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Macrofaunal communities and sediment structure across the Pakistan margin Oxygen Minimum Zone, North-East Arabian Sea

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ABSTRACT

Benthic macrofauna and sediment column features were sampled at five stations along a bathymetric transect (depths 140, 300, 940, 1200, 1850 m) through the Pakistan margin Oxygen Minimum Zone (OMZ) during the 2003 intermonsoon (March–May) and late-post-monsoon (August–October) periods. Objectives were to compare patterns with those described from other OMZs, particularly the Oman margin of the Arabian Sea, in order to assess the relative influence of bottom-water oxygenation and sediment organic content on macrofaunal standing stock and community structure. Macrofaunal density was highest at the 140-m station subject to monsoon-driven shoaling of the OMZ, but there was no elevation of density at the lower OMZ boundary (1200 m). Numbers was extremely low in the OMZ core (300 m) and were not readily explicable from the environmental data. There was no consistent depth-related trend in macrofaunal biomass. Macrofaunal densities were consistently lower than found off Oman but there was less contrast in biomass. A significant post-monsoon decline in macrofaunal density at 140 m was driven by selective loss of polychaete taxa. Polychaeta was the most abundant major taxon at all stations but did not dominate the macrofaunal community to the extent reported from Oman. Cirratulidae and Spionidae were major components of the polychaete fauna at most stations but Acrocirridae, Ampharetidae, Amphinomidae and Cossuridae were more important at 940 m. Polychaete assemblages at each station were almost completely distinct at the species level. Polychaete species richness was positively correlated with bottom-water dissolved oxygen and negatively correlated with sediment TOC, C:N ratio and total phytopigments. Community dominance showed the opposite pattern. The strongly inverse correlation between oxygen and measures of sediment organic content made it difficult to distinguish their relative effects. The strongly laminated sediments in the OMZ core contrasted with the homogeneous, heavily bioturbated sediments above and below this zone but were associated with minimal macrofaunal biomass rather than distinctive functional group composition. In general, data from the Oman margin were weak predictors of patterns seen off Pakistan, and results suggest the importance of local factors superimposed on the broader trends of macrofaunal community composition in OMZs.

1. Introduction

In the Arabian Sea wind-driven upwelling during the south-west monsoon (June–September) and convective mixing during the north-east monsoon (December–February) lead to two annual episodes of elevated planktonic primary production separated by more oligotrophic intermonsoon periods (Qasim, 1982; Nair et al., 1989; Madhupratap et al., 1996; Wiggert et al., 2005). High export fluxes from the euphotic zone result in accumulation of organic-rich sediments (Cowie, 2005) and generate an intense Oxygen Minimum Zone (OMZ), which impinges on the continental margin at $<$100–1300 m depth (Qasim, 1982; Helly and Levin, 2004). Owing to its perceived importance in global biogeochemical cycling (Law and Owens 1991; Owens et al., 1991; Naqvi and Jayakumar, 2000) the Arabian Sea has been the focus of several large-scale research programmes, with emphasis on both water-column (Smith, 1998, 1999, 2000, 2001, 2002; Burkill, 1999; Gaye-Haake et al., 2005) and benthic (Gage et al., 2000; Pfannkuche and Lochte, 2000) processes.

The major community patterns seen in OMZ benthos worldwide were reviewed by Levin (2003). Macrofaunal communities in OMZs typically show reduced species richness and elevated

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dominance in comparison with non-OMZ slope environments. Biomass is often reduced where oxygen levels are lowest. Patterns of faunal abundance are less consistent, but high densities are sometimes observed near upper or lower OMZ boundaries. Reduced bioturbation in OMZs may cause laminated sediments to persist in conditions of minimal biological disturbance. Data for polychaetes in the Indian and Pacific Oceans suggest that standing stock and community diversity are controlled by the interaction of dissolved oxygen and sediment organic content, with the former exerting a greater influence on species richness, and the latter mainly affecting dominance and evenness (Levin and Gage, 1998). However since dissolved oxygen levels are often closely tied to the quantity and quality of organic matter in OMZ sediments (Cowie, 2005; Cowie et al., 1999) these effects cannot always be separated. A concentration of 0.3–0.4 ml l^{-1} (13.4–17.9 μM) appears to mark a critical threshold below which dissolved oxygen exerts the strongest influence on community composition and diversity (Levin, 2003). In some localities benthos may be exposed to seasonal changes that cross this oxygenation threshold (Gutiérrez et al., 2000). However, much less is known about OMZ boundary processes than about seasonal or anthropogenic hypoxia in shallow-water ecosystems (Diaz and Rosenberg, 1995; Rabalais and Turner, 2001).

The ecological consequences of environmental forcing in OMZ macrofaunal communities are also complex. On the Oman margin Smith et al. (2000) found that some indices of bioturbation (for example, diversity of burrow types) were strongly correlated with bottom-water dissolved oxygen while others (such as ^{210}Pb mixed-layer depth) appeared insensitive. Functional group composition of the macrofauna appears to be more important than numbers and biomass in determining community bioturbation potential (Smith et al., 2000; Levin et al., 2002).

Data from the Arabian Sea coasts of India and Pakistan (Qasim, 1982) indicate some important environmental differences from the Oman margin, including lower pelagic productivity and a seasonal upslope movement of the OMZ driven by the south-west monsoon. Strongly laminated sediments described from 200 to 1000 m depth on the Pakistan margin (Cowie et al., 1999; Staubwasser and Sirocko, 2001) contrast with the more heavily bioturbated sediments recorded off Oman (Smith et al., 2000), and suggest marked differences in community biomass and/or composition. Biomass data (Qasim, 1982) support the hypothesis that benthic populations are sparse along the eastern Arabian Sea margin but provide only a coarse depth resolution and give no details of community structure.

In this paper we describe patterns in macrofaunal abundance, biomass, community composition, diversity and sediment structure along a bathymetric transect from 140 to 1850 m depth through the Pakistan margin OMZ. The underlying rationale was to use the contrasts between this area and the Oman margin to identify the key environmental controls on OMZ macrofaunal communities. Higher-resolution data on changes in community and sediment structure across the lower OMZ boundary are discussed by Levin et al. (2009).

We structure our analysis around the following hypotheses, framed using published information on OMZ macrofauna and the Pakistan margin environment:

1. Standing stock:
   (a) Lower primary productivity along the Pakistan margin will be reflected in lower macrofaunal standing stocks than found at comparable water depths on the Oman margin.
   (b) Macrofaunal standing stock will be lowest in the OMZ core. Highest values will be found near the upper and lower OMZ boundaries.
2. Composition and diversity
   (a) Macrofauna in the OMZ will be dominated by soft-bodied taxa, particularly annelids, with very low representation of calcified groups (molluscs, crustaceans, echinoderms).
   (b) Macrofaunal communities in the OMZ will show lower species richness, lower evenness and higher dominance than communities above and below the OMZ.
3. Temporal change
   (a) At shelf depths subject to monsoon-driven shoaling of the OMZ, macrofaunal density will decline significantly after the south-west monsoon owing to mortality of hypoxia-sensitive taxa such as echinoderms and crustaceans.
   (b) Temporal changes will be small or absent in the OMZ core and at the deeper stations below it.
4. Sediment structure
   (a) Between-station differences in bioturbation intensity will reflect contrasts in functional composition of macrofauna rather than changes in numbers or biomass alone.
   (b) At stations with laminated sediments, macrofauna will consist almost entirely of surface-feeding epifauna or small tubicolous taxa. Deep-dwelling bioturbators ('conveyor-belt' or subsurface deposit-feeders) will be rare or absent.

2. Methods

2.1. Study sites

Sampling took place in 2003 from the RRS *Charles Darwin* on cruises CD 145/146 (12 March–30 May, intermonsoon period) and CD 150/151 (22 August–20 October, late south-west monsoon, extending into post-monsoon period). Five stations at target depths of 140, 300, 940, 1200 and 1850 m were sampled, extending from the shelf through and beyond the OMZ. Cowie and Levin (2009) discuss environmental characteristics of the stations during the two sampling periods and define a zonation scheme for the Pakistan margin OMZ. A brief summary is presented here in Table 1. Dissolved oxygen concentrations were consistently lowest at 300 m depth, slightly higher at 940 m and increased at greater depths. The deepest station (1850 m) lay below the lower OMZ boundary (dissolved oxygen >0.5 ml l^{-1} or 22.3 μM). Little temporal change was observed at any of these stations. In contrast, at the shallowest station (140 m), a >19-fold decrease in dissolved oxygen between the intermonsoon and late-post-monsoon sampling intervals indicates a strong upslope movement of the oxygen-deficient water mass.

Sediments at all stations were overwhelmingly fine-grained, with sand content (of disaggregated sediment) near zero in the upper 0–1 cm. Within the silt-clay fraction, mean and median particle sizes decreased consistently with increasing water depth. Percentage TOC of surface sediment was highest within the OMZ (300, 940 and 1200 m, range 2.55–4.12%), lowest below the OMZ at 1850 m (~1.14%), and intermediate at 140 m (~1.49%) Carbon:-nitrogen ratio followed a similar pattern. Intermonsoon and late-post-monsoon values showed little change for either parameter. Total phytopigment concentration of surface sediment was very low below the OMZ at (~1 μg g^{-1} at 1850 m), higher at 140 m (~7 μg g^{-1}), and consistently much higher at 300 and 940 m (>25 μg g^{-1}). At 1200 m the intermonsoon phytopigment concentration was close to that recorded at 140 m, but the late-post-monsoon value was much higher, rising 3.5-fold to >30 μg g^{-1}).

2.2. Macrofaunal sampling and analysis

Macrofaunal samples were collected using the megacorer, a hydraulically damped device based on the SMBA multiple corer

Table 1
Summary environmental data for sampling stations..

Zone		140 m Seasonally hypoxic	300 m OMZ core	940 m Lower OMZ transition	1200 m Lower OMZ boundary	1850 m Below OMZ
Bottom water						
Temperature, °C	Intermonsoon	22.3	15.3	9.0	7.3	3.4
	Late-post-monsoon	18.2	14.9	9.3	7.3	3.7
Salinity, psu	Intermonsoon	36.4	36.1	35.5	35.2	34.9
	Late-post-monsoon	36.0	36.0	35.4	35.2	34.9
Dissolved O_2, ml l^{-1} (CTD sensor)	Intermonsoon	2.12	0.10	0.13	0.34	1.78
	Late-post-monsoon	0.11	0.11	0.17	0.36	1.65
Sediment						
% Sand (0–0.5 cm)		0.16	0.00	0.00	0.00	0.00
% Silt (0–0.5 cm)		69.55	65.74	63.70	62.38	60.60
%Clay (0–0.5 cm)		30.29	34.26	36.30	37.62	39.40
Mean grain size, μm (0–0.5 cm)		7.02	5.19	4.27	4.20	3.89
Median grain size, μm (0–0.5 cm)		4.17	3.45	3.16	3.04	2.82
% Total organic carbon (0–2 cm)	Intermonsoon	1.52	2.55	3.53	3.42	1.18
	Late-post-monsoon	1.47	2.71	3.69	4.12	1.09
C:N ratio (0–2 cm)	Intermonsoon	9.16	9.97	9.70	9.63	8.44
	Late-post-monsoon	8.94	9.65	9.82	9.70	7.65
Total phytopigments, μg g^{-1} (0–1.5 cm)	Intermonsoon	8.2	32.8	26.8	8.9	0.7
	Late-post-monsoon	6.4	40.0	29.3	31.1	1.4

Bottom water temperature, salinity and dissolved oxygen data from T. Brand, sediment grain size data from G. Law, % TOC and C:N data from G. Cowie, pigment data from C. Woulds. Zone definitions from Cowie and Levin (2009).

(Barnett et al., 1984). Internal core diameter was 9.6 cm. At each station sampling was aimed at a single target position, with drift of the ship generating haphazard spatial variability between replicate drops. On deck, recovered cores were extruded and the uppermost 10 cm fixed in 10% buffered formaldehyde solution with Rose Bengal stain. A subset of cores from each depth were sectioned more finely (0–1, 1–3, 3–5, 5–10 cm, >10 cm) for analysis of distribution down the sediment column. Table 2 lists the macrofaunal samples collected and analysed in this study.

In the laboratory, sediment samples were washed through a 300-μm sieve and the retained material preserved in 90% ethanol with 2% propylene glycol before sorting under a binocular dissecting microscope. Nematodes, harpacticoids and other meiofaunal taxa were excluded from analysis. Non-polychaete macrofauna were identified to major taxon. Polychaetes from all cores were classified to family level and in a subset of cores were identified further to the level of nominal species. Polychaetes were classified into feeding type and lifestyle categories according to Fauchald and Jumars (1979). Wet-weight biomass of major taxa within individual cores was measured on a Sartorius top-pan electronic balance. Alcohol-preserved specimens were rehydrated in fresh water and carefully blotted on absorbant paper to remove surface liquid before weighing. Calcareous shells were not removed.

For each depth station, megacorer drops were treated as replicate data points. Where macrofaunal abundance and biomass data were available from more than one core per drop, mean values (±SD) were calculated for the drop and then used to estimate station means. Polychaete species diversity was analysed using the PRIMER™ Version 5 statistical package (Clarke and Warwick, 2001).

2.3. X-radiography of sediment core sections

Megacores from each station were subsampled during cruises CD 146 and CD 151 with short (69 × 9 × 145 mm) or long (80 × 12 × 240 mm or 70 × 10 × 200 mm) slab subcores made of transparent plexiglass. One to three megacores were sampled per station on each cruise, each from a different corer drop. In some instances slabs were collected for X-raying from tubes in the same corer drop. Where this occurred, we present the mean values for the drop.

Slabs were stored in the cold room until images were taken (within 24 h of collection) on board ship using a portable ACONA PX-20N X-ray unit. 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 slab thickness and sediment texture. X-radiographs were developed on board ship (5 min developer (Kodak D-19), 1 min stop bath, 5 min fixer, 1 min active rinse, 5 min passive rinse).

Preliminary observations on X-radiographs were made aboard ship using natural light. To quantify features within the X-radiographs, digital images, generated using a Nikon Coolpix 995 camera (3.3 MP), were enlarged and contrast was enhanced using Adobe Photoshop software. We recorded the presence/absence and thickness of laminae, the depth of a visual mixed layer, and numbers of burrows (biogenic cavities lacking a discrete outer wall) and tubes (cavities enclosed within a discrete wall of proteinaceous material or agglutinated sediment grains). We also recorded the number of types of biogenic structures, and primary burrow dimensions. Because each slab was a slightly different size, and some megacores were shallower than others, we normalized data to 10 cm^2 and limited counts to a depth of 10 cm. Observations are given for sediments below this depth where appropriate. The limited amount of true replication (from separate drops) at most stations prevented statistical testing of station differences, so we present only a description of X-radiographs and summary data for quantifiable features.

3. Results

3.1. Total macrofaunal abundance, biomass and body size

Total macrofaunal density was much greater at 140 m (mean values ~10,000–15,000 ind m^{-2}) than at any deeper station (Fig. 1). The fauna at 300 m was extremely sparse, with mean

Table 2
Summary of macrofaunal samples collected on the Pakistan margin on R.V. *Charles Darwin* cruises CD 145/146 (intermonsoon) and CD 150/151 (late-post-monsoon).

Target depth (m)	Station number	Date	Depth (m)	Latitude (°N)	Longitude (°E)	Number of cores
Intermonsoon samples (cruises CD 145/146)						
140	55901#08	20 April 03	140	23 16.77	66 42.58	1
	55901#09	21 April 03	140	23 16.85	66 42.72	2 (1)
	55901#10	21 April 03	140	23 16.78	66 42.89	1
	55901#14	23 April 03	140	23 16.75	66 42.63	1
	55901#16	23 April 03	140	23 16.66	66 42.72	3 (1)
300	55803#06	21 March 03	311	23 12.25	66 33.98	1
	55813#01	24 March 03	308	23 12.57	66 33.77	1
	55902#02	25 March 03	300	23 12.50	66 34.02	2
	55902#08	26 March 03	300	23 12.47	66 33.92	1
940	55918#02	15 May 03	940	22 53.50	66 36.63	2 (1)
	55918#04	16 May 03	940	22 53.56	66 36.69	2 (1)
	55918#05	16 May 03	940	22 53.50	66 36.71	2 (1)
	55918#09	17 May 03	940	22 53.54	66 36.64	4 (1)
	55918#10	17 May 03	940	22 53.48	66 36.68	2 (1)
1200	55819#02	26 March 03	1197	22 59.95	66 24.44	2 (1)
	55822#01	27 March 03	1200	22 59.97	66 24.44	2 (1)
	55836#01	30 March 03	1214	22 59.89	66 24.12	2 (1)
	55911#07	10 May 03	1200	23 00.01	66 24.47	2 (1)
	55911#10	11 May 03	1200	23 00.07	66 24.57	1
1850	55827#03	28 March 03	1870	22 51.35	66 00.09	1
	55827#04	28 March 03	1867	22 51.50	66 00.10	1 (1)
	55830#01	29 March 03	1874	22 50.84	65 59.72	1
	55838#01	31 March 03	1871	22 51.31	66 00.03	1
	55904#05	4 May 03	1860	22 52.38	66 00.12	2
Late-post-monsoon samples (cruises CD 150/151)						
140	56016#03	28 Aug 03	135	23 16.92	66 42.74	2
	56031#02	31 Aug 03	136	23 16.56	66 42.51	2
	56031#03	31 Aug 03	134	23 16.52	66 42.40	2
	56033#04	1 Sept 03	136	23 16.76	66 42.64	1 (1)
	56101#02	19 Sept 03	133	23 16.80	66 42.71	1 (1)
300	56021#01	29 Aug 03	307	23 12.51	66 34.04	1
	56025#07	30 Aug 03	305	23 12.51	66 34.18	1
	56040#01	3 Sept 03	306	23 12.54	66 34.10	1
	56040#02	3 Sept 03	307	23 12.52	66 34.07	1
	56107#02	28 Sept 03	318	23 12.48	66 33.99	1
940	56012#02	27 Aug 03	951	22 55.90	66 36.16	4 (1)
	56012#03	27 Aug 03	956	22 55.84	66 36.10	3 (1)
	56015#01	28 Aug 03	962	22 56.17	66 36.11	1
	56015#02	28 Aug 03	958	22 55.90	66 36.12	1 (1)
	56015#03	28 Aug 03	960	22 55.88	66 36.09	1 (1)
	56116#10	6 Oct 03	943	22 56.49	66 36.66	3 (1)
1200	56007#03	26 Aug 03	1205	22 59.91	66 24.41	1
	56007#04	26 Aug 03	1203	22 59.79	66 24.49	2 (1)
	56011#03	27 Aug 03	1202	22 59.98	66 24.43	1
	56044#01	4 Sept 03	1198	23 00.07	66 24.45	2 (1)
	56139#01	14 Oct 03	1255	22 59.99	66 24.41	2
	56139#02	14 Oct 03	1255	22 59.98	66 24.43	1 (1)
1850	56001#02	24 Aug 03	1862	22 52.38	65 59.99	1 (1)
	56005#02	25 Aug 03	1860	22 52.52	66 00.01	1
	56005#03	25 Aug 03	1859	22 52.60	65 59.99	2 (1)
	56005#04	25 Aug 03	1864	22 52.26	65 59.80	1
	56137#01	12 Oct 03	1853	22 52.41	66 00.04	1
	56137#02	12 Oct 03	1853	22 52.41	66 00.04	1

Each line in the table represents a megacorer deployment. The total number of cores analysed for macrofauna is given in the final column, with the number in parentheses representing the number of cores fine-sectioned for macrofaunal depth distribution.

(±SD) densities of 159±122 (intermonsoon) and 486±817 (late-post-monsoon) ind m^{-2}. Numbers of macrofauna per core ranged from zero (in four out of ten cores examined) to 15, giving a maximum estimated density of 1920 ind m^{-2}.

Mean densities at 940 and 1850 m were similar (~3300–5200 ind m^{-2}), with lower values observed at 1200 m (~1000 ind m^{-2}). Two-way ANOVA of density data found the main effects DEPTH and TIME (both $P<0.001$) and the DEPTH × TIME interaction ($P<0.01$) to be highly significant. Two-sample *t*-tests for each depth station showed that late-post-monsoon densities were significantly lower than intermonsoon values at 140 m ($t_6 = 3.91$, $P<0.01$) and 940 m ($t_8 = 4.06$, $P<0.01$). Temporal changes were non-significant at 300, 1200 and 1850 m.

Wet-weight biomass m^{-2} was extremely variable among replicate corer drops at each station owing to the sporadic occurrence of larger-bodied individuals (Table 3). This was particularly evident at 940 m, where burrowing anemones were major contributors to biomass. Sample biomass from 300 m was below measurement limits. The wide within-sample variability meant that no statistically significant differences between depths or time intervals could be detected, but mean biomass was much higher at 940 m (both cruises) than at any other station. The high macrofaunal density at 140 m was associated with the lowest values for mean individual size (Table 3), indicating that small-bodied animals predominated at this depth.

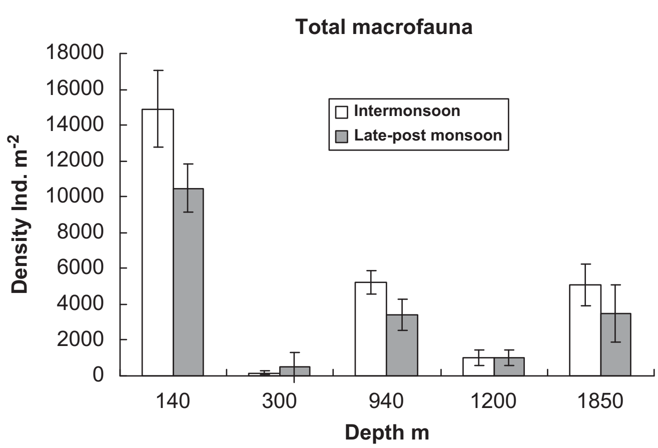

Fig. 1. Mean density (±SD) for total macrofauna (>300 μm) from stations on the Pakistan margin sampled in 2003. Data are shown separately for intermonsoon (March–May) and late-post-monsoon (August–October) sampling intervals.

3.2. Higher-taxon community composition

Polychaeta was by far the largest contributor to macrofaunal numbers at 140 m, constituting 87% and 76% of the total in intermonsoon and late-post-monsoon samples, respectively (Fig. 2). The sparse fauna collected at 300 m consisted of polychaetes and nemerteans in approximately equal numbers. Polychaeta was also the largest single group at 940, 1200 and 1850 m, but percentage contribution was lower than at 140 m owing to a greater abundance of crustaceans and molluscs. The crustaceans were largely amphipods at 940 and 1200 m, and isopods and tanaids at 1850 m. Echinoderm macrofauna were rare at all depths.

The statistically significant temporal changes in total macrofaunal density at 140 and 940 m were not uniform across major taxa. At both stations the changes were driven by declines in polychaete abundance (38% numerical decline at 140 m, 53% at 940 m), while numbers of other macrofaunal taxa remained approximately constant. Statistical support for this trend was provided by crossed ANOVA with main effects DEPTH, TIME and TAXON (macrofauna classed as polychaete or non-polychaete). A significant three-way interaction (DEPTH × TIME × TAXON, $F = 5.60$, 1 d.f., $P<0.05$) confirmed that polychaetes showed a different temporal pattern to other taxa and that the decline was significantly greater at 940 than at 140 m.

3.3. Macrofaunal distribution in the sediment column

At the 140 m station the macrofauna was overwhelmingly (83–94%) concentrated in the uppermost 3 cm of the sediment column, with very few animals occurring deeper than this (Fig. 3). Downcore distribution was more even at 940 m, with similar proportions of the total fauna found in the 0–1, 1–3 and 3–5 cm depth horizons. At 1200 and 1850 m the uppermost 1 cm of sediment contained the highest proportion of the total fauna, but with significant numbers of animals occurring down to 5 cm. Sample sizes were too low for statistical testing of temporal changes, the only apparent trend being a downward shift in the distribution of animals within the uppermost 3 cm of sediment at the 140 m station following the south-west monsoon (Fig. 3).

3.4. Polychaete community composition and diversity

The number of polychaete families recorded was highest at the upper and lower ends of the depth transect (total 27 families at 140 m, 28 at 1850 m), with lower numbers at the intermediate

Table 3
Total biomass and mean individual biomass for macrofauna (>300 μm).

Station depth (m)	Cruise	Number of corer drops	Total biomass (g WW m^{-2})	Mean individual biomass (mg WW)
140	Intermonsoon	2	6.79±3.46	0.36±0.25
	Late-post-monsoon	4	4.26±1.39	0.38±0.19
940	Intermonsoon	5	66.46±41.51	13.70±7.40
	Late-post-monsoon	4	25.01±19.77	6.84±7.37
1200	Intermonsoon	5	0.36±0.81	0.41±0.91
	Late-post-monsoon	6	5.27±8.13	15.00±16.40
1850	Intermonsoon	5	9.28±14.39	3.67±6.96
	Late-post-monsoon	5	1.57±0.81	0.57±0.17

Data for total biomass are mean values (±SD) with individual corer drops as replicates. Mean individual values are derived from pooled biomass from individual cores. No data are presented for the 300 m station where numbers of animals per sample were too low for biomass measurement.

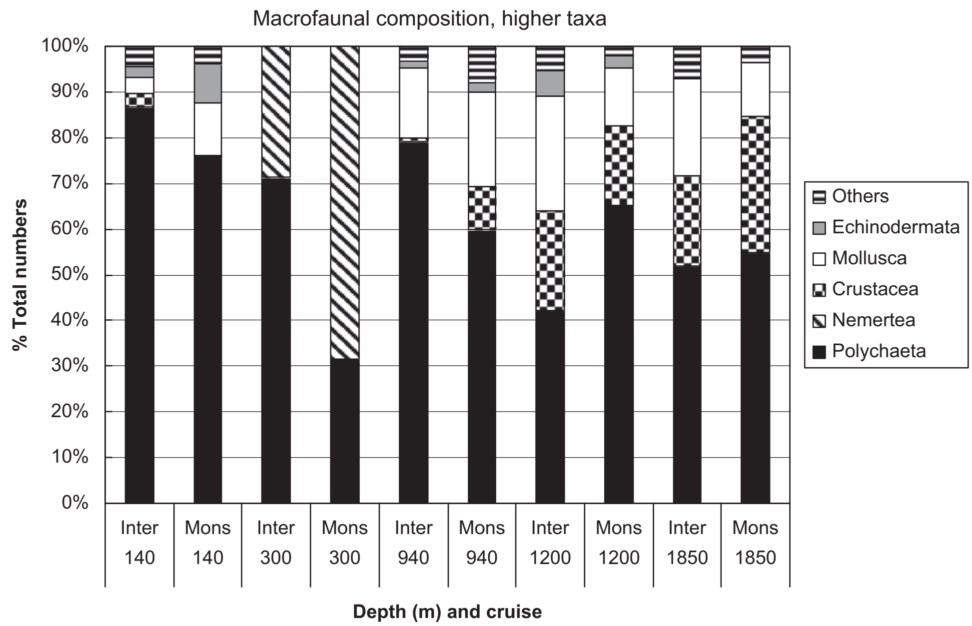

Fig. 2. Higher-taxon composition of Pakistan margin macrofauna from each depth station. Data are shown separately for intermonsoon (Inter) and late-post-monsoon (Mons) sampling intervals.

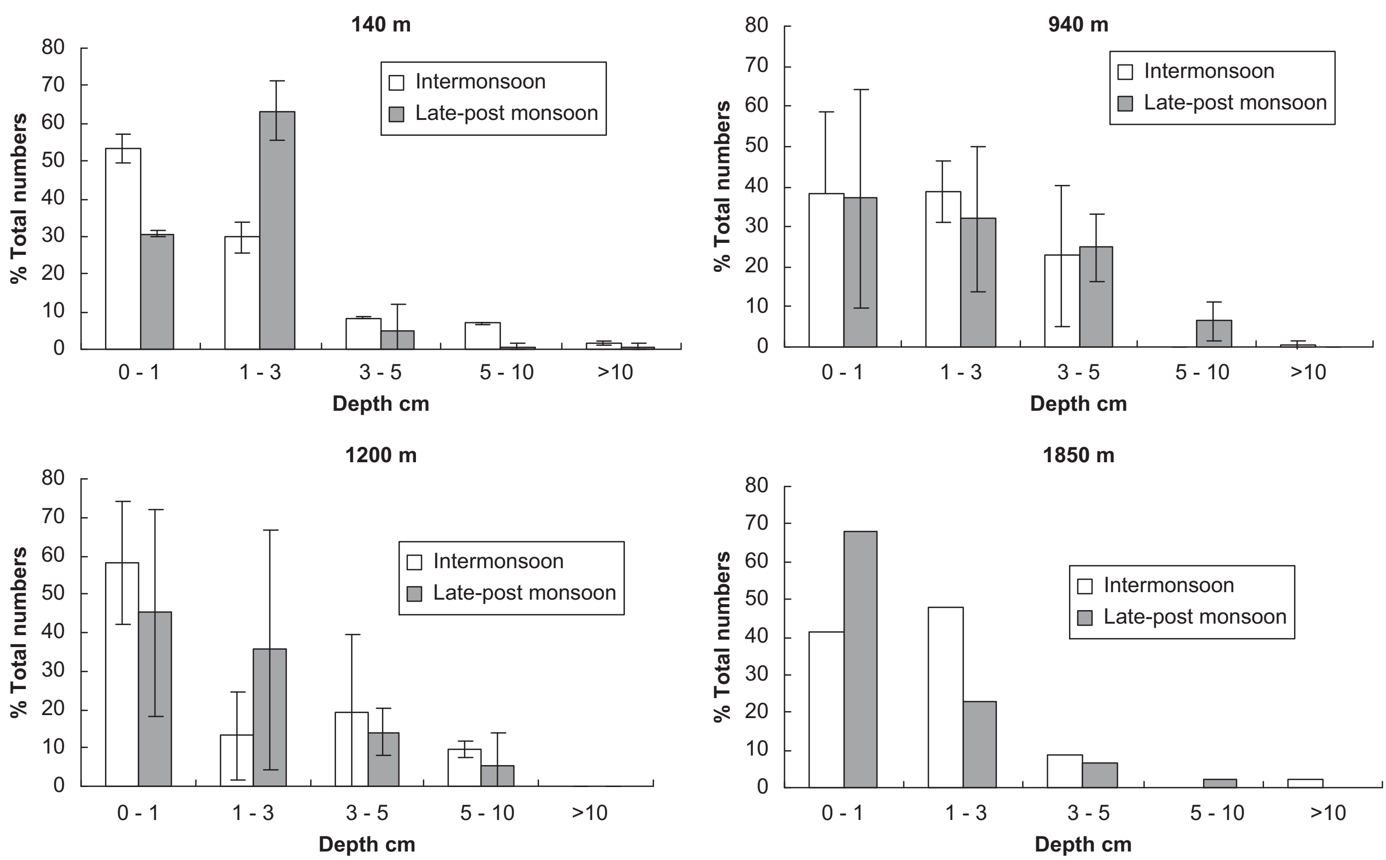

Fig. 3. Vertical distribution of macrofauna in the sediment column at four stations on the Pakistan margin. Columns represent mean (±SD) percentages of the total fauna occurring in each specified depth horizon. The histogram for 1850 m lacks error bars as only one core per sampling interval was sectioned at this station.

depths (Table 4). Only three families (Paraonidae, Pilargidae, Spionidae) were recorded at 300 m. The numerically dominant families varied among stations (Table 4). Cirratulids were abundant at 140, 1200 and 1850 m. Spionids were also important at 140 and 1200 m, but were rare at 1850 m. Paraonids were abundant at 140 and 1850 m. These three families were poorly represented at 940 m, where the assemblage was dominated by Acrocirridae, Ampharetidae, Amphinomidae and Cossuridae.

The total number of families recorded at each sampling interval did not change significantly at any station (Table 4).

Table 4
Family-level composition of the polychaete fauna at four depth stations and two sampling intervals.

Depth Cruise	140 m Intermonsoon	140 m Late-post-monsoon	940 m Intermonsoon	940 m Late-post-monsoon	1200 m Intermonsoon	1200 m Late-post-monsoon	1850 m Intermonsoon	1850 m Late-post-monsoon
Total families represented	21	25	12	12	8	9	21	20
Acrocirridae			16.8 ± 5.5					
Ampharetidae			21.0 ± 8.2	32.1 ± 13.6				
Amphinomidae			29.3 ± 5.7	6.1 ± 13.9				
Capitellidae	9.6 ± 6.7	12.5 ± 11.4			10.2 ± 10.0			
Cirratulidae	29.2 ± 7.3	40.9 ± 10.4			26.2 ± 22.8	27.6 ± 11.8	23.6 ± 9.6	21.4 ± 8.4
Cossuridae			22.5 ± 5.7	34.2 ± 10.4	22.4 ± 17.9			
Flabelligeridae	9.2 ± 4.7							
Hesionidae						5.3 ± 10.0		
Opheliidae								8.3 ± 7.7
Paraonidae	9.9 ± 1.9	12.5 ± 4.4					14.9 ± 12.5	19.3 ± 14.9
Sabellidae							8.6 ± 9.6	
Sigalionidae							10.8 ± 10.8	12.2 ± 10.7
Spionidae	22.9 ± 5.1	6.7 ± 4.2			12.4 ± 11.4	52.6 ± 20.8		6.6 ± 11.7
Terebellidae				6.0 ± 5.6				
Others	19.3 ± 4.1	27.3 ± 3.5	10.5 ± 7.2	21.6 ± 6.5	28.7 ± 19.4	14.6 ± 18.1	42.1 ± 19.1	32.2 ± 16.9

Data for individual families represent mean percentages (± SD) of the total number of polychaetes recorded, using individual corer drops as replicates. Values are given only for individual families constituting >5% of the total polychaete fauna in a given sample.

Table 5
Sample sizes and indices of species diversity and dominance for polychaete assemblages from four depth stations on the Pakistan margin.

Station depth (m)	Cruise	Number of individuals speciated	Number of nominal species	R1D (%)	Family identity of species R1D	Shannon H' ($\log_e$)	Fisher α	Pielou J' ($\log_e$)
140	Intermonsoon	458	54	20.9	Cirratulidae	3.08	15.91	0.77
	Late-post-monsoon	280	44	19.0	Cirratulidae	3.01	14.67	0.80
940	Pooled	227	21	26.2	Amphinomidae	2.15	5.65	0.71
1200	Pooled	40	15	22.5	Spionidae	2.37	8.72	0.88
1850	Pooled	144	69	6.6	Sigalionidae	3.98	52.01	0.94

However, the significant post-monsoon declines in polychaete density at 140 and 940 m were not uniform across all families. Of the five most abundant families at 140 m, Flabelligeridae (mean ± SD 1222 ± 788 ind m^{-2} to 200 ± 162 m^{-2}) and Spionidae (2827 ± 822 m^{-2} to 546 ± 401 m^{-2}) declined, while numbers of Capitellidae, Cirratulidae and Paraonidae showed little change. The differential family response was statistically significant (two-way ANOVA, TIME × FAMILY interaction, $F = 3.25$, 4 d.f., $P < 0.05$). The interaction term was non-significant (TIME × FAMILY, $F = 2.44$, 4 d.f., $P = 0.062$), in ANOVA of data for the five most abundant families at 940 m, indicating a more uniform decline in polychaete numbers.

Numbers of nominal species identified ranged from 15 to 69 per station (Table 5). To compensate for small and uneven sample sizes at 940, 1200 and 1850 m, diversity indices were calculated for pooled data from both cruises. At 140 m, where polychaete families showed differential patterns of temporal change, cruise data were considered separately. Numbers of animals collected at 300 m (only 11 polychaetes in total) were too low for any meaningful analysis of diversity. Values for the Shannon–Wiener index (H') were highest (>3.0) at the shallowest and deepest stations and lower at intermediate depths. Fisher's α, which is less sample-size dependent than H' (Magurran, 1988) showed an accentuation of this pattern, with a much higher value at 1850 m than at any other station. Pielou's index of evenness (J') was relatively poor at discriminating the stations, but showed slightly higher values at 1200 and 1850 m than at the two shallower stations. Percentage contribution of the single most abundant species (R1D), showed a major contrast between the 1850 m station (6.6%) and the three shallower depths (19–26%) (Table 5). Intermonsoon and late-post-monsoon samples from 140 m were very similar for all diversity measures, and data were therefore pooled for analysis of species rank accumulation curves (Fig. 4). These confirmed that evenness was highest at 1850 m and lowest at the 940 and 1200-m stations. The 140-m station was intermediate between these two extremes.

Cluster analysis of Bray–Curtis similarities (Fig. 5) and two-dimensional MDS using untransformed polychaete abundance data (Fig. 6) unambiguously distinguished the four depth stations at a high level of statistical significance. Values of R for pairwise comparisons in ANOSIM ranged from 0.72 to 0.99, with all depth pairs significantly different ($P = 0.01$). Intermonsoon and late-post-monsoon samples did not cluster separately at any depth (Fig. 5) and two-way crossed ANOSIM gave an R-value of only 0.15 for the TIME factor, indicating that the depth contrasts were maintained between successive cruises.

The distinct clustering of samples by station depth reflects the fact that of the 152 nominal polychaete species distinguished, 132 (87% of the total) occurred at only a single depth. Seventeen species were recorded at two depths, and three species at three depths. No species were recorded at all sampling stations, although one (an ampharetid) occurred at 140, 940 and 1850 m, spanning the full extent of the bathymetric transect.

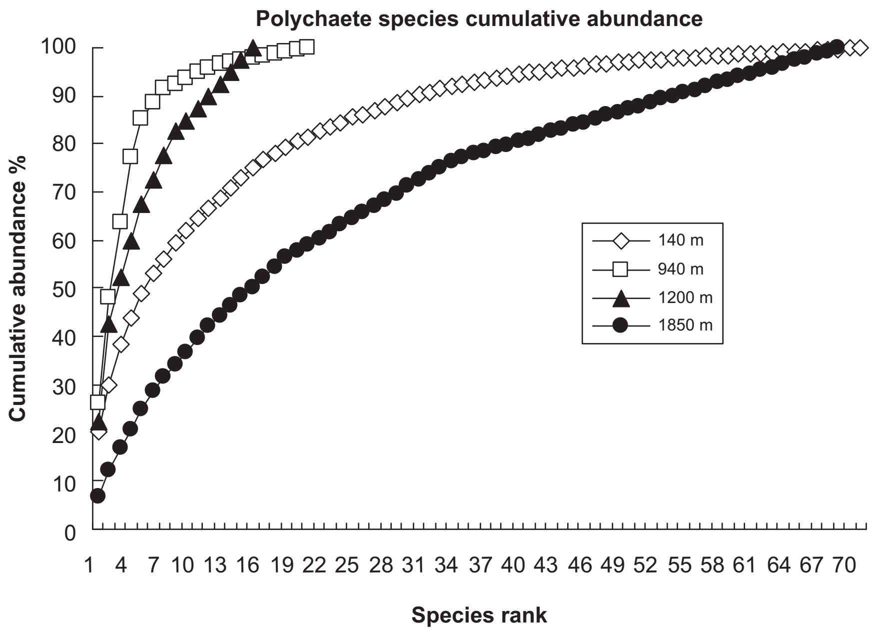

Fig. 4. Species rank-accumulation (*k*-dominance) curves for Polychaeta at four stations on the Pakistan margin, using pooled data from intermonsoon and late-post-monsoon cruises.

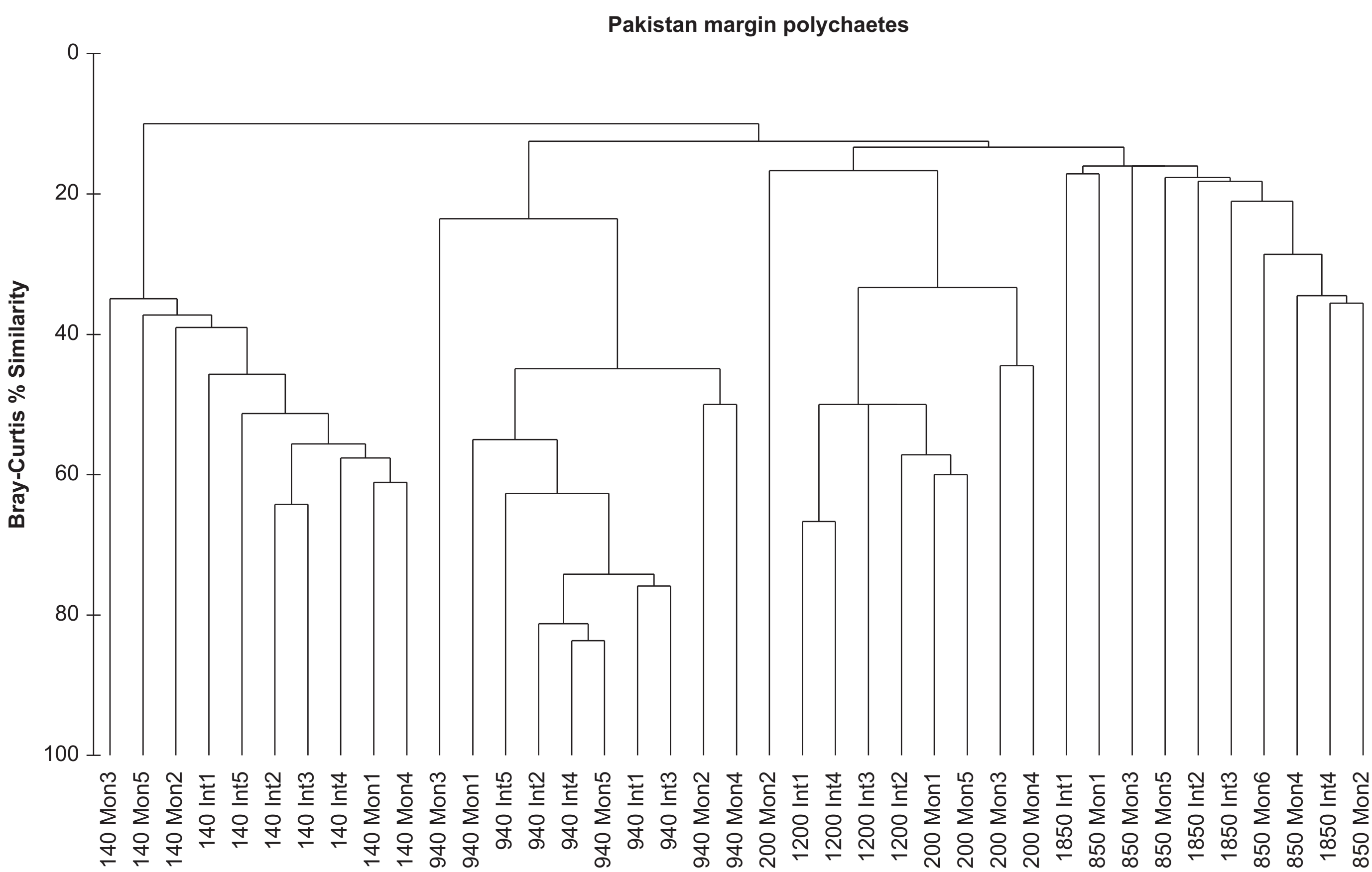

Fig. 5. Cluster analysis, using Bray-Curtis similarity indices, for polychaete assemblages from the Pakistan margin. Each sample in the cluster analysis is an individual megacorer deployment, with frequencies of polychaete species standardized to numbers per core. No data transformation has been applied. Samples are labelled by depth (140, 940, 1200, 1850), cruise (Inter, intermonsoon; Mons, late-post-monsoon) and corer deployment (4–6 per depth and cruise).

3.5. *Polychaete feeding types and modes of life*

Polychaete assemblages at all depths were dominated numerically by deposit- or interface-feeders, with carnivores/omnivores playing a smaller role and suspension-feeders generally rare (Fig. 7). Surface-deposit and interface-feeders were much more abundant than subsurface deposit-feeders at 140 m, and roughly equally abundant at 940 and 1850 m. The only notable temporal change was a greater relative importance of surface-deposit/interface-feeders in the late-post-monsoon sample from 1200 m, driven by an increased abundance of Cirratulidae and Spionidae.

Burrowing polychaetes were slightly less numerous than tube-dwellers at 140 m and slightly more numerous at 940 m (Fig. 8). The two functional groups were approximately equally represented at 1850 m. No station was clearly dominated by one functional group. The post-monsoon increase in abundance of cirratulids and spionids at 1200 m was reflected in a higher representation of tubicolous relative to burrowing polychaetes at that sampling interval. Epifaunal polychaetes were present in insignificant numbers at all stations.

3.6. Sediment structure visible in X-radiographs

X-radiographs from the five stations each exhibited different biogenic and mixing features (Fig. 9, Table 6). The 140-m sections appeared homogeneous to a depth of 12–18 cm, with a dense network of burrows visible to 6–7 cm. Multiple types of burrow and tubes, with a range of dimensions, were evident. Burrow densities ($13–34 \times 10\,cm^{-2}$) were much higher than tube densities ($1–3 \times 10\,cm^{-2}$). Within the OMZ core at 300 m irregular laminations 0.5–1 mm thick were present to at least 12 cm. Laminae were often interrupted or discontinuous. No tubes were present but a surprising number of burrows were evident. In the lower OMZ (940 m) faint laminations were present throughout the slabs (to 22 cm depth in some cases). These were overlain by vertical and horizontal burrows, 1–2 mm wide, and up to 3 cm long. These are probably attributable to the very abundant amphinomid polychaete *Linopherus* sp. Burrow densities were greatest at this station, with counts of $50–100 \times 10\,cm^{-2}$ (Table 6). Vertical burrows formed a dense network extending to 5–6 cm depth in the core. Just below these was a dense 1-cm-thick layer of light-coloured clay (Fig. 9). Few biogenic structures were present below this feature. The clay layer probably represents a relatively local event such as a turbidity flow, slump or flood deposition. Thyasirid bivalve shells were visible in several X-radiographs. At 1200 m, sediments were heavily bioturbated throughout the cores (to 13–22 cm). Sediments appeared mottled with high- and low-density patches. This site exhibited a diversity of biogenic structures including tubes up to 4 mm diameter, voids, and fine burrows (0.2–1.0 mm diameter), present to 15 cm depth. Burrow counts were low ($10–43 \times 10\,cm^{-2}$). Tube counts were maximal at this station ($3–7 \times 10\,cm^{-2}$) during the intermonsoon period. Below the OMZ at 1850 m, sediments appeared fully bioturbated to 12–17 cm, with the heaviest concentration of biogenic structures in the upper 5–6 cm. A network of vertical and horizontal burrows was evident in some cores, with burrow diameters ranging from 0.5 to 4.0 mm. Tubes and burrows were evident in most cores, but the diversity of structures was typically low.

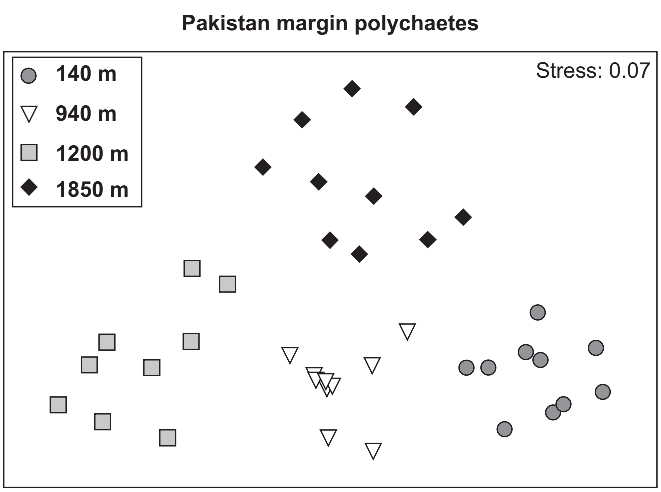

Fig. 6. Two-dimensional MDS plot of polychaete assemblages from the Pakistan margin. Each data point represents an individual megacorer deployment, with frequencies of polychaete species standardized to numbers per core. No data transformation has been applied.

3.7. Relationship of macrofaunal community parameters to environmental variables

Total macrofaunal density and biomass were only weakly correlated with environmental variables (Table 7). A statistically significant positive correlation was found between density and median grain size, although significance thresholds must be treated with caution given the possibility of Type I error when making multiple comparisons (Zar, 1984). Measures of polychaete

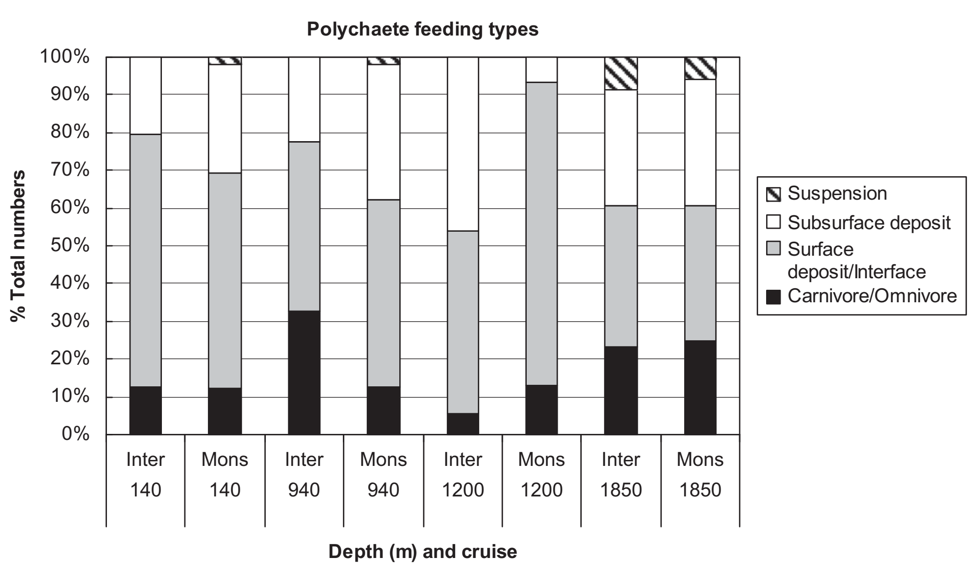

Fig. 7. Feeding-type composition of polychaete assemblages from four depth stations on the Pakistan margin. Data are shown separately for intermonsoon (Inter) and late-post-monsoon (Mons) sampling intervals.

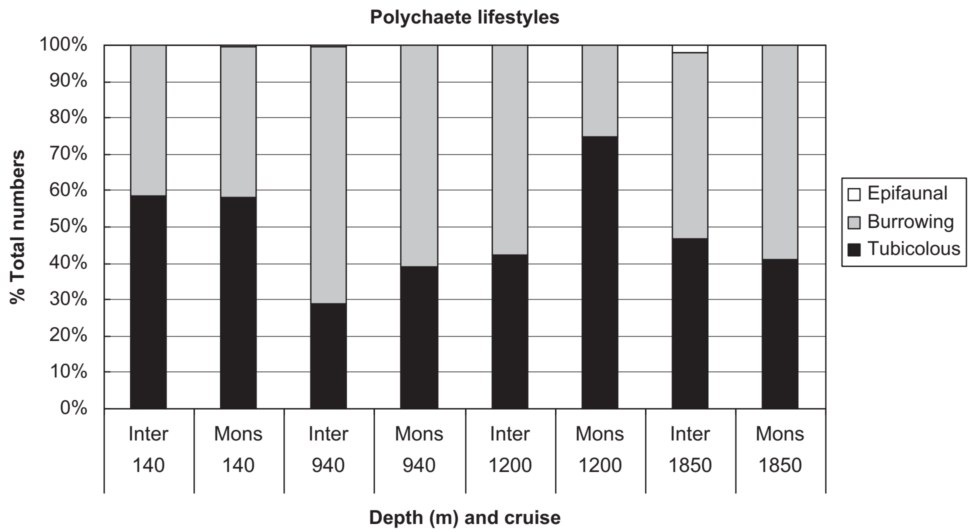

Fig. 8. Mode of life representation of polychaete assemblages from four depth stations on the Pakistan margin. Data are shown separately for intermonsoon (Inter) and late-post-monsoon (Mons) sampling intervals.

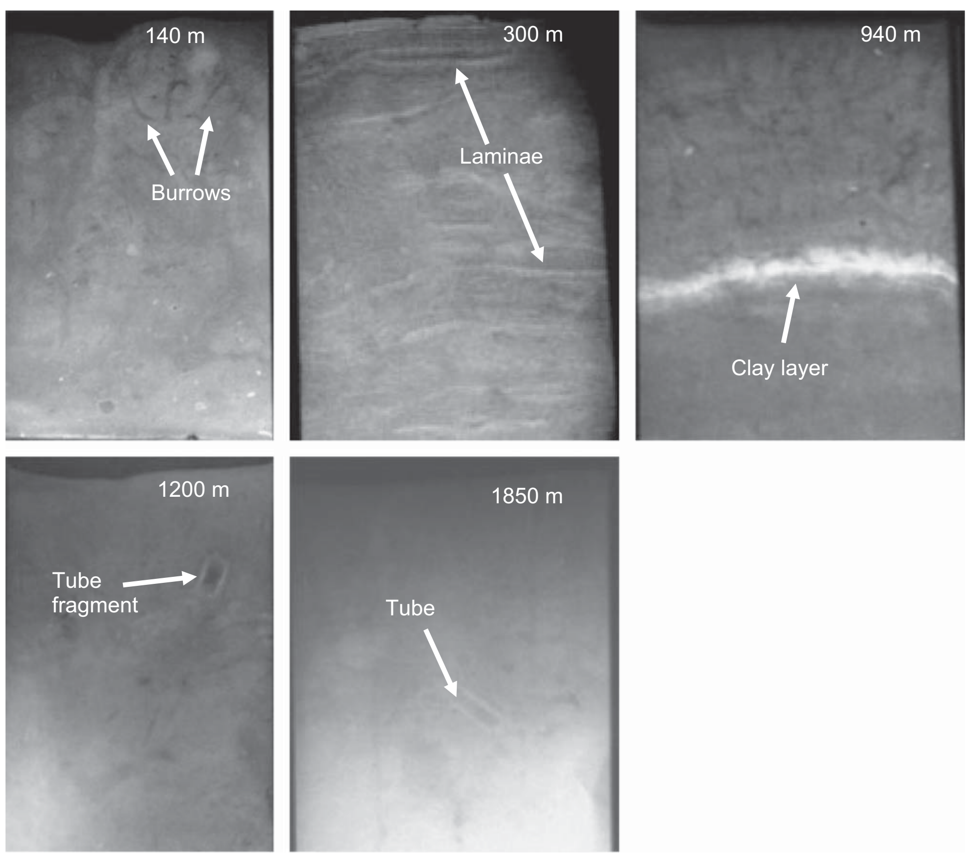

Fig. 9. Sample X-radiographs taken from five depth stations on the Pakistan margin during Spring 2003 (cruise CD 146). Features of interest are indicated. Dimensions of X-ray sections: 140 m (71 × 125 mm), 300 m (71 × 100 mm), 940 m (71 × 90 mm), 1200 m (71 × 100 mm), 1850 m (81 × 100 mm).

diversity and dominance showed the strongest relationships with environmental variables. Fisher's species richness index (α, here used in preference to Shannon–Wiener H' owing to its lower dependence on sample size) was significantly negatively correlated with % TOC and C:N ratio. As would be expected, the index of polychaete community dominance (R1D) showed the opposite pattern. Dominance was negatively correlated with dissolved oxygen, and positively correlated with % TOC and C:N ratio. Pielou's index of evenness showed a significant positive correlation with water depth but not with any other parameter.

Sediment structure indices were poorly correlated with environmental factors, the strongest being a negative relationship between the depth of the bioturbated layer and total phytopigment concentration. Correlations between measures of bioturbation intensity and macrofaunal density, biomass and polychaete diversity were generally weak and non-significant (values ranged

Table 6
Sediment structure observed in X-radiographs of megacore sections from the Pakistan margin.

Station depth (m)	Cruise	Number of corer drops (X-ray sections)	Sediment lamination	Number of biogenic structure types (section [1])	Total biogenic structures (0 cm^{-2})	Number of burrow types (section [1])	Burrows (0 cm^{-2})	Tubes (10 cm^{-2})
140	Intermonsoon	1 (3)	None	4–6	40	3–4	34	2
	Late-post-monsoon	2 (2)	None	5–6	21±6	2–4	15±2	1±1
300	Intermonsoon	2 (5)	Heavy, to 12 cm depth	1–4	37±10	1–3	35±9	0
	Late-post-monsoon	1 (1)	Heavy, to 12 cm depth	1	9	1	9	0
940	Intermonsoon	2 (3)	Faint	2–3	44±6	2–3	68±7	0
	Late-post-monsoon	2 (2)	Faint	2–4	78±34	2–3	76±32	0
1200	Intermonsoon	3 (3)	None	3–6	32±15	2–4	27±17	5±2
	Late-post-monsoon	1 (1)	None	1	1	0	0	1
1850	Intermonsoon	1 (2)	None	3	39±27	2–3	39±27	1±1
	Late-post-monsoon	1 (1)	None	3	10	1	6	4

Table 7
Pearson correlation coefficients and *P* values for comparisons of environmental parameters with indices of macrofaunal community and sediment structure in samples from the Pakistan margin.

	Total macrofaunal density	Total macrofaunal biomass	Polychaetes fisher α	Polychaetes R1D (%)	Polychaetes (Pielou J')	Depth of bioturbated layer	Burrow density	Total biogenic structure density
Depth	0.32 NS	0.07 NS	0.62 NS	−0.49 NS	0.78 $P<0.05$	0.49 NS	−0.02 NS	−0.06 NS
Dissolved oxygen	0.53 NS	−0.22 NS	0.69 NS	−0.69 NS	0.30 NS	0.47 NS	−0.13 NS	−0.03 NS
Median grain size	0.71 $P<0.05$	−0.15 NS	−0.36 NS	0.19 NS	−0.64 NS	−0.19 NS	−0.07 NS	0.02 NS
% TOC	−0.53 NS	0.37 NS	−0.72 $P<0.05$	0.78 $P<0.05$	−0.18 NS	−0.25 NS	0.27 NS	0.16 NS
C:N ratio	−0.30 NS	0.24 NS	−0.80 $P<0.05$	0.91 $P<0.01$	−0.47 NS	−0.49 NS	0.35 NS	0.30 NS
Total phytopigments	−0.53 NS	0.20 NS	−0.67 NS	0.70 NS	−0.39 NS	−0.63 NS	0.11 NS	−0.01 NS

NS = non-significant.

from −0.52 to 0.47) A stronger, significantly positive association (0.72, $P<0.05$) was found between burrow density and macrofaunal biomass.

Bottom-water dissolved oxygen and measures of sediment organic content (% TOC, C:N ratio, surface pigments) were all highly correlated with each other (absolute values for Pearson coefficients were in the range 0.65–0.90). Low oxygen levels were associated with high % TOC, high C:N ratio and high phytopigment concentration. Non-independence of environmental variables and the small data set preclude the use of multiple regression (Zar, 1984), but the broad pattern was for stations with high dissolved oxygen/low TOC to show higher polychaete species richness (Fisher's α) than stations with low dissolved oxygen/high TOC (Fig. 10). Replacing Fisher's α with R1D reversed the direction of the relationship. Samples grouped consistently for both environmental parameters with one exception. Post-monsoon shoaling of the OMZ gave a combination of low dissolved oxygen and low TOC at the 140 m station (Table 1). Polychaete species richness and dominance showed no post-monsoon change and indices retained values characteristic of the high oxygen/low TOC group.

4. Discussion

The data presented here are sufficient to identify the broad trends in macrofaunal standing stock and community structure across the Pakistan margin. However, the small sample sizes available, particularly from the 300 and 1200-m stations, mean that detailed interpretations must be regarded as provisional and subject to revision by additional study. Also, the coarse depth resolution of our stations does not allow resolution of fine-scale biotic gradients across the critical lower boundary of the OMZ, for which Levin et al. (2009) should be consulted.

4.1. Macrofaunal standing stock

Table 8 compares macrofaunal numbers and biomass across the Pakistan margin with published data from the Oman margin (Levin et al., 2000) and from Volcano 7 in the eastern Pacific, where the OMZ has a similar depth distribution to the Arabian Sea OMZ (Levin et al., 1991). Additional comparative data are

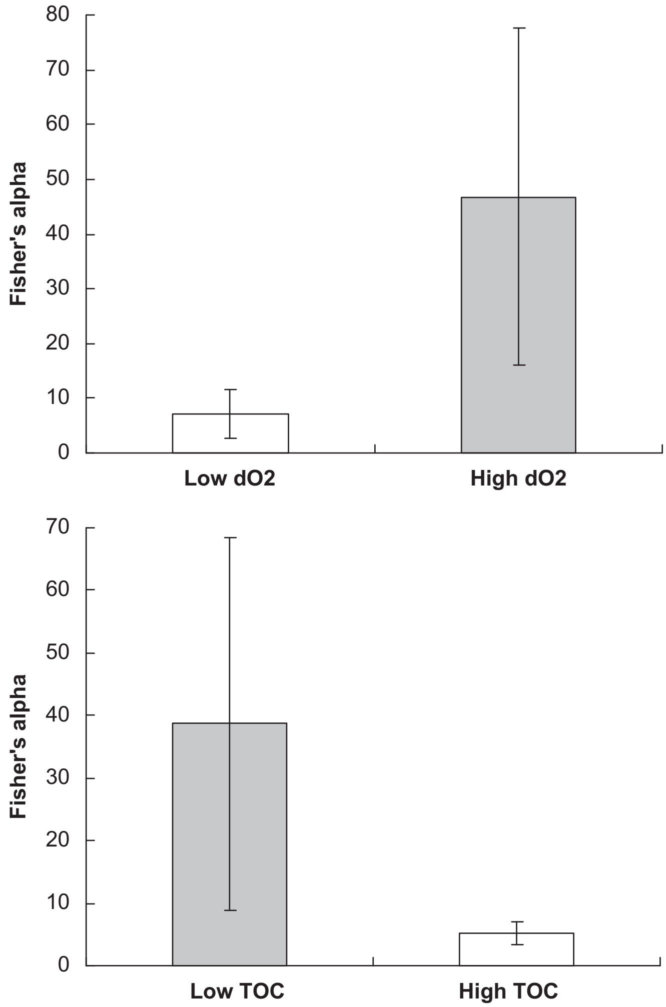

Fig. 10. Histograms showing mean values (±SD) for Fisher's α for polychaete samples from the Pakistan margin stations in relation to environmental parameters at the time of sampling. Samples are categorized by bottom-water dissolved oxygen (Low, $<0.5\,ml\,l^{-1}$ or 22.3 µM, $n=5$ samples; High, $>1.5\,ml\,l^{-1}$ or 66.9 µM, $n=3$ samples) and sediment total organic content (Low, <1.5%, $n=4$ samples; High, >3.5%, $n=4$ samples).

presented by Levin (2003, Table 1). Macrofaunal density in the Pakistan OMZ core (300 m) is extremely low when compared with the stations off Oman at 400 m and on the summit of Volcano 7 (~750 m), all with similar dissolved oxygen concentrations. Such low densities have previously been reported only from the OMZs off northern Chile (Gallardo et al., unpublished data cited in Levin, 2003) and central Peru (Gutiérrez, pers. comm. cited in Levin, 2003), both associated with dissolved oxygen concentrations approximately double those recorded from 300 m off Pakistan. Recorded densities in the lower OMZ (900–1000 m) are similar off Pakistan and Oman although the boxcorer used in the latter area may have undersampled the fauna to some extent (Bett et al., 1994; Hughes and Gage, 2004). Biomass estimates can be heavily influenced by sporadic occurrence of large-bodied individual animals (Gage et al., 2002), a confounding factor likely to operate in the small samples discussed here, and possibly as a result there apears to be no consistent trend towards higher biomass on the Oman margin. Hypothesis 1a, predicting a consistently higher standing stock on the Oman than the Pakistan margin, is therefore not supported for macrofaunal biomass and only weakly supported with respect to abundance.

Hypothesis 1b, predicting lowest standing stock in the OMZ core and elevated densities at the OMZ boundaries, is supported by the extreme scarcity of macrofauna at the 300-m station, but not by the boundary data. Density, but not biomass, was highest at the upper OMZ boundary at 140 m, but neither parameter showed any elevation near the lower boundary (1200 m). Instead, maximal biomass was observed at 850–940 m (Levin et al., 2009). Our data support the conclusion (Levin et al., 2009) that there are threshold effects governing the standing stock of macrofauna within OMZs. The boundary effect reviewed by Levin (2003) may be associated with phase shifts occurring not at the nominal OMZ boundary of $0.5\,ml\,l^{-1}$ (22.3 µM), but closer to the oxygen thresholds critical for macro- and megafauna (0.1–0.2 ml l^{-1} or 4.5–8.9 µM).

Oxygen concentration alone does not appear to explain the extremely low macrofaunal standing stock at 300 m off Pakistan, where oxygenation was only slightly lower than at the much more densely populated 940-m station. Similarly, population densities were very different at the Pakistan 300-m and Oman 400-m stations despite only a small difference in oxygenation (Table 8). Oman sediments had a much higher phytopigment content, with

Table 8
Comparison of macrofaunal standing stock, represented as mean numerical density (ind m^{-2}) and biomass (g WW m^{-2}, in parentheses) through the OMZs of the Pakistan and Oman margins, and from Volcano 7, an eastern Pacific locality with an OMZ of similar vertical extent to the Arabian Sea (Levin et al., 1991).

Depth (m)	Dissolved O_2 ($ml\,l^{-1}$)	Pakistan margin (this study)	Oman margin (Levin et al., 2000)	Volcano 7 (Levin et al., 1991)
140	2.12	14894 (6.8)		
	0.11	10464 (4.3)		
300	0.11	323 (<0.1)		
400	0.13		12362 (14.2)	
700	0.16		16283 (59.7)	
745–767	0.09			1854
788–857	0.13			8457
850	0.20		19193 (18.2)	
940	0.13	5222 (66.5)		
	0.17	3380 (25.0)		
1000	0.27		5818 (43.5)	
1200	0.35	1003 (3.0)		
1250	6.70		2485 (3.6)	
1316–1790	0.81			2165
1850	1.72	8513 (5.4)		

Samples are listed in order of increasing water depth, with corresponding dissolved oxygen levels also shown. Dissolved oxygen values refer only to the sites for which standing stock data are listed in the same row, not to all localities. For the Pakistan margin, mean values for intermonsoon and late-post-monsoon samples are given where no significant difference was found between cruises. Both values are given where temporal change in density was statistically significant. All data refer to macrofauna retained on a 300 µm sieve mesh. Biomass data were not available for samples from Volcano 7.

770 μg g^{-1} (0–0.5 cm) at 400 m (Levin et al., 2000), compared with only 33–40 μg g^{-1} (0–1.5 cm) at 300 m off Pakistan (Woulds and Cowie, 2009). Phytopigments in Pakistan margin sediments are also relatively degraded, with fresh material (chlorophyll-*a*) making up only a small percentage of the total (Woulds and Cowie, 2009; Shankle et al., 2002). However, the lack of evidence for consistently lower biomass across the Pakistan margin argues against food availability as a general explanation for the contrasts in standing stock in the OMZ core stations. Periodic disturbance by sediment slides and turbidity flows could potentially affect macrofaunal communities in continental margin environments (Levin et al., 2001). The probable turbidite in X-radiographs from 940 m shows that downslope events do occur on the Pakistan margin, but no comparable features were visible in sections from 300 m. On present evidence the unusually low macrofaunal standing stock in the Pakistan margin OMZ core is not readily explicable by station environmental data or by comparison with the Oman margin, and further study is clearly required to determine its causes.

4.2. Community structure and species diversity

On the Oman margin, polychaetes accounted for 90–96% of macrofaunal numbers across the OMZ, falling to 71% at the lower OMZ boundary (1260 m) (Levin et al., 2000). Their contribution was more variable off Pakistan (32–87%), with highest representation at the seasonally hypoxic 140 m station (76–87%). As expected, the sparse macrofauna at the most oxygen-deficient Pakistan station (300 m) was entirely soft-bodied, including a high proportion of nemerteans, a group also well-represented in the Oman OMZ (Levin et al., 2000). There was no counterpart to the community composed largely of gutless, symbiont-bearing oligochaetes found in conditions of extreme hypoxia at 305 m depth off Peru (Levin et al., 2002), or to the aplacophoran-dominated system on the summit of Volcano 7, eastern Pacific (Levin et al., 1991). Hypothesis 2a, predicting dominance of the Pakistan margin OMZ by soft-bodied macrofauna is supported by taxonomic composition at the core 300-m station (with appropriate caution, given the low sample sizes obtained here) but is a less accurate descriptor of patterns at other depths, where annelid dominance was lower than reported from the Oman and Peru margins.

Levin (2003) noted that OMZs worldwide differ in the relative importance of major polychaete families, with patterns reflecting hydrodynamic, bathymetric or geochemical factors rather than dissolved oxygen levels alone. Spionidae is one of the most consistently well-represented families, and along with Cirratulidae dominated the upper OMZ (400–700 m) off Oman (Levin et al., 2000). Both families were also important at the shallowest Pakistan station (140 m), near the lower OMZ boundary (1200 m) and below the OMZ at 1850 m, but not at 940 m, where a distinctive assemblage dominated by Acrocirridae, Ampharetidae, Amphinomidae and Cossuridae was found. The first three of these families were important nowhere else, and the Cossuridae only in the 1200 m intermonsoon sample. There is no obvious correlate for this pattern in the environmental data from 940 m (Table 1), and knowledge of the natural history of deep-sea polychaetes is inadequate to suggest a cause. Cossurids are important components of OMZ polychaete faunas off central Chile (Gallardo et al., 2004; Palma et al., 2005). The importance of capitellids at 140 and 1200 m off Pakistan contrasts with Oman (Levin et al., 2000) but is also paralleled on the Chile margin (Gallardo et al., 2004).

Species diversity comparisons between the Pakistan and Oman margins must be made with caution since the Pakistan data refer to polychaetes alone and not to the total macrofauna (Levin et al., 2000). Low sample sizes at the Pakistan stations, particularly at 1200 m, also may lead to overestimates of community dominance (Gray, 2001). With these provisos, at comparable depths, Shannon–Wiener diversity (at common logarithmic base 2) was higher on the Oman margin (for example, 4.1 at 1000 m off Oman compared with ~2.0 at 940 m off Pakistan). Shannon–Wiener diversity was relatively high in the zone of seasonal hypoxia at 140 m depth, although dominance was closer to that seen at 940 and 1200 m than to the very low 1850-m value. The small sample sizes from the OMZ core precluded analysis of community diversity, and Hypothesis 2b can therefore be considered only partially supported by the available data. Richness was lower within the Pakistan margin OMZ than above or below it, but reduced dominance (R1D) was seen only below the OMZ at 1850 m.

The almost complete species-level separation of polychaete faunas seen in the Pakistan data set was also observed for macrofauna from Oman (Levin et al., 2000) and Chile (Gallardo et al., 2004) with similar levels of divergence present in the cluster analysis of Bray-Curtis similarities. These patterns suggest the occurrence of distinct polychaete assemblages at each depth off Pakistan but must be interpreted with caution. Small sample sizes at some stations create the potential for sampling artefacts, especially with regard to rare species. In Oman, greater within-station heterogeneity was noted in samples from below the OMZ, indicated by a wider scatter of points in the two-dimensional MDS plot. This was not seen in the Pakistan data, where levels of scatter were approximately equal for all four depths investigated. Intercomparison of nominal polychaete species distinguished off Oman and Pakistan was beyond the scope of our study but should be pursued to quantify the degree of overlap in community composition and determine whether bathymetric ranges differ in the two areas.

4.3. Temporal change

Levin and Gage (1998) noted that separating the effects of oxygen availability and organic matter enrichment on faunal diversity measures is difficult owing to the strong inverse relationship often found between them in OMZ settings. On the Oman margin the lack of correlation between TOC and dissolved oxygen allowed estimation of the contribution of each to the variance in community diversity indices (Levin et al., 2000). This was not possible for the Pakistan stations, where bottom-water dissolved oxygen showed a strong inverse correlation with measures of sediment organic content. The 140-m station, where oxygenation declined sharply during the south-west monsoon but sediment organic content showed little change, provides a partial exception. The significant taxon-specific reduction in macrofaunal density in the late-post-monsoon sample suggests loss of sensitive fauna as reported in many coastal systems subject to seasonal or anthropogenic hypoxia (Diaz and Rosenberg, 1995). Without more intensive sampling at shelf depths it is premature to regard the affected polychaete taxa as shallow-water taxa, eliminated by the monsoon-driven shoaling of the OMZ, but their observed depth distribution is consistent with this interpretation. Flabelligerids were not recorded at 300, 940 or 1200 m, and were present only in very low numbers at 1850 m. The decline in Spionidae was driven by the loss or near-loss of four nominal species, none of which were recorded from any deeper station. Hypothesis 3a, predicting a post-monsoon reduction in macrofaunal density at 140 m, is therefore supported, but the taxa affected were unexpectedly soft-bodied rather than calcified forms.

Hypothesis 3b, predicting no temporal change in the permanent OMZ is contradicted by the statistically significant decline in macrofaunal density at 940 m. This apparent temporal change is confounded with spatial variation, as the nominal intermonsoon station was approximately 4.7 km distant from the central position occupied during the later cruise. Sediment properties at the two sites (Table 1) gave no indication of environmental differences that could affect macrofaunal abundance, and the apparent change might simply be a stochastic result of the limited number of samples obtained.

4.4. Sediment structure and bioturbation

Comparisons of sediment mixing depths and extent of bioturbation from X-radiographs must be made with caution, as under steady-state conditions relic tubes and burrows remain visible far into the historical layer. The visual assessments presented here should therefore be considered alongside quantitative estimates of mixing depth from radionuclide profiles by Shimmield et al. (unpublished data). The most conspicuous visible contrast in sediment structure across the bathymetric transect was between the strong lamination in the OMZ core (300 m) and the homogeneous, heavily bioturbated sediment column at 140, 1200 and 1850 m. Sediment in the lower OMZ transition zone (940 m) was intermediate in structure, showing faint laminations overlain by dense burrow networks. Overall, stations between 700 and 1200 m show a clear transition in burrow size, depth and density, with concomitant reductions in the degree of lamination (Levin et al., 2009). Although there was more apparent biogenic structure at 300 and 940 m than described in previous studies (Cowie et al., 1999; Staubwasser and Sirocko, 2001), the expected presence of laminated sediments in the most oxygen-deficient OMZ region was confirmed. The strong lamination at 300 m is consistent with the extremely low macrofaunal standing stock at this depth, but the putative relationship is less clear when other stations are considered. The faint laminations at 940 m co-occurred with the highest macrofaunal biomass, whereas the homogeneous, bioturbated sediment columns at 140, 1200 and 1850 m were associated with much lower biomass values. Broad functional group composition of the polychaete assemblages at each depth provided no obvious explanation for these patterns. Hypotheses 4a and 4b concerning macrofaunal community composition and sediment structure are therefore not supported by the Pakistan data set. In contradiction to Hypothesis 4a, the most distinctive sediment structure (at 300 m) was associated with minimal biomass rather than with biomass-independent divergence in functional group composition.

4.5. Conclusions

This study demonstrates several novel characters of the macrofaunal communities of the Pakistan margin, notably the numerical response to seasonal hypoxia on the shelf, the extremely low abundance in the OMZ core and the distinctive polychaete family assemblage recorded at 940 m. In general, results from the neighbouring Oman margin were weak predictors of the patterns detected, suggesting that local factors superimposed on the broad trends identified by Levin (2003) are important in the control of OMZ macrofaunal communities. The most striking contrast between the Pakistan and Oman macrofaunas—standing stock in the OMZ core—should be addressed in future studies to identify the environmental factors driving this distinctive feature of the Pakistan margin.

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