1 dominance) or biogenic variables (number of burrows, depth of burrowing, number of biogenic structures) were examined by means of simple linear correlation analyses ($\alpha = 0.05$) and multiple regression. Pairs with correlations of $P < 0.10$ were investigated further using both a forward linear stepwise method (JMP) and generalized additive models (GAMs) using a Poisson log link function and the R Gam library in the program Brodgar v.2.5.2 (Hastie and Tibshirani, 1990). The following abiotic and sediment parameters were significantly correlated with each other: % C_{org} with TN, oxygen with % clay and $\delta^{13}C$, THAA with β-alanine and AA, and DI with $\delta^{15}N$ during CD 146. In each case the former parameter was retained and the latter parameter was removed from the linear and generalized additive models.

For macrofaunal assemblages, multidimensional scaling analyses (MDS) and diversity indices (species richness, H' log base 2, J') were determined using PRIMER Software v. 5.1 (Clarke and Warwick, 2001).

3. Results

3.1. Oxygen gradients

Bottom-water oxygen concentrations between 700 and 1100 m ranged from 0.12 to 0.20 mL L^{-1} (5.4–8.9 μM) during the inter-monsoon period and from 0.13 to 0.23 mL L^{-1} (5.8–10.3 μM) during the post-monsoon period (Fig. 1, Table 2). The difference in oxygenation from the top (700 m) to the bottom (1100 m) of this zone was approximately 0.1 mL L^{-1} (4 μM) during each period (Table 2). However, oxygen concentration even in this deep zone appears to be dynamic. The absolute concentrations at any given depth increased by approximately 0.02–0.05 mL L^{-1} (1–2 μM)) from the inter- to post-monsoon period (Table 2). Thus the concentrations typical of 940–1000 m during the inter-monsoon period, 0.13–0.15 mL L^{-1} (5.8–6.7 μM), were present at 700–900 m during the post-monsoon period (Table 2).

3.2. Sediment organic geochemistry and granulometry

Sediment organic carbon content (0–2 cm) rose gradually from 700 m (2.4–2.6%) to a maximum between 900 and 940 m (3.5–3.6%) and declined again, leveling off at 1050–1100 m (3.1%) (Table 3). Percent TN exhibited a parallel pattern, with maximal

Table 2
Transition zone bottom-water oxygen concentrations based on CTD casts (see text).

Depth (m)	Pre monsoon (mL L^{-1})	Post monsoon (mL L^{-1})	Pre vs. post difference (mL L^{-1})
703	0.117	0.133	0.016
713	0.117	0.133	0.016
738	0.118	0.134	0.016
753	0.119	0.135	0.016
803	0.122	0.137	0.016
853	0.125	0.140	0.016
903	0.128	0.147	0.019
943	0.133	0.152	0.019
953	0.134	0.156	0.022
1003	0.146	0.174	0.028
1053	0.164	0.199	0.036

values (0.42–0.44%) at 900–940 m (Table 3). These patterns do not mirror bottom-water oxygen concentration (Table 2), indicating that there is no simple relationship between sediment organic content and dissolved oxygen.

C/N ratios ranged from 9.16 to 9.93 but exhibited no systematic trend within the lower OMZ (Table 3). They reflect a predominantly marine (and invariant) OM source. $\delta^{15}N$ values ranged from 6.73‰ to 7.98‰. These show no trend with depth but are consistent with influence of water-column denitrification. $\delta^{13}C$ values ranged from −20.08‰ to −21.15‰, and like $\delta^{15}N$, show no clear trend with depth within the lower OMZ. They are not a mirror image of % C_{org}, which was maximal at 940 m. Trends towards heavier values of $\delta^{13}C$ at 1100 m, along with a trend towards heavier values downcore (not shown), may be linked to increasing organic matter degradation state.

There was no consistent trend in sediment grain size across the lower OMZ boundary (Table 3), and no obvious relationship between % C_{org} and grain size parameters (mean, median or % clay) (e.g., $r^2 = 0.17$, $P = 0.31$). The more organic-rich sediments had slightly coarser average grain sizes. Thus grain size/surface area and OM adsorption (Keil and Cowie, 1999) do not appear to be the primary causes for the % C_{org} maximum at the lower OMZ boundary or the variability in OM content among the sites considered in this study.

Amino acid yields and DI potentially provide a variety of indices for OM quality. Total amino acid yields (THAA, C-normalized) are influenced by OM source but, for marine deposits, are a rough proxy for protein content and thus potential OM bioreactivity (Cowie and Hedges, 1992b). Values of % AA-N (percentage of N as amino acids) and % (BALA+GABA) (percentage of non-protein amino acids) are established proxies for OM degradation state (Cowie and Hedges, 1994), as is the degradation index of Dauwe and Middelburg (1998), based on PCA of amino acid distributions. Over the 700–1100 m depth range, these parameters are highly correlated with one another but do not vary consistently with station depth or bottom-water oxygen content and do not show variation linked to % C_{org} (Table 3, Appendix A). Thus, the differences in OM content across these sites are not obviously linked to differences in OM quality.

3.3. Macrobenthos

3.3.1. Density, biomass and body size

Macrofaunal densities ($t_6 = 0.36$, $P = 0.732$) and biomass ($t_8 = 0.32$, $P = 0.756$) did not vary consistently between inter- and post-monsoon periods. Densities during both sampling periods were lowest at 700–750 m (0–414 individuals (ind) m^{-2}),

Table 3
Sediment organic chemistry and granulometry for the Pakistan margin lower OMZ.

Site/depth	% C_{org}	% Total N	C:N	$\delta^{13}C$	$\delta^{15}N$	THAA[a]	% (BALA+GABA)[b]	% AA-N[c]	DI[d]	Bacterial C[e]	Chlorins (mg/g)[f]	% Clay	% Silt	% Sand
CD 146														
A700	2.64	0.31	9.93	−20.69	7.36	22.17	1.18	31.50	0.49	4.56	1.63	32.05	64.60	3.35
A750	2.74	0.35	9.20	−20.62	7.00	NA	NA	NA				34.92	62.20	2.88
A800	3.14	0.39	9.42	−21.14	6.78	16.04	1.65	19.60	0.41	5.55	2.09	35.37	63.79	0.84
A850	3.11	0.38	9.45	−20.90	7.02	15.74	1.76	19.59	0.48	3.13	1.05	30.51	65.37	4.12
A900	3.51	0.44	9.37	−20.75	7.25	16.79	1.73	20.81	0.47		0.72		0.00	0.00
A940	3.53	0.42	9.70	−20.64	7.74	NA	NA	NA		8.89		33.26	65.73	1.01
A1000	2.69	0.33	9.47	−20.62	7.11	15.19	1.82	19.09	0.84	2.67	1.39	32.58	61.43	5.99
A1050	3.10	0.38	9.41	−20.50	7.02	15.13	1.86	18.97	0.41	6.31	1.52	29.44	64.87	5.69
A1100	3.17	0.38	9.80	−20.08	7.98	20.14	1.08	26.55	0.55	2.30	2.17	26.64	68.21	5.15

Site/depth	% C_{org}	% Total N	C:N	$\delta^{13}C$	$\delta^{15}N$	THAA[a]	% (BALA +GABA)[b]	% AA-N[c]
CD 151								
A700	2.46	0.31	9.36	−21.15	7.15	18.20	1.48	21.94
A750	NA	NA	NA	NA	NA	NA	NA	NA
A800	2.78	0.35	9.37	−20.77	6.92	15.27	1.58	20.25
A850	3.14	0.36	0.38	−20.89	7.03	17.18	2.14	21.49
A900	3.49	0.44	9.16	−20.88	6.76	16.67	1.15	21.87
A940	3.61	0.44	9.70	−20.47	7.65	15.94	1.75	20.08
A1000	3.14	0.38	9.53	−20.66	7.04	14.99	1.87	19.04
A1050	3.16	0.40	9.20	−20.59	6.73	17.88	1.40	21.87
A1100	3.14	0.39	9.38	−20.29	7.75	14.97	1.65	18.61

[a] THAA = total amino acid yield, carbon-normalized. Obtained by HPLC fluorescence.
[b] (BALA+GABA) = sum of mole percentages represented by β-alanine and γ-amino butyric acid.
[c] AA-N = percentage of total N in the form of amino acids.
[d] DI = amino acid based degadation index (Dauwe and Middelburg 1998).
[e] Bacterial C-obtained from colorimetric phospholipid analysis with biomass coefficient from Findlay et al. 1989.
[f] Total chorins = sum of chlorophyll and pheopigments (obtained by bulk flourescence or by HPLC).

increased abruptly at 850–950 m (4146–6773 ind m^{-2}), and declined at 1000–1100 m (691–3732 ind m^{-2}). During both sampling seasons a dip in density was observed at 900 m (Fig. 3A). Biomass patterns did not directly mirror density. Biomass increased gradually with increasing depth, reaching a maximum at 950 m, with values exceeding 150 g m^{-2} post monsoon. However, biomass values above 50 g m^{-2} were observed between 850 and 1000 m, and there was no 900-m decline as observed for density (Fig. 3B). Inter- and post-monsoon biomass values did not differ ($t_3 = 2.52$, $P = 0.128$) (Fig. 3B). Average individual biomass (body size) ranged from 5.7 mg (750 m) to 21.2 mg (900 m) during the pre-monsoon period and from 0.3 mg (800 m) to 56.4 mg (1100 m) during the post-monsoon period, but temporal differences, tested for 900–1100 m, were not significant ($t_3 = 2.55$, $P = 0.084$) (Fig. 3C).

3.3.2. Vertical distribution

The vertical distribution of macrofauna within the sediment column varied with water depth and season (Fig. 4). Macrofauna were found exclusively in the uppermost 1 cm at 750–800 m and were recovered from successively deeper fractions in the sediment column with increasing water depth and oxygenation (Fig. 4). At 950 m ~50% of animals occurred at 2–5 cm depth in the sediments. At 1000–1050 m they again became concentrated in surface sediments. However, at 1100 m, 50% of animals were in the 5–10 cm fraction (Fig. 4). At most stations, the macrofaunal vertical distributions did not differ between inter- and post-monsoon periods. However, at 850 and 900 m, more animals (mostly an undescribed amphinomid, Linopherus sp.) were found deeper during the post- than inter-monsoon period (Fig. 4; note sample size was not large enough to conduct a statistical test of this trend).

3.3.3. Composition

During both sampling periods most of the macrofauna (97–100%) at the stations from 750 to 850 m were polychaetes (Fig. 5). Over 83% of the individuals belonged to a species in the genus Linopherus. Polychaetes comprised 61–85% of individuals at stations between 900 and 1100 m (Fig. 5), with multiple families well represented, including acrocirrids, ampharetids and cossurids at 950 m, and sphaerodorids, paraonids, and cirratulids at 1000–1100 m (Appendix B). Molluscs and crustaceans first appeared at 900 m and echinoderms (mainly ophiuroids) at 950 m (Fig. 5; Appendix B). The molluscs tolerating the lowest oxygen levels (900–950 m) were pectinid and thyasirid bivalves. Cumaceans were present in abundance at 900 and 950 m, suggesting they are the most hypoxia-tolerant crustaceans. Amphipods generally were not present at depths < 1000 m.

The inter-monsoon samples exhibited a consistent change in assemblage composition with increasing depth and oxygenation (MDS, Fig. 6A) but the post-monsoon samples did not (MDS, Fig. 6B). Communities were distinct at each 100-m interval (700–750, 800–850, 900–950, >1000 m) (Fig. 6C; ANOSIM, $P < 0.05$). Differences between the 700/750 m and the 800/850 m assemblages were driven by higher densities of Linopherus, Prionospio, Cossura and Acrocirrus at 800–850 m. Enhanced abundances of cumaceans, cirratulids and ampharetids at 900/950 m accounted for differences with shallower assemblages (SIMPER). All of these groups were more abundant above than below 1000 m. Between-season differences in lower OMZ community composition were minor (ANOSIM $P = 0.893$) and were considerably less than between-station differences.

3.3.4. Feeding modes and lifestyles

Surface feeding was the dominant feeding mode throughout the lower OMZ. There was a shift from detritivory (mainly by
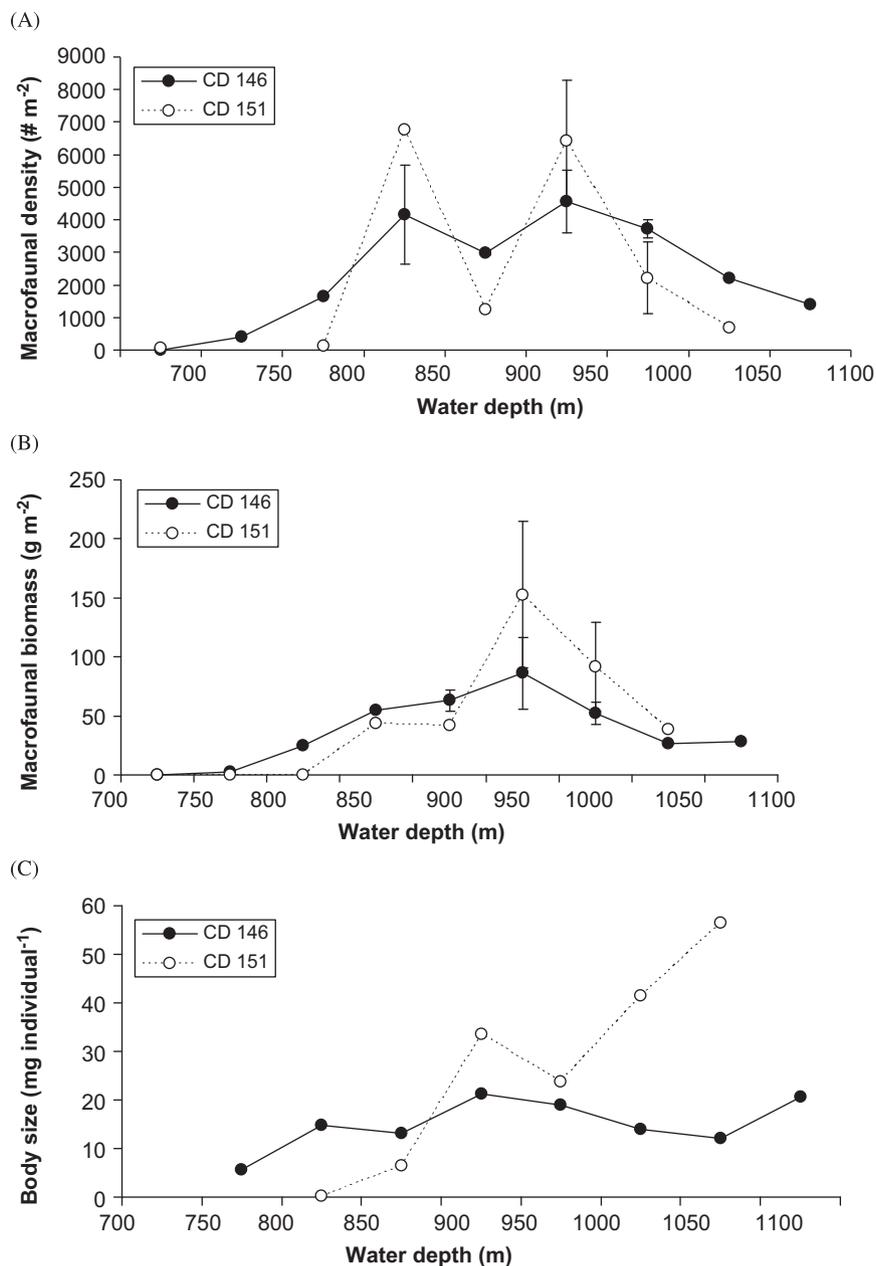
Fig. 3. Macrofaunal (>0.3 mm) (A) density, (B) biomass and (C) body size as a function of depth within the lower OMZ transition zone, 700–1100 m. Data are given for samples taken in May 2003 (inter monsoon, CD 146) and October 2003 (post monsoon, CD 151).

Linopherus sp., as determined from phytodetritus labelling experiments [Woulds et al., 2008]) at 700–900 m, to surface deposit-feeding from 950 to 1100 m, with subsurface feeding only minimally represented (Fig. 7A and B). Permanent burrows (made mainly by *Linopherus* sp.) were dominant at 750–850 m. Mobile burrowers and tube builders increased in abundance with greater oxygenation, such that the three lifestyles were fairly equally represented at the deeper end of the zone (1050–1100 m) (Fig. 7C and D).

3.3.5. Diversity and dominance

Indices of diversity (species richness [S] and H′) were low (or incalculable) between 700 and 850 m and rose sharply between 800 and 900 m (Fig. 8A and B). Maximum H′ and species richness were observed at 1000 m. High dominance was a feature of the lowest oxygen zones, with *Linopherus* sp. comprising up to 100% of animals at 800 m. Rank 1 dominance dropped sharply from 850 to

1000 m (Fig. 8C), while evenness (J′) rose from 800 m (0.49) to 1050 m (0.97) and remained high at 1100 m. There was no consistent difference in S, H′, J′ or R1D across the study zone between inter- and post-monsoon periods (paired *t*-tests, all $P > 0.10$).

3.4. Sediment structure

Uniform, unbroken, seasonal laminations (typically 0.5–1.0 mm thick) were present in sediments between 700 and 800 m (Fig. 9, Table 4). In many cases, these laminations were visible directly by eye in X-ray slabs prior to X-radiography, appearing as alternating light and dark sediment layers (not shown). The 700–750-m sediments exhibited a soupy, low-density layer several mm thick at the top of the sediment column. Burrows were visible but rare between 700 and 800 m (Table 4, Fig. 9). In X-radiographs from depths of 700–950 m there was a
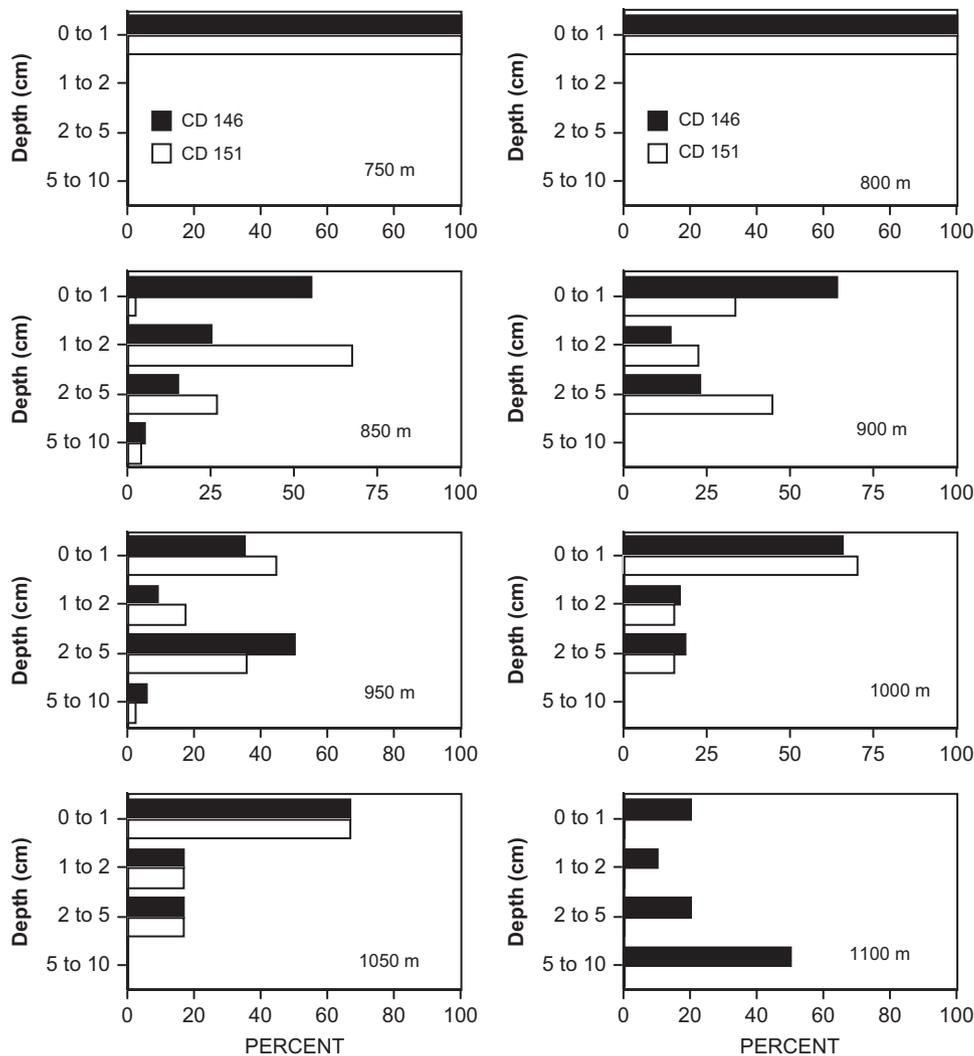
Fig. 4. The vertical distribution of macrofauna in the sediment column as a function of water depth within the lower OMZ transition zone, 700–1100 m. Data are given for samples taken in May 2003 (inter monsoon, CD 146) and October 2003 (post monsoon, CD 151).

high-density layer of light-colored clay located 5–7 cm below the sediment surface. This turbidite-like feature ranged in thickness from 2 to 9 mm and apparently reflects a local deposition event (e.g., turbidity flow, slump or flood deposition).

Burrow abundance and visibility increased at 850 m. Laminae were still visible but vertically oriented burrows (1–2 mm wide, 0.5–1.5 cm long) were abundant in the upper 6 cm of the sediment column. At 900 m, laminations grew faint, and most were thicker (4–9 mm) than at other depths. Laminations were concentrated in the upper sediments, with burrows still visible in the upper 6 cm. At 940–950 m, the diversity of biogenic structures increased. Ampharetid polychaete and ampeliscid amphipod tubes were present in cores but were not visible in X-radiographs, whereas thyasirid clam shells appeared clearly. Faint laminations remained visible downcore, with a dense network of burrows (typically 1–3 mm wide and up to 3 cm long) present in the upper 6 cm. One large, long burrow (4 mm wide, 4.8 cm long) was observed.

A state change, in which the sediments went from laminated to fully bioturbated, occurred at 1000 m and continued through 1050 and 1100 m (Fig. 9). No laminations were visible, and biogenic structures such as tubes and burrows were very faint and difficult to visualize during May 2003 (Fig. 9, Table 4). The post-monsoon cores from 1050 and 1100 m exhibited horizontal burrows in the upper few cm; at least one set was attributed to shrimp, which were visible in a lander video.

There were no consistent differences in burrow density ($t_4 = 0.90$, $P = 0.412$), depth of bioturbation ($t_4 = 0.87$, $P = 0.43$) or diversity of biogenic structures ($t_4 = 0.15$, $P = 0.21$) between inter- and post-monsoon periods. Burrow counts were greatest at 800–850 m during the inter-monsoon period and at 850–900 m during the post-monsoon period (Table 4). Most of these appeared to be made by the amphinomid polychaete *Linopherus* sp. There was no correlation of *Linopherus* density and burrow counts in either season (inter monsoon: $r^2 = 0.65$, $F_{1,2} = 3.78$, $P = 0.19$, post monsoon: $r^2 = 0.004$, $F_{1,6} = 0.02$, $P = 0.89$). The greatest diversity of burrow types (different sizes and shapes) was observed at 950 m during the inter-monsoon period and 900 m during the post-monsoon period. Void spaces were observed in about half of the X-radiographs. These were few and did not show a consistent trend with depth (Table 4). No tubes were recorded in any X-radiographs taken between 700 and 1100 m, despite the known presence (albeit low numbers) of tube-building ampharetids and ampeliscid amphipods at 940 m. This is probably due to the small volume sampled by the X-radiographs. The diversity of types of biogenic structures (mainly burrows) did not differ notably among depths, but these structures were difficult to visualize in the fully bioturbated cores from 1000, 1050 and 1100 m.

(A)

(B)
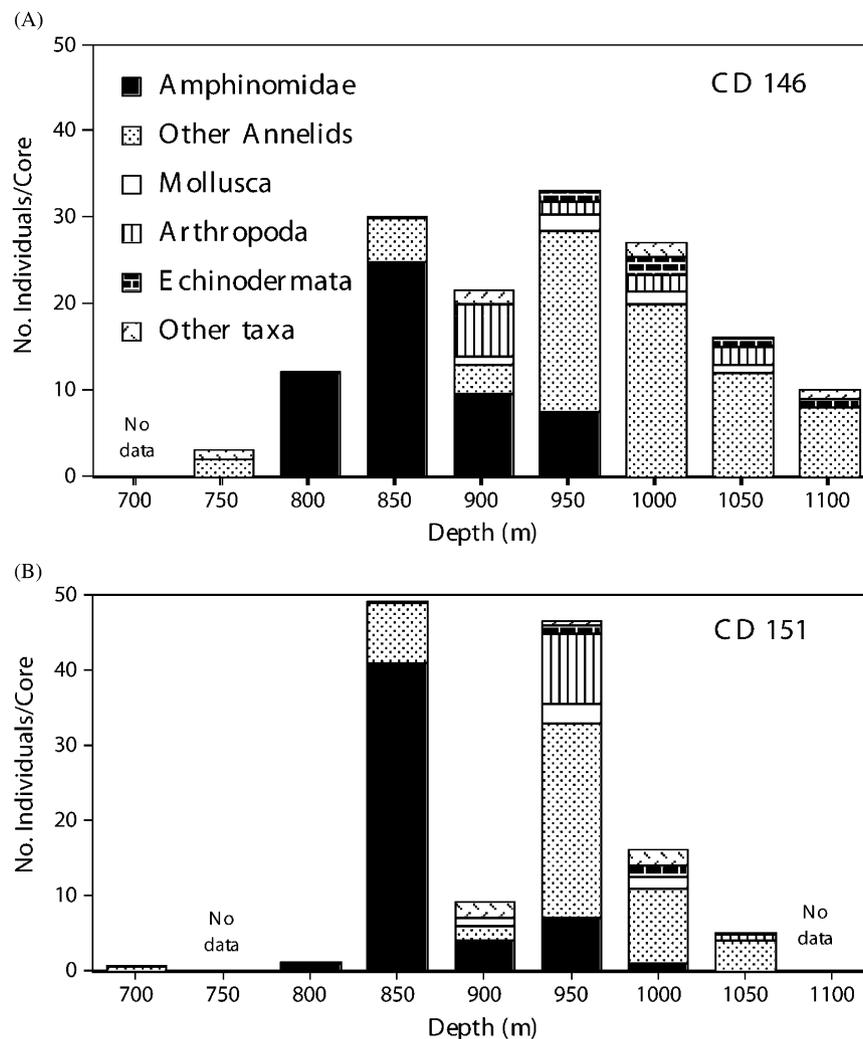
Fig. 5. Composition of macrofauna (> 0.3 mm) as a function of water depth within the lower OMZ transition zone, 700–1100 m. Data are given for samples taken in (A) May 2003 (inter monsoon, CD 146) and (B) October 2003 (post monsoon, CD 151).

3.5. Interaction of oxygen, organic matter, food quality and biological activity

There was a positive linear relationship between sediment organic carbon content and animal biomass ($r^2 = 0.51$; $P = 0.031$ for CD 146 and $r^2 = 0.48$; $P = 0.055$ for CD151) during inter- and post-monsoon periods, while density was inversely correlated with THAA during CD 146 ($r^2 = 0.61$; $P = 0.06$). Body size was positively correlated with organic matter quality during the inter-monsoon period ($r^2 = 0.65$; $P = 0.05$) but with oxygen during the post-monsoon period ($r^2 = 0.87$; $P = 0.0008$) (Table 5), suggesting a possible shift from food to environmental factors as controlling agents. Generalized additive models (GAMs) suggest that macrofaunal density is a function of bottom-water oxygen concentration, C_{org}, and THAA, and that biomass is related to C_{org} (CD 151) or C_{org} plus oxygen (CD 146), but give no fit for body size.

Diversity (H′) was positively but weakly correlated (linearly) with bottom-water oxygen concentration during both cruises ($r^2 = 0.35$, $P = 0.09$ on CD 146 and $r^2 = 0.54$, $P = 0.04$ on CD 151; Table 5). C_{org} combined with DI, a potential measure of food quality, accounted for 73% of the variance in J′ and C_{org} combined with oxygen accounted for 95% of the variance in Rank 1 Dominance (R1D) during the post-monsoon period (Table 5). Surprisingly, species richness (S) did not show linear correlations with any of the variables studied but was highly associated with C_{org} (during CD 146) using GAMs.

Burrow density was negatively correlated with bottom-water oxygen during both cruises ($r^2 = 0.46$, $P = 0.06$ on CD146 and $r^2 = 0.69$, $P = 0.01$ on CD 151). Percent C_{org} explained 65% of variance in burrow depth post monsoon based on linear regression (Table 5); GAMs suggested that both C_{org} and bottom-water oxygen concentration were significantly associated with bioturbation depth. After the monsoon, burrow density was correlated positively with macrofaunal H′ (Spearman's $\rho = 0.78$, $P = 0.037$), negatively with bottom-water oxygen concentration (Spearman's $\rho = 0.69$, $P = 0.011$) and $\delta^{13}C$ (Spearman's $\rho = 0.71$, $P = 0.009$) and negatively with faunal R1D (Spearman's $\rho = -0.79$, $P = 0.037$). The degradation index and bottom-water oxygen explained 61% and 49% of the variation in the diversity of biogenic structures during inter and post-monsoon periods, respectively (Table 5; Appendix C), whereas GAMs indicated that biogenic structure diversity was positively associated with C_{org}.

4. Discussion

4.1. Organic matter quantity and quality

When the whole Pakistan margin from 140 to 1850 m is considered, values of THAA for surficial sediments show little trend across the lower OMZ boundary, suggesting no consistent differences in relative protein content despite a 4–5-fold range in

Fig. 6. MDS plot for macrofauna (>0.3 mm) collected within the Pakistan lower OMZ transition zone, 700–1100 m. MDS analyses were conducted for samples taken in (A) May 2003 (inter monsoon, CD 146), (B) October 2003 (post monsoon, CD 151) and (C) dates combined.

at the lowest oxygen concentrations. The threshold for molluscs and crustaceans appears to be between 0.13 and 0.15 mL^{-1} (5–7 µM) while echinoderms appear to require 0.15–0.17 mL^{-1} (7–8 µM). Differential tolerance to hypoxia among invertebrate taxa (annelids > molluscs > crustaceans > echinoderms) has been noted previously in shallow and deep waters (Diaz and Rosenberg, 1995; Levin, 2003). Composition shifts across the Pakistan lower OMZ are consistent with this pattern (Fig. 5), although molluscs may be more tolerant than annelids to hypoxia in shallow water (Gray et al., 2002).

Within the eastern Pacific OMZ, macrofauna have been reported to dwell at low densities (1850 ind m^{-2}) at oxygen concentrations as low as 0.08 mL^{-1} (3.5 µM) in sandy sediments of Volcano 7 (750 m) (Levin et al., 1991) and at relatively high densities (>13,000 ind m^{-2}) at 0.02 mL L^{-1} (<1 µM) in a basin off Peru (300 m) (Levin et al., 2002). However, in the Peru basin the dominant taxon, a tubificid oligochaete, was known to possess multiple symbionts that probably enhanced survival in nearly anoxic conditions (Blazejak et al., 2005). The macrofaunal densities reported here for the lower Pakistan OMZ are within the range reported from other OMZs, with comparable oxygen levels (Hughes et al., 2008).

The sharp macrofaunal zonation we observed within the lower OMZ transition zone (Fig. 6) is a feature characteristic of other OMZ lower boundaries (Volcano 7 off Mexico—Wishner et al., 1995; Oman—Levin et al., 2000; Chile—Gallardo et al., 2004). Such zonation is also exhibited by foraminifera (Gooday et al., 2008) and megafauna (Murty et al., 2008) on the Pakistan margin, although the depths of greatest change differ among the groups (Gooday et al., 2008). Several taxa exhibited narrow depth ranges of ~100 m, forming distinct bands in the 700–1100 m transition zone. This was observed for the thyasirid bivalve *Leptaxinus indusarium* (Oliver and Levin, 2006), pectinid bivalves, burrowing anemones, and psolid holothurians (Cowie, 2003a, b). Many OMZs studied to date exhibit a dense band of ophiuroids, typically around 1000 m (Mullins et al., 1985; Thompson et al., 1985; Wishner et al., 1995; Levin et al., 2000; Gallardo et al., 2004), as well as bands of crustaceans such as spider crabs (Smallwood et al., 1999), squat lobsters (Creasey et al., 2000) or shrimp (Wishner et al., 1995) in the zones below.

Elevated total abundance (density and biomass) is a distinctive feature of the Pakistan margin transition zone (Fig. 3A and B) and reflects the edge effect phenomenon characteristic of lower OMZs. This feature is evident in macrofaunal transects off Walvis Bay, SW Africa, Mexico, Peru, California and Oman (reviewed in Levin, 2003). While macrofaunal density peaks were evident at 850 and 950 m on the Pakistan margin (Fig. 3A), the biomass maximum occurred only at the lower depth (Fig. 3B). Macrofaunal body size was positively correlated with bottom-water oxygen concentration during CD 151 (Table 5; Appendix D); oxygen effects on body size could explain the presence of only one biomass maximum in the zone studied.

It has been hypothesized that small-bodied animals, with greater surface area for O$_2$ adsorption, should be more prevalent than large-bodied taxa under conditions of permanent hypoxia. This idea is supported by a general pattern of meiofaunal and microbial dominance within OMZs (Levin, 2003). Populations of the most oxygen-tolerant macrofaunal taxon, *Linopherus* sp., mainly consisted of small individuals (juveniles?) present in the part of the transition zone with lowest oxygen concentrations (≤800 m) and larger individuals at 900–950 m (P. Lamont, pers. comm.). However, averaging across all macrofaunal taxa, body sizes are not smaller within the OMZs of the Oman (Levin et al., 2000) and Pakistan margins (this study). Rather, the abundant food supply in the lower OMZ apparently promotes larger macrofaunal body size.

% C$_{org}$ values (Vandewiele et al., 2008; Cowie and Levin, 2008). However, to varying degrees, % (BALA+GABA) and DI values show minima, and % AA-N values a maximum (i.e. less decay, or greater "quality" in all cases) at sites with organic-rich sediments within and around the OMZ, relative to oxygenated sites well above and below. This suggests that sediment OM content on the Pakistan margin is at least partially linked to degree of preservation and thus to OM quality. The absence of a strong relationship between organic matter content (C$_{org}$) and quality within the lower OMZ (Appendix A), combined with no obvious link to grain size, suggests that other influences—e.g. biological factors (abundance, diversity, bioturbation)—might be primary controls on OM distributions across this depth range.

4.2. Biotic thresholds, zonation and edge effects

The Pakistan margin differs from all other OMZ margins studied to date in the rarity of macrofauna within the OMZ core (300–600 m; 0.09–0.11 mL L^{-1} or 4–5 µM) (Hughes et al., 2008). This margin provides evidence for clear oxygen thresholds for macrofaunal abundance and burrowing activity at ~0.11–0.13 mL^{-1} (4–6 µM), suggesting that this level of oxygen is required to support macrofaunal populations, given that other conditions are favorable. Primarily spionid and amphinomid polychaetes appear

Fig. 7. Macrofaunal feeding modes (A, B) and lifestyles (C, D) as a function of water depth on the Pakistan Margin during May 2003 (inter monsoon, CD 146) and October 2003 (post monsoon, CD 151).

4.3. Lifestyles under hypoxia

The Pakistan margin stations with lowest bottom-water oxygen concentrations studied here (700–850 m; 0.11–0.13 mL L^{-1}; 5–6 µM) hosted almost exclusively the burrowing amphinomid species *Linopherus*, which can exceed 1 cm in length. The amphinomid burrows are >1 cm long, and appear to be relatively permanent (and possibly recent), as the sediment laminations remain visible despite *Linopherus* sp. densities of 4–6000 ind m^{-2} (Fig. 9, 850–950 m). Were these worms mobile, subsurface-deposit feeders, the laminations would have been obliterated by bioturbation. *In situ* video tapes of the sediment surface made by a camera within a benthic lander revealed that this species is highly motile and frequently swims out of its burrows, up into the water column and back down into burrows (although this could be a response to disturbance) (P. Lamont, O. Pepe, unpublished data). Thus *Linopherus* has an interface habitat, dwelling in both the upper 5 cm of the sediment column and the few cm of water immediately overlying the sediment. It is not a classic infaunal, deposit-feeding burrower, but rather feeds on phytodetritus and will rapidly ingest artificially placed diatom slurry (Woulds et al., 2007, 2008). This species has extensive branchial development, presumably to enhance surface area for oxygen diffusion (unpublished observations), but the swimming behavior may also facilitate oxygen

exposure. The only other polychaete recorded from the OMZ core (<700 m) based on live sorting of cores on board ship was a small tube-building spionid polychate (*Prionospio* sp.), but these were rare.

Burrowing was the dominant lifestyle in an anoxic basin off Peru (300 m; 0.02 mL L^{-1}), but in this case the burrower was a symbiont-bearing (non-feeding) tubificid oligochaete, *Olavius crassitunicatus*, comprising 83% of the macrofauna (Levin et al., 2003). On Volcano 7 off Mexico (750 m; 0.08 mL L^{-1}) burrowing aplacophorans comprised 47% of the macrofauna (Levin et al., 1991). In both these instances the burrowers bioturbated sediments, and laminations were not evident.

Slight increases in oxygen and organic matter (at 950 m) were associated with a greater diversity of lifestyles including tube-building ampeliscid amphipod, ampharetid, and acrocirrid polychaetes, burrowing species (edwardsiid anemones and aplacophorans), bivalved pectinids and thyasirids, and mobile cumaceans. At 1000–1100 m, the infaunal community was typical of deep-sea sediments, with burrowing polychaetes known to feed on phytodetritus (cirratulids and paraonids) and small psolid holothurians and ophiuroids, which may be suspension feeders. The presence of a dense band of ophiuroids near 1000 m is a feature of most OMZs studied (e.g., off Oman), though the 1000 m zone off Pakistan may experience lower oxygen concentrations (0.14–0.17 mL L^{-1}; 6–8 µM) than in many other OMZ settings.
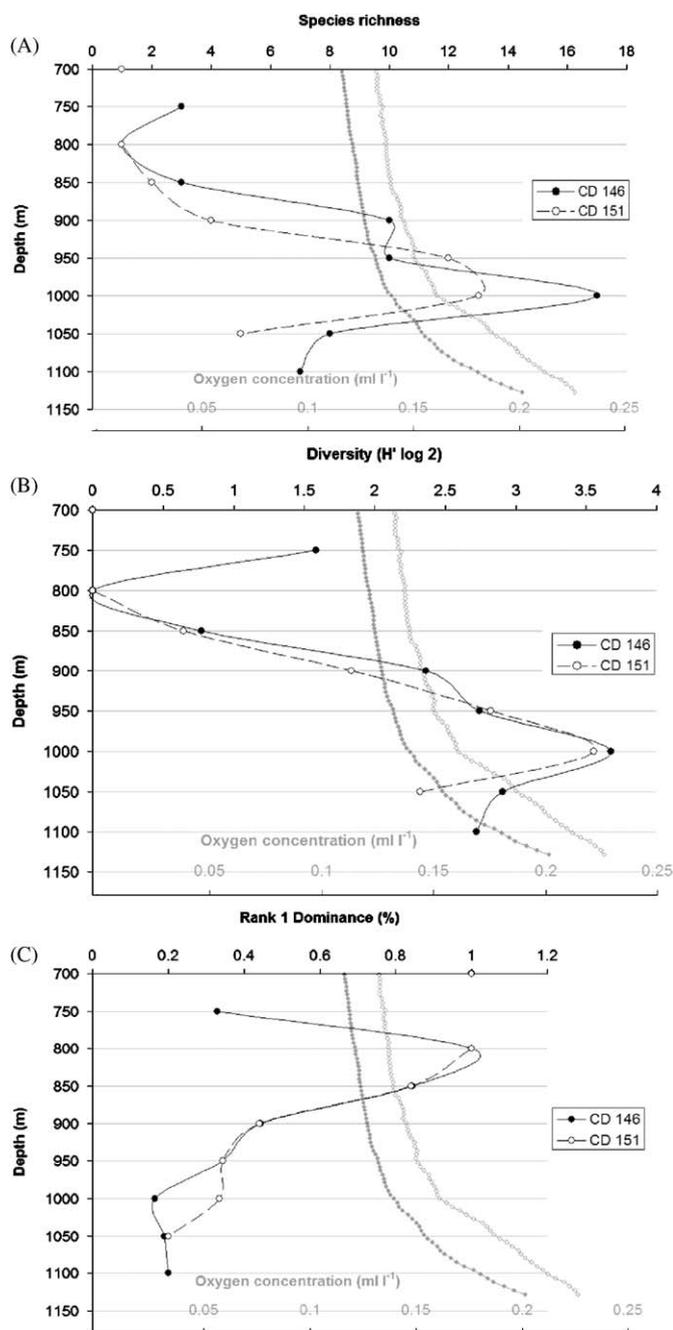
Fig. 8. (A) Macrofaunal species richness (S), (B) Diversity (H′ log base 2), and (C) Rank 1 dominance (proportion of the most abundant species) as a function of water depth within the lower OMZ transition zone, 700–1100 m. Data are given for samples taken in May 2003 (inter monsoon, CD 146, closed symbols) and October 2003 (post monsoon, CD 151, open symbols). Bottom-water oxygen concentrations for each period are plotted on the opposing axis.

4.4. Bioturbation and oxygenation

On the Pakistan margin the transition from completely laminated to fully bioturbated sediments (Fig. 9) took place over a 300 m depth range with an oxygen increase of only $\sim 0.10\,\mathrm{mL\,L^{-1}}$. A threshold for the development of macrofaunal communities capable of bioturbation occurs between 0.1 and $0.2\,\mathrm{mL\,L^{-1}}$ (4–$9\,\mu M$) on the Pakistan margin. This oxygen range is typically referred to as exaerobic (Savrda and Bottjer, 1987) or dysaerobic (Savrda et al., 1984; Thompson et al., 1985).

The Pakistan margin is more oligotrophic, with greater mineral input (from the Indus River) than the other OMZs studied off Mexico (Levin et al., 1991), Peru (Levin et al., 2002), Chile (Gallardo et al., 2004) and Oman (Qasim, 1982; Levin et al., 2000). Our data suggest that organic matter supply and quality, along with oxygen, are associated with the amount and depth of bioturbation as well as the diversity of structures (Table 5; Appendix D). Smith et al. (2000) observed a strong correlation between diversity of burrow types and bottom-water oxygen concentration on the Oman margin (0.13–$2.00\,\mathrm{mL\,L^{-1}}$ or 6–$9\,\mu M$) but no clear relationship between oxygen and mixing depth or mixing rate (Db). We hypothesize that animals can thrive and bioturbate sediments under lower oxygen levels when food supply is plentiful and/or quality is high. Positive correlations between burrow abundance and animal diversity (H′) as well as depth of bioturbation were evident only post monsoon (Appendix C). Both deposit feeders and chemoautotrophs should be more common in organic-rich sediments, and should dwell deeper within them. The Pakistan margin surface sediments, with organic C concentrations of 2.5–3.6% (Table 3), have a lower organic carbon content than the margins off Peru (up to 17% at 300 m; Levin et al., 2002) or Oman (4.0% at 850 m; Levin et al., 2000).

Burrow counts in X-radiographs exhibited a distinct maximum at 850 m (Table 4) corresponding to *Linopherus* abundance maxima (Fig. 5). Burrows were not readily visible in heavily bioturbated sediments below 1000 m (Fig. 9; Table 4), suggesting that semi-permanent, open burrows, of the sort made by *Linopherus*, were not present at these depths. The presence of burrows appears to be uncoupled to particle mixing and bioturbation but they may be an important conduit for passive deposition and active subduction of freshly deposited organic matter. In ^{13}C tracer experiments, *Linopherus* was a voracious consumer of fresh phytodetritus (Woulds et al., 2007, 2008) but was not observed to enact massive subduction of phytodetritus, as is known for maldanids (e.g., Levin et al., 1997a).

4.5. Temporal stability of the lower OMZ

Most of the biotic parameters measured across the lower OMZ transition zone did not vary substantially between inter- and post-monsoon periods. This was true of macrofaunal density, composition, dominance patterns and burrow counts, although lack of replication within stations makes quantitative comparisons difficult. Our data suggest there could be post-monsoon changes in macrofaunal biomass (950–1050 m; Fig. 3C) and vertical distribution (850–900 m, Fig. 4), as well as a trend for greater body size at stations below 850 m (Fig. 3C). Species may time reproduction such that juveniles are present at the time of the monsoon to take advantage of increased food availability. The relatively minor temporal variations observed within the lower OMZ stand in sharp contrast to the uppermost boundary of the OMZ (140 m), where seasonal fluctuations drive conditions from oxic to hypoxic, with corresponding changes in faunal composition and carbon processing pathways (Woulds et al., 2007, 2008).

4.6. Low oxygen biofacies and paleoecological implications

Bottom-water oxygen concentration is recognized to control the abundance, size and diversity of structures made by infauna (Savrda and Bottjer, 1986, 1991; Ekdale and Mason, 1988). Distinct oxygen-associated biofacies have been described. These include the dysaerobic zone (0.1–$0.3\,\mathrm{mL\,L^{-1}}$ [4.5–$13\,\mu M$] sensu Thompson et al., 1985; Rhoads et al., 1991; Savrda and Bottjer, 1991), which is characterized by small, burrowing, soft-bodied invertebrates comprising low-diversity assemblages. In this zone body fossils
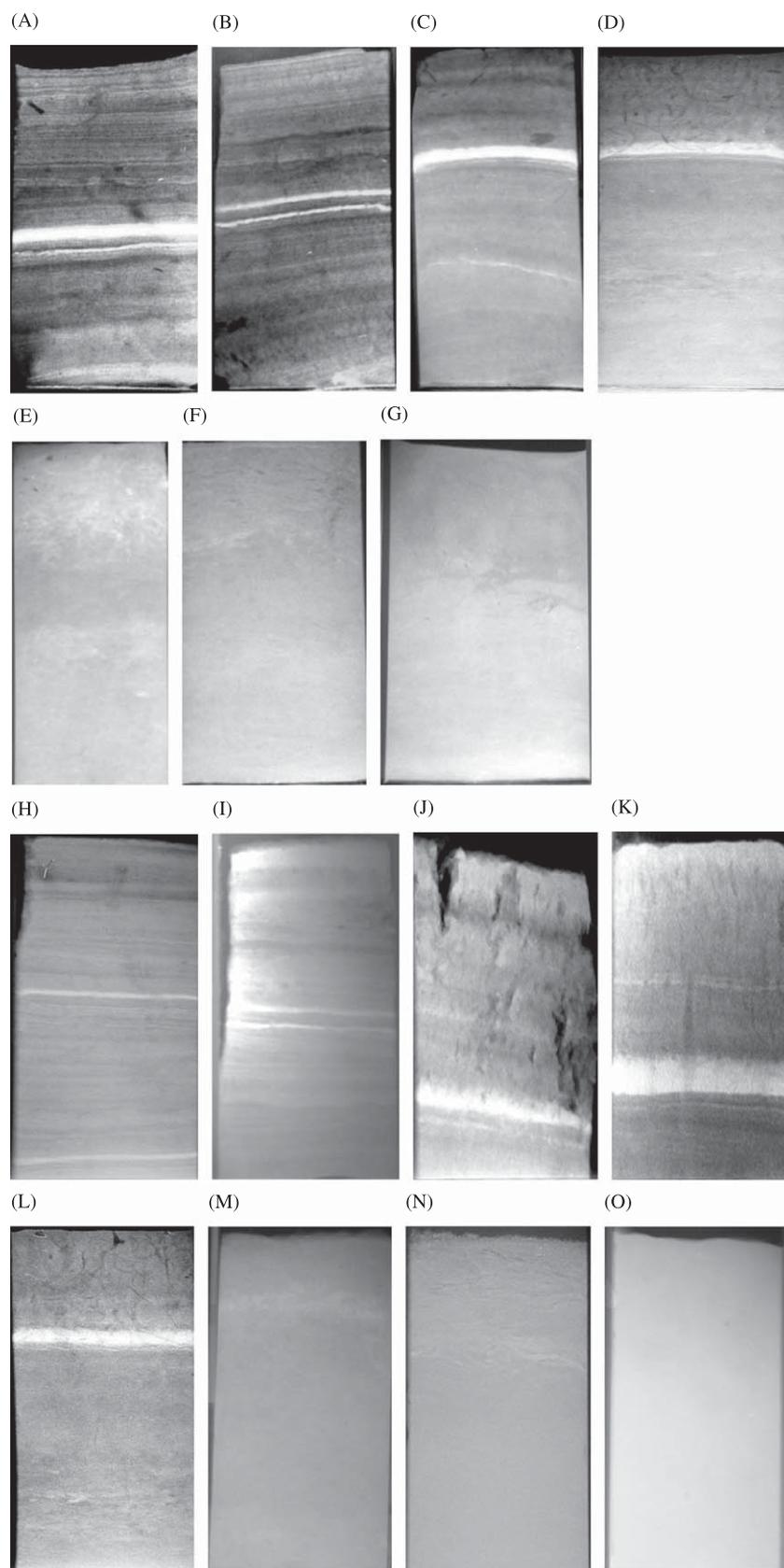
Fig. 9. Photographs of X-radiographs of Pakistan margin sediments taken in May 2003 (CD 146; inter monsoon): (A) 737 m, (B) 850 m, (C) 900 m, (D) 950 m, (E) 1000 m, (F) 1050 m, (G) 1100 m, and in October 2003 (CD 151; post monsoon) (H) 700 m, (I) 800 m, (J) 850 m, (K) 900 m, (L) 940 m, (M) 1000 m, (N) 1050 m and (O) 1100 m. All of the slabs shown are short slabs (6.9 × 0.9 × 14.5 cm) except CD146 900 m, 1000 m and CD151 1000, 1050 and 1100 m which are long slabs (8 × 1.2 × 24 cm; 7 × 1.0 × 20 cm).

Table 4
Measurements of sediment and biogenic structures made on X-radiographs from the Pakistan margin lower OMZ in May 2003 (CD 146) and October 2003 (CD 151).

Depth (m)	Core surface area (cm^{-2})	Lamination thickness (mm)	Depth of white deposition layer (top) (mm)	Thickness of white deposition layer (mm)	Visual depth of bioturbated layer (mm)	Total no. of burrows visible	Total no. of burrows visible per 10 cm^{-2}	No. of burrow types	Total no. of void spaces	No. of voids per 10 cm^{-2}	Number of types of biogenic structures
CD 146											
712	7.81	0.5–1.0	82	3	67	16	20	2	2	0.003	4
737	6.39	0.5–1.0	65	5	65	17	27	2	1	0.002	4
800	6.39	0.5–1.0	57	6	75	103	161	1	0	0.000	2
850	6.39	0.5–1.0	52	5	103	120	188	2	2	0.003	4
900	8.91	0.5–2.0	66	9	65	85	95	2	1	0.001	3
940	6.39	0.5–1.5	49	5	55	40	63	3	0	0.000	3
950	6.39	0.5–1.5	51	6	57	33	52	2	0	0.000	2
950	7.81	0.5	52	8	>100	79	101	4	0	0.000	5
950	6.39	Not visible	54	6	>100	60	94	2	0	0.000	3
1000	8.91	Not visible	Not visible	Not visible	>100	0	0	0	4	0.004	2
1050	6.39	Not visible	32	2	>100	94	147	3	0	0.000	3
1100	6.39	Not visible	Not visible	Not visible	>100	51	80	2	0	0.000	2
CD 151											
700	7.81	0.5–5.0	73	1.5	50	16	20	3	2	0.002	4
800	7.81	0.5–1.0	70	3	70	49	63	3	3	0.003	4
850	6.39	1.0–2.0	70	6	85	86	135	2	6	0.006	3
900	6.39	0.5–1.0	49	8	50	75	117	4	1	0.001	5
940	7.81	1.0–2.0	48	8	>100	77	99	3	0	0.000	4
1000	8.91	Not visible	20	13	>100	Not visible	0	0	4	0.004	1
1050	8.69	Not visible	Not visible	Not visible	>100	Not visible	0	0	1	0.001	1
1100	9.24	Not visible	Not visible	Not visible	>100	Not visible	0	0	0	0.000	1

Data are for upper 10 cm of X-ray slabs and are normalized to 10 cm^2 surface area.

Table 5
Regression of biotic variables against environmental data.

Abundance		Density	Biomass	Body size	
CD146	Inter monsoon	$r^2 = 0.61$ (0.039) THAA (0.061, −)	$r^2 = 0.51$ (0.031) C_{org} (0.031, +)	$r^2 = 0.65$ (0.054) THAA (0.054, +)	
CD 151	Post monsoon	NO FIT	$r^2 = 0.48$ (0.055) C_{org} (0.055, +)	$r^2 = 0.87$ (0.0008) oxygen (0.0008, +)	

Diversity		Species richness	H′	J′	R1D
CD146	Inter monsoon	No fit	$r^2 = 0.35$ (0.094) oxygen (0.094, +)	No fit	No fit
CD 151	Post monsoon	No fit	$r^2 = 0.54$ (0.038) oxygen (0.038, +)	$r^2 = 0.73$ (0.067) C_{org} (0.096, +) DI (0.051, +)	$r^2 = 0.95$ (0.003) C_{org} (0.006, −) oxygen (0.010, −)

Sediment Structure		Burrow density	Depth bioturbation	Biogenic structure diversity	
CD146	Inter monsoon	$r^2 = 0.46$ (0.064) oxygen (0.064, +)	No fit	$r^2 = 0.61$ (0.065) DI (0.065, +)	
CD 151	Post monsoon	$r^2 = 0.69$ (0.011**) oxygen (0.011**, −)	$r^2 = 0.65$ (0.011) C_{org} (0.011, +)	$r^2 = 0.49$ (0.053**) oxygen (0.053**, +)	

( ) give *P* values for whole model and *P* values and direction of relationship for each abiotic parameter.
BALA = mole percentage of β-alanine (amino acid), C_{org} = percent organic carbon, clay = percent clay, salinity adjusted, DI = amino acid based degradation index (Dauwe and Middelburg, 1998), oxygen = bottom water oxygen concentrations (mL L^{-1}).
　** Spearman's ρ is given because normality of these parameters could not be achieved through transformations.

are rare, bioturbation is low, and laminations are minimal. An exaerobic zone (0.1–0.2 mL L^{-1} [4.5–9 μM]) has been defined that is comprised of meiofauna and chemosynthetic, symbiont-bearing taxa that are often shelly, epibenthic forms (Savrda and Bottjer, 1987). These occur in association with microbial mats and limited large burrows. The Pakistan margin lower OMZ transition zone exhibits elements of these two facies. The 900–950 m region in particular has shelly pectinids and thyasirids (Oliver and Levin, 2006; Hughes et al., 2008; Appendix B), although a chemosynthesis-

based nutrition has not been established for these taxa. Filamentous sulfur bacteria were present (unpublished observations) and large burrows are made by *Linopherus* sp.

At even lower oxygen concentrations (<0.1 mL L^{-1} [4.5 μM]), the quasi-anerobic zone has been defined, with characteristic low diversity of meiofauna and small polychaetes, microscopic burrows and persistent laminae (reviewed in Levin et al., 2000). The sparse fauna of spionid polychaetes and nemerteans that occupies the 300–700 m region of the Pakistan margin, where

sediments are laminated, appears to match this zone (this study; Hughes et al., 2008).

There has been debate about which faunal lifestyles and associated trace fossils are characteristic of low oxygen (Ekdale and Mason, 1988, 1989; Wheatcroft, 1989). The sequence predicted by Ekdale and Mason (1988) encompasses the transition from fodonichnia (structures made by sessile deposit feeders that mine sediments in one place) at lowest oxygen levels to pasichnia (mobile deposit feeders producing grazing trails) at moderately low levels, to domichnia (permanent dwelling structures) in aerobic conditions. Wheatcroft (1989) argued that dense tube builders are more likely to occur in low oxygen zones, and observations of abundant tubes and dwelling structures at $0.13–0.16 \, mL \, L^{-1}$ [5.8–7.1 µM] on the Oman margin supported this contention (Levin et al., 1997a, 2000).

The Pakistan margin suggests yet another lifestyle might dominate under exaerobic conditions—that of large, mobile detritivores residing in permanent burrows. Excursions into the overlying water may facilitate oxygen exposure, provide access to food even before it falls to the seafloor, and irrigate burrows. The Pakistan margin lower OMZ sediments exhibit a notably elevated incidence of large burrows and a near absence of tubes compared to the better-oxygenated zones above the OMZ (140 m) and at 1200 and 1850 m (this study; Hughes et al., 2008). Lower productivity and higher riverine mineral input than observed on the Oman margin (Qasim, 1982) could possibly generate the lifestyle differences observed between the Western (Oman) and Eastern (Pakistan) sides of the Arabian Sea.

In a shallow Swedish fjord, sediment profiling imagery revealed changes in RPD, raised tube position then loss of tube builders as oxygen concentrations fell below $0.7 \, mL \, L^{-1}$, with greatest hypoxia tolerance by thyasirids, capitellids and amphar-etids (Nilsson and Rosenberg, 2000). The loss of tube builders and early recolonization by burrowers resembles patterns within the lower Pakistan margin OMZ, as does the abundance of thyasirids and ampharetids, which were common at 950 m off Pakistan (Appendix B, Hughes et al., 2008).

4.7. Oxygen vs. organic matter as macrofaunal influences

For both inter- and post-monsoon periods, measures of macrofaunal abundance (density, biomass), species richness, burrow density and bioturbation depth were most closely associated with measures of sediment OM content or quality (Table 5, Appendix D). In contrast, variation in macrofaunal diversity (H′) and dominance (R1D) could be explained by a combination of bottom-water oxygen concentration and organic matter content (Table 5), though in the case of species richness, by organic matter content and quality alone (GAM results for cruises combined). These results differ somewhat from those of Levin and Gage (1998), who suggested, based on analysis of polychaetes from OMZs in the eastern Pacific and Indian Oceans, that oxygen was more likely to control species richness while OM influenced measures of evenness and dominance. Body size and biogenic structure diversity (richness) on the Pakistan margin appeared correlated with OM quality during the inter-monsoon period and

with oxygen during the post-monsoon period (Table 5), introducing the possibility that these factors are at times affected by food supply, but that after monsoon-associated food input, oxygen becomes limiting.

Organic enrichment and hypoxia often co-occur in shallow water under conditions of eutrophication, with the organic deposition generating oxygen depletion in sediments (Pearson and Rosenberg, 1978; Gray et al., 2002). Often this depletion is seasonal or episodic (Diaz and Rosenberg, 2001). As a result, we find diverse, well-developed animal communities within lower OMZs (e.g., $0.3–0.5 \, mL \, L^{-1}$ [13–22 µM]) at oxygen concentrations that would exclude most metazoan macrofauna in shallow water (Diaz and Rosenberg, 1995; Rabalais et al., 2001a). A broad review indicates that where both occur, hypoxia rather than organic enrichment drives the majority of benthic faunal responses in shallow water (Gray et al., 2002). Our results indicate that within the OMZ, where animals have evolved to cope with permanent low oxygen, OM supply and quality may play a more important role in structuring benthic communities.

Appendix A

See Table A1.

Appendix B

See Table B1.

Appendix C

See Table C1.

Appendix D

See Table D1.

Table A1
Correlations [r^2] with P values in ( ) between sediment and organic-matter parameters.

Parameters	Total N	C:N	$\delta^{13}C$	$\delta^{15}N$	Bottom oxygen	THAA	Bacterial C	DI	% Clay	% (BALA+GABA)	% AA-N	C_{org}
CD 146												
Total N												
C:N	0.06 (0.52)	0.13 (0.34)										
$\delta^{13}C$	0.01 (0.76)											
$\delta^{15}N$	0.02 (0.69)	**0.51 (0.03)**	**0.54 (0.02)**									
Bottom oxygen	0.01 (0.82)	0.08 (0.45)	**0.69 (0.005)**	0.34 (0.10)								
THAA	0.17 (0.36)	**0.88 (0.002)**	0.13 (0.43)	0.47 (0.08)	0.01 (0.87)							
Bacterial C	0.32 (0.19)	0.00 (0.98)	0.06 (0.59)	0.00 (0.96)	0.11 (0.46)	0.04 (0.69)						
DI	0.00 (0.95)	0.36 (0.15)	0.36 (0.15)	**0.70 (0.02)**	0.10 (0.50)	0.53 (0.06)	0.28 (0.28)					
% Clay	0.01 (0.85)	0.19 (0.29)	**0.54 (0.04)**	0.31 (0.15)	**0.69 (0.01)**	0.07 (0.60)	0.21 (0.30)	0.56 (0.09)				
% (BALA+GABA)	0.13 (0.42)	**0.86 (0.002)**	0.26 (0.25)	**0.65 (0.03)**	0.12 (0.44)	**0.86 (0.002)**	0.11 (0.52)	0.45 (0.10)	0.15 (0.44)			
% AA-N	0.27 (0.23)	**0.93 (0.0005)**	0.14 (0.40)	0.44 (0.11)	0.01 (0.87)	**0.98 (0<0.0001)**	0.03 (0.73)	0.46 (0.09)	0.07 (0.62)	**0.83 (0.004)**		
C_{org}	**0.95 (0.0001)**	0.00 (0.93)	0.00 (0.94)	0.11 (0.39)	0.03 (0.67)	0.07 (0.58)	0.34 (0.17)	0.03 (0.71)	0.04 (0.65)	0.04 (0.66)	0.14 (0.40)	
CD151												
Total N												
C:N	0.04 (0.65)											
$\delta^{13}C$	0.31 (0.15)	0.08 (0.49)										
$\delta^{15}N$	0.01 (0.80)	0.01 (0.74)	0.33 (0.13)									
Bottom oxygen	0.0 (0.45)	0.08 (0.51)	**0.64 (0.02)**	0.11 (0.40)								
THAA	0.08 (0.51)	0.07 (0.52)	0.39 (0.10)	0.19 (0.28)	0.10 (0.45)							
Bacterial C	0.18 (0.34)	0.10 (0.48)	0.00 (0.86)	0.00 (0.94)	0.08 (0.53)	0.05 (0.63)						
DI	0.34 (0.13)	0.00 (0.89)	0.08 (0.50)	0.20 (0.27)	0.04 (0.65)	0.22 (0.24)	0.02 (0.75)					
% Clay	0.04 (0.68)	0.03 (0.73)	0.19 (0.33)	0.10 (0.49)	**0.66 (0.01)**	0.01 (0.80)	0.21 (0.30)	0.00 (0.82)				
% (BALA+GABA)	0.06 (0.58)	0.38 (0.11)	0.03 (0.68)	0.14 (0.36)	0.00 (0.93)	0.08 (0.51)	0.12 (0.45)	0.01 (0.79)	0.00 (0.94)			
% AA-N	0.02 (0.73)	0.08 (0.49)	**0.53 (0.04)**	0.42 (0.08)	0.27 (0.18)	**0.82 (0.001)**	0.10 (0.49)	0.04 (0.61)	0.17 (0.31)	0.02 (0.76)		
C_{org}	**0.94 (<0.0001)**	0.00 (0.96)	0.30 (0.16)	0.03 (0.16)	0.03 (0.69)	0.06 (0.55)	0.09 (0.48)	0.11 (0.46)	0.31 (0.15)	0.03 (0.70)	0.03 (0.70)	0.03 (0.68)

P values <0.05 are shown in bold.

Table B1
Lifestyles, feeding modes and counts for Pakistan margin macrofauna.

Taxon	Lifestyle	Cruise Depth (m) / Feeding mode	CD146 700 55919#1 mgc10	CD146 750 55922#2 mgc5	CD146 800 55915#1 mgc9	CD146 850 55914#3 mgc3	CD146 850 55921#1 mgc1	CD146 900 55909#1 mgc7	CD146 900 55909#1 mgc ?	CD146 950 55918#1 mgc3	CD146 950 55929#1 mgc1	CD146 1000 55920#1 mgc3	CD146 1000 55907#1 mgc1	CD146 1050 55906#1 mgc ?
Annelida														
Tubificidae	Burrower	ssdf	0	0	0	2	0	0	0	0	0	0	0	0
Prionospio (Minuspio) sp.	Tube builder	sdf	0	1	0	6	2	2	0	1	0	0	0	0
Linopherus sp. nov.	Permanent Burrower	Detritivore	0	0	12	33	17	7	12	12	3	0	0	0
Hesionidae juv.	Mobile	Omnivore	0	0	0	0	0	1	0	0	0	0	0	0
Polynoidae sp a	Mobile	Carnivore	0	0	0	0	0	1	0	0	0	0	0	0
Acrocirrus sp. a	Tube builder	sdf	0	0	0	0	0	0	1	15	4	0	0	0
Ampharete cf. parvidentata	Tube builder	sdf	0	0	0	0	0	0	2	1	8	1	0	2
Cossura spp.	Permanent Burrower	sdf	0	0	0	0	0	0	0	5	5	5	2	2
Sphaerodoropsis sp. a	Burrower	ssdf	0	0	0	0	0	0	0	0	0	5	4	0
Aricidea sp. a	Burrower	Detritivore	0	0	0	0	0	0	0	0	0	2	1	3
Hesionidae sp. a	Mobile	Omnivore	0	0	0	0	0	0	0	0	0	2	0	0
Cirratulidae sp. A	Burrower	sdf	0	0	0	0	0	0	0	0	0	1	0	0
Flabelligeridae sp. a	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	1	0
Tharyx sp.	Permanent Burrower	sdf	0	0	0	0	0	0	0	0	0	4	4	3
Cirratulidae unid sp.	Permanent Burrower	sdf	0	0	0	0	0	0	0	0	0	0	1	0
Sabellidae, unid sp.	Tube builder	filter/sdf	0	0	0	0	0	0	0	0	0	4	1	0
Ampharetidae, unid juv	Tube builder	sdf	0	0	0	0	0	0	0	1	0	0	0	0
Nephtyidae, unid juv	Mobile	Omnivore	0	0	0	0	0	0	0	0	0	0	0	0
Paraonidae, unid juv	Burrower	Detritivore	0	0	0	0	0	0	0	0	0	0	0	2
Syllidae, unid. Juv.	Mobile	Carnivore	0	0	0	0	0	0	0	0	0	0	2	0
Sabellidae, unid. Juv.	Tube builder	Filter/sdf	0	0	0	0	0	0	0	1	1	0	0	0
Unid. Polychaeta juv.	Unknown	Unknown	0	1	0	0	0	0	0	0	0	0	0	0
Crustacea														
Gammarid sp. a	Burrower	sdf	0	0	0	0	0	0	0	0	0	2	0	0
Gammarid sp. b	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	1	0
Gammarid sp. c	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	1	0
Unid gammarid	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea sp. a	Burrower	Filter/sdf	0	0	0	0	0	7	5	0	0	0	0	0
Ampelisca sp. a	Tube builder	Omnivore	0	0	0	0	0	0	0	3	0	0	0	2
Mollusca														
Pectinid sp. A	Burrower	sdf	0	0	0	0	0	1	1	0	0	0	0	0
Leptaxinus indusarium	Permanent Burrower	sdf	0	0	0	0	0	0	0	1	3	0	0	0
Unid. aplacophoran	Burrower	Omnivore	0	0	0	0	0	0	0	0	0	1	2	1
Sipuncula	Burrower	ssdf	0	0	0	0	0	1	0	0	0	0	0	0
Echinodermata														
Unid holothurid	Mobile	sdf	0	0	0	0	0	0	0	0	2	0	0	0
Ophiurid sp. A	Mobile	sdf	0	0	0	0	0	0	0	0	0	2	2	1
Anthozoan unid	Permanent burrower	Carnivore	0	0	0	0	0	2	0	0	0	0	0	0
Anthozoa	Permanent burrower	Carnivore	0	0	0	0	0	0	0	0	0	0	3	0
Nemertean	Mobile	Carnivore	0	0	0	0	0	0	0	0	0	0	0	0

Table B1 (continued)

Taxon	Lifestyle	Cruise Depth (m) Feeding mode	CD146 700 55919#1 mgc10	CD146 750 55922#2 mgc5	CD146 800 55915#1 mgc9	CD146 850 55914#3 mgc3	CD146 850 55921#1 mgc1	CD146 900 55909#1 mgc7	CD146 900 55909#1 mgc ?	CD146 950 55918#1 mgc3	CD146 950 55929#1 mgc1	CD146 1000 55920#1 mgc3	CD146 1000 55907#1 mgc1	CD146 1050 55906#1 mgc ?
Unid. metazoan	Unknown	Unknown	0	1	0	0	0	0	0	0	0	0	0	0
Phoronida	Tube builder	Filter feeder	0	0	0	0	0	0	0	0	0	0	0	0
Tunicata	Permanent burrower	Filter feeder	0	0	0	0	0	0	0	0	0	0	0	0
Total			0	3	12	41	19	22	21	40	26	29	25	16

Taxon	Lifestyle	Cruise Depth (m) Feeding mode	CD146 1100 55905#2 mgc7	CD151 700 56113#2 mgc3	CD151 700 56113#1 mgc	CD151 800 56123#1 mgc8	CD151 850 56114#5 mgc6	CD151 900 56121#2 mgc7	CD151 950 56116#4 mgc4	CD151 950 56136#1 mgc1	CD151 1000 56119#3 mgc9	CD151 1000 56122#1 mgc2	CD151 1050 56142#1 mgc2
Annelida													
Tubificidae	Burrower	ssdf	0	0	0	0	0	0	0	0	0	0	0
Prionospio (Minuspio) sp.	Tube builder	sdf	0	0	0	0	8	2	0	0	0	0	0
Linopherus sp. nov.	Permanent Burrower	Detritivore	0	0	0	1	41	4	5	9	0	2	0
Hesionidae juv.	Mobile	Omnivore	0	0	0	0	0	0	0	0	0	0	0
Polynoidae sp a	Mobile	Carnivore	0	0	0	0	0	0	0	0	0	0	0
Acrocirrus sp. a	Tube builder	sdf	0	0	0	0	0	0	9	0	0	1	1
Ampharete cf. parvidentata	Tube builder	sdf	0	0	0	0	0	0	3	7	0	3	0
Cossura spp.	Permanent Burrower	sdf	2	0	0	0	0	0	13	16	1	1	0
Sphaerodoropsis sp. a	Burrower	ssdf	1	0	0	0	0	0	0	0	0	3	0
Aricidea sp. a	Burrower	Detritivore	2	0	0	0	0	0	0	0	0	2	1
Hesionidae sp. a	Mobile	Omnivore	0	0	0	0	0	0	0	1	0	0	0
Cirratulidae sp. A	Burrower	sdf	0	0	0	0	0	0	0	3	0	1	0
Flabelligeridae sp. a	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	0
Tharyx sp.	Permanent Burrower	sdf	0	0	0	0	0	0	0	0	4	0	0
Cirratulidae unid sp.	Permanent Burrower	sdf	1	0	0	0	0	0	0	0	0	0	1
Sabellidae, unid sp.	Tube builder	filter/sdf	0	0	0	0	0	0	0	0	0	4	1
Ampharetidae, unid juv	Tube builder	sdf	0	0	0	0	0	0	0	0	0	0	0
Nephtyidae, unid juv	Mobile	Omnivore	2	0	0	0	0	0	0	0	0	0	0
Paraonidae, unid juv	Burrower	Detritivore	0	0	0	0	0	0	0	0	0	0	0
Syllidae, unid. Juv.	Mobile	Carnivore	0	0	0	0	0	0	0	0	0	0	0
Sabellidae, unid. Juv.	Tube builder	Filter/sdf	0	0	0	0	0	0	0	0	0	0	0
Unid. Polychaeta juv.	Unknown	Unknown	0	0	1	0	0	0	0	0	0	0	0
Crustacea													
Gammarid sp. a	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	0
Gammarid sp. b	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	0
Gammarid sp. c	Burrower	sdf	0	0	0	0	0	0	0	0	0	0	0
Unid gammarid	Burrower	sdf	0	0	0	0	0	0	0	1	0	0	1
Cumacea sp. a	Burrower	Filter/sdf	0	0	0	0	0	0	0	18	0	0	0
Ampelisca sp. a	Tube builder	Omnivore	0	0	0	0	0	0	0	0	0	0	0

Mollusca

Pectinid sp. A	Burrower	sdf	0	0	0	0	0	1	0	0	0	0	0
Leptaxinus indusarium	Permanent Burrower	sdf	0	0	0	0	0	0	2	2	0	1	0
Unid. aplacophoran	Burrower	Omnivore	0	0	0	0	0	0	0	1	1	1	0
Sipuncula	Burrower	ssdf	0	0	0	0	0	2	0	0	0	0	0
Echinodermata													
Unid holothurid	Mobile	sdf	0	0	0	0	0	0	0	0	0	0	0
Ophiurid sp. A	Mobile	sdf	1	0	0	0	0	0	0	2	2	1	0
Anthozoan unid	Permanent burrower	Carnivore	0	0	0	0	0	0	0	0	0	0	0
Anthozoa	Permanent burrower	Carnivore	0	0	0	0	0	0	0	0	0	0	0
Nemertean	Mobile	Carnivore	1	0	0	0	0	0	0	0	0	0	0
Unid. metazoan	Unknown	Unknown	0	0	0	0	0	0	0	0	0	0	0
Phoronida	Tube builder	Filter feeder	0	0	0	0	0	0	1	0	0	0	0
Tunicata	Permanent burrower	Filter feeder	0	0	0	0	0	0	0	0	0	4	0
Total			10	0	1	1	49	9	33	60	8	24	5

Counts are given as number per core (9.6 cm diam × 10 cm deep).

ssdf = sub-surface deposit feeder, sdf = surface deposit feeder, filter = filter feeder.

Table C1
Correlations (r^2) with P value in ( ) between biological and biogenic structure parameters on the Pakistan margin.

Parameters	Body size	Biomass	Density	Species richness	R1D arcsine	J'	H' log base 2	Depth of bioturbated layer	# of biogenic structures	# of burrows (log 10)
CD 146										
Body size										
Biomass	0.41 (0.09)									
Density	0.16 (0.33)	**0.89 (0.0001)**								
Species richness	0.12 (0.40)	0.39 (0.07)	0.38 (0.08)							
R1D arcsine	0.00 (0.92)	0.00 (0.99)	0.01 (0.86)	0.47 (0.06)						
J'	0.05 (0.62)	0.05 (0.61)	0.05 (0.59)	0.32 (0.15)	**0.85 (0.003)**					
H' log base 2	0.07 (0.54)	0.23 (0.19)	0.21 (0.21)	**0.84 (0.0005)**	**0.86 (0.0009)**	**0.67 (0.01)**				
Depth of bioturbated layer	0.05 (0.61)	0.04 (0.65)	0.07 (0.54)	0.10 (0.45)	0.47 (0.09)	0.00 (0.99)	0.09 (0.48)			
# of biogenic structures	0.24 (0.27)	0.20 (0.26)	0.18 (0.30)	0.34 (0.13)	0.00 (0.92)	0.26 (0.24)	0.18 (0.29)	0.00 (0.98)		
# of burrows (log 10)	0.01 (0.83)	0.10 (0.44)	0.35 (0.12)	0.16 (0.33)	0.01 (0.85)	0.15 (0.35)	0.01 (0.85)	0.08 (0.50)	0.05 (0.58)	
CD151										
Body size										
Biomass	0.21 (0.26)									
Density	0.00 (0.98)	**0.50 (0.05)**								
Species richness	0.37 (0.11)	**0.85 (0.0005)**	0.19 (0.28)							
R1D arc sine	**0.61 (0.02)**	0.24 (0.21)	0.00 (0.88)	0.30 (0.16)						
J'	0.75 (0.06)	0.38 (0.27)	0.11 (0.58)	0.42 (0.24)	**0.77 (0.05)**					
H' log base 2	**0.70 (0.009)**	0.68 **(0.01)**	0.11 (0.42)	**0.88 (0.0006)**	0.49 **(0.05)**	0.66 **(0.09)**				
Depth of bioturbated layer	0.34 (0.30)	0.20 (0.45)	0.48 (0.19)	0.10 (0.60)	0.33 (0.31)	0.77 (0.12)	0.28 (0.36)			
# of biogenic structures**	0.50 (0.25)	0.05 (0.91)	0.22 (0.63)	0.10 (0.81)	0.73 (0.06)	0.21 (0.74)	0.45 (0.31)	0.22 (0.71)		
# of burrows**	0.64 (0.12)	0.36 (0.38)	0.51 (0.25)	0.40 (0.32)	**0.79 (0.04)**	0.47 (0.41)	**0.78 (0.04)**	0.89 **(0.003)**	0.78 **(0.02)**	

P values <0.05 are shown in bold.
** Spearman's ρ is given because normality of these parameters could not be achieved through transformations.

Table D1
Correlations [r^2] with P value in ( ) between biological and organic matter/sediment parameters on the Pakistan margin.

CD 146

Parameters	Body size	Biomass	Density	Species richness	R1D	J′	H′ (log base 2)	Depth of bioturbated layer	# of biogenic structures	# of burrows
Total N	0.43 (0.08)	**0.48 (0.04)**	0.30 (0.13)	0.04 (0.61)	0.03 (0.66)	0.14 (0.36)	0.05 (0.55)	0.36 (0.11)	0.09 (0.48)	0.00 (0.93)
C:N	**0.52 (0.04)**	0.00 (0.96)	0.02 (0.72)	0.01 (0.76)	0.04 (0.65)	0.29 (0.17)	0.01 (0.76)	0.09 (0.48)	0.00 (0.88)	0.01 (0.84)
$\delta^{13}C$	0.05 (0.61)	0.01 (0.82)	0.03 (0.66)	0.12 (0.36)	**0.68 (0.01)**	0.24 (0.22)	0.39 (0.07)	0.29 (0.17)	0.04 (0.64)	0.01 (0.80)
$\delta^{15}N$	0.43 (0.08)	0.08 (0.47)	0.00 (0.86)	0.05 (0.55)	0.27 (0.18)	0.00 (0.89)	0.14 (0.31)	0.18 (0.29)	0.00 (0.97)	0.04 (0.62)
Bottom oxygen	0.15 (0.34)	0.00 (0.94)	0.00 (0.99)	0.13 (0.33)	0.26 (0.19)	0.27 (0.19)	0.35 (0.09)	0.01 (0.82)	0.17 (0.31)	0.46 (0.06)
THAA	**0.65 (0.05)**	0.39 (0.13)	**0.61 (0.04)**	0.23 (0.27)	0.03 (0.75)	0.37 (0.20)	0.15 (0.39)	0.16 (0.43)	0.35 (0.21)	0.46 (0.13)
Bacterial C	0.00 (0.92)	0.14 (0.42)	0.05 (0.62)	0.00 (0.92)	0.00 (0.93)	0.00 (0.90)	0.00 (0.99)	0.00 (0.94)	0.05 (0.66)	0.15 (0.45)
DI	0.56 (0.09)	0.00 (0.95)	0.07 (0.57)	0.01 (0.84)	0.22 (0.35)	0.10 (0.54)	0.00 (0.89)	0.02 (0.80)	0.61 (0.06)	0.19 (0.39)
% clay	0.23 (0.27)	0.00 (0.90)	0.00 (0.90)	0.03 (0.67)	0.19 (0.32)	0.01 (0.86)	0.14 (0.36)	0.10 (0.49)	0.08 (0.54)	0.50 (0.08)
% (BALA+GABA)	0.42 (0.17)	0.38 (0.14)	**0.57 (0.05)**	0.17 (0.35)	0.02 (0.80)	0.11 (0.51)	0.07 (0.57)	0.17 (0.41)	0.23 (0.39)	0.42 (0.16)
% AA-N	0.55 (0.09)	0.47 (0.09)	**0.64 (0.03)**	0.20 (0.32)	0.08 (0.58)	0.39 (0.18)	0.12 (0.44)	0.24 (0.32)	0.32 (0.24)	0.36 (0.21)
C_{org}	**0.57 (0.03)**	**0.51 (0.03)**	0.29 (0.13)	0.03 (0.64	0.02 (0.75)	0.07 (0.52)	0.05 (0.58)	0.32 (0.14)	0.09 (0.47)	0.00 (0.91)

Parameters	Body size	Biomass	Density	Species richness	R1D	J′	H′ (log base 2)	Depth of bioturbated layer	# of biogenic structures**	# of burrows**

CD 151

	Body size	Biomass	Density	Species richness	R1D	J′	H′ (log base 2)	Depth of bioturbated layer	# of biogenic structures**	# of burrows**
Total N	0.42 (0.11)	0.38 (0.10)	0.12 (0.44)	0.26 (0.20)	**0.71 (0.02)**	0.70 (0.08)	0.52 (0.07)	0.47 (0.20)	0.01 (0.81)	0.10 (0.44)
C:N	0.11 (0.48)	0.00 (0.89)	0.38 (0.14)	0.06 (0.55)	0.03 (0.73)	0.00 (0.96)	0.10 (0.49)	0.34 (0.30)	0.04 (0.63)	0.32 (0.15)
$\delta^{13}C$	0.36 (0.15)	0.01 (0.45)	0.12 (0.45)	0.08 (0.50)	0.50 (0.08)	0.45 (0.16)	0.54 (0.06)	0.19 (0.47)	0.25 (0.21)	**0.71 (0.009)**
$\delta^{15}N$	0.10 (0.50)	0.06 (0.54)	0.38 (0.14)	0.01 (0.83)	0.00 (0.96)	0.02 (0.83)	0.03 (0.70)	0.01 (0.87)	0.02 (0.72)	0.09 (0.48)
Bottom oxygen	**0.87 (0.0008)**	0.00 (0.99)	0.00 (0.92)	0.01 (0.80)	0.38 (0.10)	0.55 (0.15)	**0.54 (0.04)**	0.41 (0.25)	**0.49 (0.05)**	**0.69 (0.01)**
THAA	0.00 (0.97)	0.04 (0.65)	0.02 (0.78)	0.08 (0.51)	0.02 (0.79)	0.72 (0.07)	0.14 (0.40)	0.06 (0.68)	0.09 (0.47)	0.22 (0.24)
Bacterial C	0.02 (0.81)	0.27 (0.23)	0.02 (0.79)	0.12 (0.44)	0.06 (0.64)	0.00 (0.98)	0.03 (0.76)	0.00 (0.97)	0.29 (0.21)	0.00 (0.93)
DI	0.35 (0.16)	0.05 (0.58)	0.00 (0.91)	0.15 (0.35)	0.32 (0.18)	**0.87 (0.02)**	0.30 (0.20)	0.46 (0.16)	0.01 (0.81)	0.00 (0.95)
% Clay	0.31 (0.19)	0.01 (0.79)	0.08 (0.55)	0.02 (0.74)	0.05 (0.62)	0.06 (0.76)	0.12 (0.45)	0.15 (0.61)	0.48 (0.08)	0.10 (0.49)
% (BALA+GABA)	0.08 (0.54)	0.09 (0.46)	0.50 (0.08)	0.05 (0.58)	0.01 (0.86)	0.01 (0.91)	0.00 (0.89)	0.09 (0.63)	0.16 (0.33)	0.10 (0.49)
% AA-N	0.01 (0.87)	0.04 (0.65)	0.04 (0.66)	0.08 (0.48)	0.03 (0.70)	0.31 (0.33)	0.26 (0.24)	0.00 (0.97)	0.23 (0.23)	0.21 (0.25)
C_{org}	0.31 (0.19)	**0.48 (0.05)**	0.32 (0.19)	0.29 (0.17)	**0.68 (0.02)**	**0.76 (0.05)**	0.50 (0.08)	0.65 (0.10)	0.00 (0.91)	0.20 (0.27)

P values <0.05 are shown in bold.
** Spearman's ρ is given because normality of these parameters could not be achieved through transformations.

References

Bett, B.J., 2004a. RRS "Charles Darwin" Cruise 145, 12 Mar–09 Apr 2003. Benthic Ecology and Biogeochemistry of the Pakistan Margin, Southampton Oceanography Centre Cruise Report, No. 50, 161pp.

Bett, B.J., 2004b. RRS "Charles Darwin" Cruise 150, 22 Aug–15 Sep 2003. Benthic Ecology and Biogeochemistry of the Pakistan Margin, Southampton Oceanography Centre Cruise Report, No. 51, 144pp.

Blazejak, A., Erseus, C., Amann, R., Dubilier, N., 2005. Coexistence of bacterial sulfide oxidizers, sulfate reducers, and spirochetes in a gutless worm (Oligochaeta) from the Peru margin. Applied and Environmental Microbiology 71, 1553–1561.

Brand, T.D., Griffiths, C., 2008. Seasonality in the hydrography and biogeochemistry across the Pakistan Margin of the NE Arabian Sea. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.05.036].

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. PRIMER-E, Plymouth.

Cook, A.A., Lambshead, P.J.D., Hawkins, L.E., Mitchell, N., Levin, L.A., 2000. Nematode abundance at the oxygen minimum zone in the Arabian Sea. Deep-Sea Research Part II 47, 75–85.

Cowie, G.L., 2005. The biogeochemistry of Arabian Sea surficial sediments: a review of recent studies. Progress in Oceanography 65, 260–289.

Cowie, G.L., 2003a. RRS "Charles Darwin Cruise 146: 12 April–30 May 2003. Benthic Ecology and Biogeochemistry of the Pakistan Margin. Cruise Report, 124pp.

Cowie, G.L., 2003b. RRS Charles Darwin Cruise 151: 15 September–20 October 2003. Benthic Ecology and Biogeochemistry of the Pakistan Margin. Cruise Report, 123pp.

Cowie, G.L., Hedges, J.I., 1992a. Improved quantification of amino acids in environmental samples—reduced analysis time and charge-matched recovery standards. Marine Chemistry 37, 223–238.

Cowie, G.L., Hedges, J.I., 1992b. Sources and reactivities of amino acids in a coastal marine environment. Limnology and Oceanography 37, 703–724.

Cowie, G.L., Hedges, J.I., 1994. Biochemical indicators of diagenetic alteration in natural organic mixtures. Nature 369, 304–307.

Cowie, G.L., Levin, L.A., 2008. Benthic biological and biogeochemical patterns and processes across an oxygen minimum zone (Pakistan Margin, NE Arabian Sea). Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.06.001].

Creasey, S., Rogers, A.D., Tyler, P., Gage, J., Jollivet, D., 2000. Genetic and morphometric comparisons of squat lobster, Munidopsis scobina (Decapoda: Anomura: Galatheidae) populations, with notes on the phylogeny of the genus Munidopsis. Deep-Sea Research II 47, 87–118.

Dauwe, B., Middelburg, J.J., 1998. Amino acids and hexosamines as indicators of organic matter degradation state in North Sea sediments. Limnology and Oceanography 43, 782–798.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology: An Annual Review 33, 245–303.

Diaz, R.J., Rosenberg, R., 2001. Overview of anthropogenically induced hypoxic effects on marine benthic fauna. In: Rabalais, N.N., Turner, R.E. (Eds.), Coastal Hypoxia: Consequences for Living Resources and Ecosystems. American Geophysical Union, Washington, DC, pp. 129–146.

Ekdale, A.A., Mason, T.R., 1988. Characteristic trace-fossil associations in oxygen-poor sedimentary environments. Geology 16, 720–723.

Ekdale, A.A., Mason, T.R., 1989. Commentary and reply on "Characteristic trace-fossil associations in oxygen-poor sedimentary environments". Geology 17, 674–676.

Findlay, R.H., King, G.M., Watling, L., 1989. Efficacy of phospholipid analysis in determining microbial biomass in sediments. Applied and Environmental Microbiology 55, 2888–2893.

Gallardo, V.A., Palma, M., Carrasco, F.D., Gutiérrez, D., Levin, L.A., Cañete, J.I., 2004. Macrobenthic zonation caused by the oxygen minimum zone on the shelf and slope off central Chile. Deep-Sea Research II 51, 2475–2490.

Gooday, A.J., Levin, L.A., Aranda da Silva, A., Bett, B.J., Cowie, G.L., Dissard, D., Gage, J.D., Hughes, D.J., Jeffreys, R., Lamont, P.A., Larkin, K.A., Murty, S.J., Schumacher, S., Whitcraft, C., Woulds, C., 2008. Faunal responses to oxygen gradients on the Pakistan margin: a comparison of foraminifera, macrofauna and megafauna. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.10.003].

Gray, J., Wu, R.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. Marine Ecology Progress Series 238, 249–279.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman & Hall, New York.

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

Hughes, D.J., Lamont, P.A., Levin, L.A., Packer, M., Gage, J.D., 2008. Macrofaunal communities and sediment structure across the Pakistan Margin oxygen minimum zone, north-east Arabian Sea. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.05.030].

Keil, R.G., Cowie, G.L., 1999. Organic matter preservation through the oxygen minimum zone of the NE Arabian Sea, as discerned by mineral–organic interactions. Marine Geology 161, 13–22.

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanography and Marine Biology: An Annual Review 41, 1–45.

Levin, L.A., Gage, J.D., 1998. Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. Deep-Sea Research II 45, 129–163.

Levin, L.A., Thomas, C.L., Wishner, K., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. Journal of Marine Research 49, 763–800.

Levin, L.A., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C., 1997. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina Slope. Journal of Marine Research 55, 595–611.

Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. Deep-Sea Research Special Volume: Benthic Processes in the Arabian Sea. Deep-Sea Research II 47, 189–226.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and Systematics 132, 51–93.

Levin, L.A., Gutiérrez, D., Rathburn, A., Neira, C., Sellanes, J., Muñoz, P., Gallardo, V.M., Salamanca, M., 2002. Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997-98 El Niño. Progress in Oceanography 53, 1–27.

Levin, L.A., Rathburn, A.E., Gutierrez, D., Muñoz, P., Shankle, A., 2003. Bioturbation by symbiont-bearing annelids in near-anoxic sediments: implications for biofacies models and paleo-oxygen assessments. Palaeogeography, Palaeoclimatology, Palaeoecology 199, 129–140.

Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen minimum zone edge effects, evidence from the central California coastal upwelling system. Geology 13, 491–494.

Murty, S., Bett, B., Gooday, A., 2008. Megafaunal response to strong oxygen gradients on the Pakistan Margin of the Arabian Sea. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.05.029].

Neira, C., Sellanes, J., Levin, L.A., Arntz, W.E., 2001a. Meiofaunal distributions on the Peru margin: relationships to oxygen and organic matter availability. Deep-Sea Research I 48, 2453–2472.

Neira, C., Sellanes, J., Soto, A., Guitierrez, D., Gallardo, V.A., 2001b. Meiofauna and sedimentary organic matter off central Chile: response to changes caused by the 1997–98 El Niño. Oceanologica Acta 24, 313–328.

Nilsson, H.C., Rosenberg, R., 2000. Succession in marine benthic habitats and fauna in response to oxygen deficiency analysed by sediment profile-imaging and by grab samples. Marine Ecology Progress Series 197, 139–149.

Oliver, P.G., Levin, L., 2006. A new species of the family Thyasiridae (Mollusca: Bivalvia) from the oxygen minimum zone of the Pakistan margin. Journal of the Marine Biological Association of the United Kingdom 86, 411–416.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16, 229–311.

Qasim, S.Z., 1982. Oceanography of the northern Arabian Sea. Deep-Sea Research A A29, 1041–1068.

Rabalais, N.N., Harper Jr., D.E., Turner, R.E., 2001a. Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In: Rabalais, N.N., Turner, R.E. (Eds.), Coastal Hypoxia: Consequences for Living Resources and Ecosystems. American Geophysical Union, Washington, DC, pp. 115–128.

Rabalais, N.N., Smith, L.E., Harper Jr., D.E., Justic, D., 2001b. Effects of seasonal hypoxia on continental shelf benthos. In: Rabalais, N.N., Turner, R.E. (Eds.), Coastal Hypoxia: Consequences for Living Resources and Ecosystems. American Geophysical Union, Washington, DC, pp. 211–240.

Rhoads, D.C., Mulsow, S.G., Gutschick, R., Baldwin, C.T., Stolz, J.F., 1991. The dysaerobic zone revisited, a magnetic facies? In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society, Tulsa, OK, pp. 187–199.

Rosenberg, R., Nilsson, H.C., Diaz, R.J., 2001. Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. Estuarine, Coastal and Shelf Science 53, 343–350.

Rosenberg, R., Agrenius, S., Hellman, B., Nilsson, H.C., Norling, K., 2002. Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. Marine Ecology Progress Series 234, 43–53.

Rowe, G.T., 1983. Biomass and production of the deep-sea macrobenthos. In: Rowe, G.T. (Ed.), Deep-Sea Biology, Vol. 8 The Sea. Wiley, New York, pp. 453–472.

Savrda, C.E., Bottjer, D.J., 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology 14, 3–6.

Savrda, C.E., Bottjer, D.J., 1987. The exaerobic zone, a new oxygen-deficient marine biofacies. Nature 327, 54–56.

Savrda, C.E., Bottjer, D.J., 1991. Oxygen-related biofacies in marine strata. An overview and update. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. The Geological Society of London, London, pp. 201–219.

Savrda, C.E., Bottjer, D.J., Gorsline, D., 1984. Development of a comprehensive oxygen-deficient marine biofacies model, evidence from Santa Monica, San Pedro, and Santa Barbara Basins, California Continental Borderland. American Association of Petroleum Geologists Bulletin 68, 1179–1192.

Smallwood, B.J., Wolff, G.A., Smith, C.R., Hoover, D., Gage, J.D., Patience, A., 1999. Megafauna can control the quality of organic matter in marine sediments. Naturwissenschaften 86, 320–324.

Smith, C.R., Levin, L.A., Hoover, D.J., McMurtry, G., 2000. Variations in bioturbation across the oxygen minimum zone in the northwest Arabian Sea. Deep-Sea Research II 47, 227–257.

Thompson, J.B., Mullins, H.T., Newton, C.R., Vercoutere, T., 1985. Alternative biofacies model for dysaerobic communities. Lethaia 18, 167–179.

Vandewiele, S., Cowie, G., Middelburg, J.J., Soetart, K., 2008. Amino acid biogeochemistry and organic matter quality across the Pakistan Margin

oxygen minimum zone. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.05.035].

Wheatcroft, R.A., 1989. Characteristic trace-fossil associations in oxygen-poor sedimentary environments: discussion. Geology 17, 674.

Wishner, K.F., Ashjian, C.J., Gelfman, C., Gowing, M., Kann, L., Levin, L.A., Mullineaux, L.S., Saltzman, J., 1995. Pelagic and benthic ecology of the lower interface of the eastern tropical Pacific oxygen minimum zone. Deep-Sea Research I 42, 93–115.

Woulds, C., Andersson, J.H., Cowie, G., Middelburg, J.J., Levin, L.A., 2008. The short-term fate of organic carbon in marine sediments: comparing the Pakistan Margin to other regions. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2008.10.008].

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