



Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Benthic biological and biogeochemical patterns and processes across an oxygen minimum zone (Pakistan margin, NE Arabian Sea)

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ARTICLE INFO

Keywords:

Sediment
Carbon
Continental margin
Oxygen minimum
Benthos
Fauna

ABSTRACT

Oxygen minimum zones (OMZs) impinging on continental margins present sharp gradients ideal for testing environmental factors thought to influence C cycling and other benthic processes, and for identifying the roles that biota play in these processes. Here we introduce the objectives and initial results of a multinational research program designed to address the influences of water depth, the OMZ (~150–1300 m), and organic matter (OM) availability on benthic communities and processes across the Pakistan Margin of the Arabian Sea. Hydrologic, sediment, and faunal characterizations were combined with *in-situ* and shipboard experiments to quantify and compare biogeochemical processes and fluxes, OM burial efficiency, and the contributions of benthic communities, across the OMZ. In this introductory paper, we briefly review previous related work in the Arabian Sea, building the rationale for integrative biogeochemical and ecological process studies. This is followed by a summary of individual volume contributions and a brief synthesis of results.

Five primary stations were studied, at 140, 300, 940, 1200 and 1850 m water depth, with sampling in March–May (intermonsoon) and August–October (late-to-postmonsoon) 2003. Taken together, the contributed papers demonstrate distinct cross-margin gradients, not only in oxygenation and sediment OM content, but in benthic community structure and function, including microbial processes, the extent of bioturbation, and faunal roles in C cycling. Hydrographic studies demonstrated changes in the intensity and extent of the OMZ during the SW monsoon, with a shoaling of the upper OMZ boundary that engulfed the previously oxygenated 140-m site. Oxygen profiling and microbial process rate determinations demonstrated dramatic differences in oxygen penetration and consumption across the margin, and in the relative importance of anaerobic processes, but surprisingly little seasonal change. A broad maximum in sediment OM content occurred on the upper slope, roughly coincident with the OMZ; but the otherwise poor correlation with bottom-water oxygen concentrations indicated that other factors are important in determining sediment OM distributions. Downcore profiles generally showed little clear evidence of *in-situ* OM alteration, and there was little sign of OM enrichment resulting from the southwest monsoon in sediments collected in the late-to-postmonsoon sampling. This is interpreted to be due to rapid cycling of labile OM. Organic geochemical studies confirmed that sediment OM is overwhelmingly of marine origin across the margin, but also that it is heavily altered, with only small changes in degradation state across the OMZ. More negative stable C isotopic compositions in surficial sediments at hypoxic sites within the OMZ core are attributed to a chemosynthetic bacterial imprint. Dramatic changes in benthic community structure occurred across the lower OMZ transition, apparently related to OM availability and quality as well as to DO concentrations. High-resolution sampling, biomarkers and isotope tracer studies revealed that oxygen availability appears to exert threshold-type controls on benthic community structure and early faunal C processing. Biomarker studies also provided evidence of faunal influence on sediment OM composition. Together, the results offer strong evidence that benthic fauna at sites across the margin play important roles in the early cycling of sediment OM through differential feeding and bioturbation activities.

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1. Introduction and scientific context

Processes occurring across the water–sediment interface and within surficial sediments of the world's continental margins are of major biogeochemical importance. They form a primary control

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on the make-up of sedimentary records, and burial in margin sediments represents the largest long-term sink for C on the planet (Bernier, 1982; Walsh, 1991). Processes such as sedimentary denitrification and anammox, as well as authigenic phosphorite formation, also are important and variable terms in the global N and P cycles (Follmi, 1996; Hulth et al., 2005; Ingall et al., 2005; Codispoti, 2007). Benthic solute fluxes, into or out of the sediments, including nutrients, gases, organic matter (OM) and metals, may significantly influence total ocean inventories and, through benthic–pelagic coupling, may represent positive or negative feedback controls on ocean productivity and, ultimately, climate (Burdige et al., 1992; Ganeshram et al., 1995; Holcombe et al., 2001; Berelson et al., 2003).

An enormous variety of organisms live on or within the sediments, ranging from bacteria to large, mobile megafauna, and these organisms are also diverse in lifestyle and feeding modes. Through feeding and digestion, as well as burrowing activity and associated mixing, irrigation and ventilation of the sediments, the benthos directly and indirectly influence not just OM cycling and burial, but the texture and composition of the sediments, as well as the redox conditions, associated microbial activity, and benthic solute fluxes (McCall and Tevesz, 1982; Aller, 1994; Aller and Aller, 1998). Consequently, understanding the identity of these organisms and their feeding, digestion, bioturbation and bioirrigation activities is central to a wider, mechanistic understanding of benthic biogeochemical processes.

As a result of the remote location of the deep-sea floor, benthic communities and processes, as well as the roles that organisms play in these processes, remain poorly characterized and quantified relative to counterparts in the surface ocean. Most process information has been inferred from sediment cores and studies of sediment and porewater geochemistry. Our knowledge of deep-sea benthic organisms is even more limited. For example, while it has been established that both O₂ availability and food supply are key determinants of benthic community composition in coastal environments (e.g., Pearson and Rosenberg, 1978), it is uncertain how these and other factors, including depth, interact to influence distributions and diversity of benthic fauna in the deep sea (Levin and Gage, 1998). Information on how organisms behave, in terms of feeding and bioturbation, and the consequences for OM cycling and other sedimentary processes, is even more limited (Gage, 2003). Traditionally, benthic ecologists and geochemists have worked independently, leading to a paucity of studies that integrate species-level biological information with detailed analyses of chemical pathways and transformations. Over the last two decades, there have been major advances in the development of remotely-deployed vehicles and research platforms, as well as instruments, experimental equipment and tracers. These have led to important progress in the detailed characterization of sediments and porewaters (e.g., microelectrode and optode profiling) as well as *in-situ* experimentation with seafloor biogeochemical processes.

This volume presents first results from a multidisciplinary project involving linked benthic biological and geochemical investigations, including experimental process studies at sites across the Pakistan Margin of the Arabian Sea. The project, funded by the UK Natural Environment Research Council, the Leverhulme Trust, the US National Science Foundation International Program, and the Netherlands Organization for Scientific Research, involved geochemists and biologists from four UK institutions and collaborators from the USA, the Netherlands, India and Pakistan. The Arabian Sea was selected for study for numerous reasons. Reversing monsoons generate upwelling and unusually high and strongly seasonal primary productivity (Quasim, 1982; Sen Gupta and Naqvi, 1984). Resulting export of organic debris to depth (Nair et al., 1989), combined with limited deep-water ventilation,

generates a layer of intensely O₂-depleted water (Wyrтки, 1973). At the depths where this “oxygen minimum zone” (OMZ; ca. 150–1300 m) impinges on the margins, an exceptionally large belt of hypoxic sediments is created (Helly and Levin, 2004). Organic-rich, reducing sediments typical of upwelling regions are of particular importance in terms of OM cycling and burial as well as benthic solute fluxes (Bernier 1982; Walsh, 1991; Hedges and Keil, 1995), giving the margins of the Arabian Sea disproportionate biogeochemical significance. Benthic conditions range from fully oxygenated well above and below the OMZ to strongly reducing at its core, and sites thus show broad spectra of redox conditions and benthic communities (Gage et al., 2000 and papers therein). Detailed cross-margin studies therefore permit assessment of depth and O₂ availability as controls on sediment geochemistry, benthic biology, benthic biogeochemical processes, and their interactions, in a region where these processes and interactions are particularly significant. Similarly, studies under monsoon and intermonsoon conditions permit assessment of the effects of seasonal differences in OM deposition (i.e. food supply) on benthic processes and community function.

2. Arabian Sea margin biology and biogeochemistry, and objectives of the project

A full synthesis of biological and geochemical studies in the Arabian Sea through the start of the 21st Century is given by Cowie (2005). The mid-water OMZ in the Arabian Sea was noted early in the 20th century; soon after, spatial correspondence was observed between the OMZ and a belt of sediments on the continental slope that were rich in OM but poor in, or even devoid of, larger fauna (Sewell, 1934a,b). These findings provided some of the earliest evidence for the assertion that O₂ depletion is the main determinant of organic C burial in marine sediments (e.g. Demaison and Moore, 1980; and references therein). However, this is now much debated, and other factors, including OM supply, organic–mineral interactions (e.g. Hedges and Keil, 1995) and, potentially, benthic faunal activity (or its absence), also may contribute.

Early research on the Arabian Sea benthos, conducted by Russian scientists following WWII, documented a strong negative impact of the OMZ on faunal biomass (Neymann et al., 1973). This built on the landmark work of Howard Sanders (1969), who first quantified the powerful influence of the west African OMZ and associated high food inputs in reducing faunal diversity. But detailed studies of Arabian Sea benthic community structure and composition were not conducted until the latter part of the 20th century, when the region became a focus for global biogeochemical studies. Several major expeditions were conducted under the umbrella of international JGOFS programs. Most of these focused on water-column or abyssal organisms and processes (Herring et al., 1998; Pfannkuche and Lochte, 2000; Smith, 2001), but the Netherlands Indian Ocean Program 1992–1993 (van Weering et al., 1997) and the UK Arabesque cruises (Gage et al., 2000) provided outstanding descriptions of benthos. Focused studies addressed foraminifera (Goody et al., 2000a), gromiids (Goody et al., 2000b; Aranda da Silva et al., 2006), metazoan meiofauna (Cook et al., 2000), macrofauna (Levin et al., 2000; Lamont and Gage, 2000), and selected megafauna (Young and Vazquez, 1997; Creasey et al., 1997) within and beneath the Oman Margin OMZ. Consequences of animal activity such as bioturbation (Smith et al., 2000; Meadows et al., 2000), modification of OM (Smallwood et al., 1999), and mass mortality (Billett et al., 2006) were examined. These initial benthic investigations revealed dramatic environmental gradients and strong biological and geochemical patterns on the Oman Margin, but little OMZ influence off Yemen,

Somalia and Kenya, where O₂ depletion is less intense (Duineveld et al., 1997).

The above projects and others, including studies on the Pakistan and Indian margins (e.g., von Rad et al., 1995; Calvert et al., 1995), also included various assessments of the organic and inorganic geochemistry of surficial sediments and porewaters. As summarized by Cowie (2005), these generally showed a basin-wide influence of monsoon-driven productivity and the OMZ on the organic content, redox state and wider geochemistry of Arabian Sea sediments relative to typical abyssal and margin settings in other ocean regions. Many studies addressed the mid-slope maxima observed in sedimentary OM content and the ongoing debate over the environmental factors responsible for these. With the exception of German studies primarily focused on the abyssal plain (Pfannkuche and Lochte, 2000), and Dutch studies on the Kenya–Yemen margins (Van Weering et al., 1997), very few studies of benthic geochemistry included characterisation or quantification of biogeochemical process rates, especially across the continental slope and OMZ.

Two key themes emerged from these early biological studies. One involves the potential for OMZ regulation of faunal community structure, especially diversity, via gradients in DO and food supply. The other concerns the differential abundance responses to O₂ depletion of different biotic groups. Smaller organisms were clearly more tolerant to hypoxia than larger ones. Most of the previous studies represented snapshots in time and did not explore the mechanisms, process rates or dynamics underlying the biological patterns on the margin. The dynamic nature of O₂ and food supply as influences on the Arabian Sea benthos, and the consequences of different faunal responses, had yet to be revealed, and provide one focus of the Pakistan Margin research presented here. The initial Oman Margin studies, however, provided a fundamental basis of comparison for the Pakistan Margin system, and in this context, go far in revealing the heterogeneity of OMZ biological systems.

What had not been done previously, and has been attempted here for the Pakistan Margin, is a thorough, focused integration of geochemical and biological information from the same sediments. The study was designed to assess the environmental controls on OM cycling and burial as part of a broader study of benthic biogeochemistry across an OMZ. The specific region chosen for study, off the Indus River, was selected to allow comparison with results from the Oman/Somali margins, and because a previous German cruise to the same location (F.S. Sonne 1993) had demonstrated more intense O₂ depletion and extreme sediment characteristics and benthic communities across the OMZ (von Rad et al., 1995).

Overarching hypotheses tested on the Pakistan Margin were that:

- Environmental parameters—most notably water depth, O₂ availability and supply of reactive OM—determine the community structure, activity and distribution of benthos across the Pakistan Margin.
- The benthos, in turn, exert distinct and major controls on sediment OM distributions, cycling and burial, on microbial processes and redox conditions, and on the fate of nutrients and redox-sensitive metals.

The broader objectives of the project were:

- a. To investigate an interrelated suite of geochemical and faunal characteristics in contrasting settings across the Indus Margin OMZ, specifically:
 - Faunal community structure (meiofauna to megafauna) and trophic relationships.

- Faunal depth distributions within the sediments and adaptations to hypoxia.
- Sediment and porewater geochemistry (organic and inorganic).
- b. To conduct *in-situ* and on-deck process studies to determine:
 - Sediment accumulation, mixing and irrigation rates.
 - Fluxes of O₂ and dissolved OM, nutrients and metals across the sediment–water interface.
 - Rates and relative importance of aerobic, suboxic and anaerobic microbial processes.
 - Rates of OM accumulation, cycling and burial.
 - Short-term OM cycling and sediment mixing and irrigation by benthic communities.
- c. To combine the above in order to quantify and compare biogeochemical processes and fluxes, OM burial efficiency, and the roles of benthic communities across the OMZ, and to produce refined biological terms for geochemical process models.

This volume is a collection of papers that represent the first suite of biological, geochemical and experimental results; they address a significant subset of the objectives outlined above.

3. Cruise, site and sampling summaries

The field program took place on the Pakistan Margin, primarily in the area immediately north of the Indus River Canyon (Fig. 1) over two pairs of cruises aboard the R.R.S. *Charles Darwin* (CD) in 2003. The first pair of cruises took place in the spring intermonsoon season—CD 145 (12 March–9 April) and CD 146 (12 April–29 May); the second pair took place during the late- and immediate post-southwest-monsoon season (CD 150; 22 August–15 September; and CD 151; 17 September–20 October). Investigations were designed to provide comprehensive assessment of benthic communities, sediment biogeochemistry and benthic system function at sites with contrasting redox conditions across the mid-slope OMZ in monsoon vs. intermonsoon conditions of contrasting productivity. Sampling on the first cruise in each set focused mainly on characterisation of benthic communities and sediment properties, while the second in each pair was used primarily to conduct shipboard and *in-situ* process studies. The latter included determinations of sediment mixing and accumulation rates, microbial process rates (aerobic through sulfate reduction), benthic solute fluxes and isotope tracer studies of early benthic OM cycling. Notably, ¹³C pulse-chase tracer experiments represented the first comparative, holistic study of short-term C uptake and cycling that contrasts activities of whole benthic communities across a continental slope and OMZ.

Participants included scientists and students from the University of Edinburgh (UK), the UK National Oceanography Centre (Southampton), the Scottish Association for Marine Sciences (Oban, UK), the University of Liverpool (UK), Scripps Institution of Oceanography (USA), the University of Hawaii (USA), the Netherlands Institute of Ecology, and the National Institute of Oceanography of Pakistan (Karachi). Full cruise details are provided in cruise reports by the Principal Scientific Officers (Bett, 2003a, b; CD 145 and 150; Cowie, 2003a, b; CD 146 and 151).

Five primary stations were studied on all cruises (Fig. 1); the depths and oxygenation nomenclature adopted throughout the volume are 140 m (seasonally hypoxic), 300 m (OMZ core), 940 and 1200 m (lower OMZ transition) and 1850 m (below OMZ). These definitions are based on a combination of dissolved oxygen (DO) concentrations (from water-column profiles obtained with a Seabird DO sensor attached to a CTD) and sediment properties, as distinguished by abundance of macrofauna and extent of visible

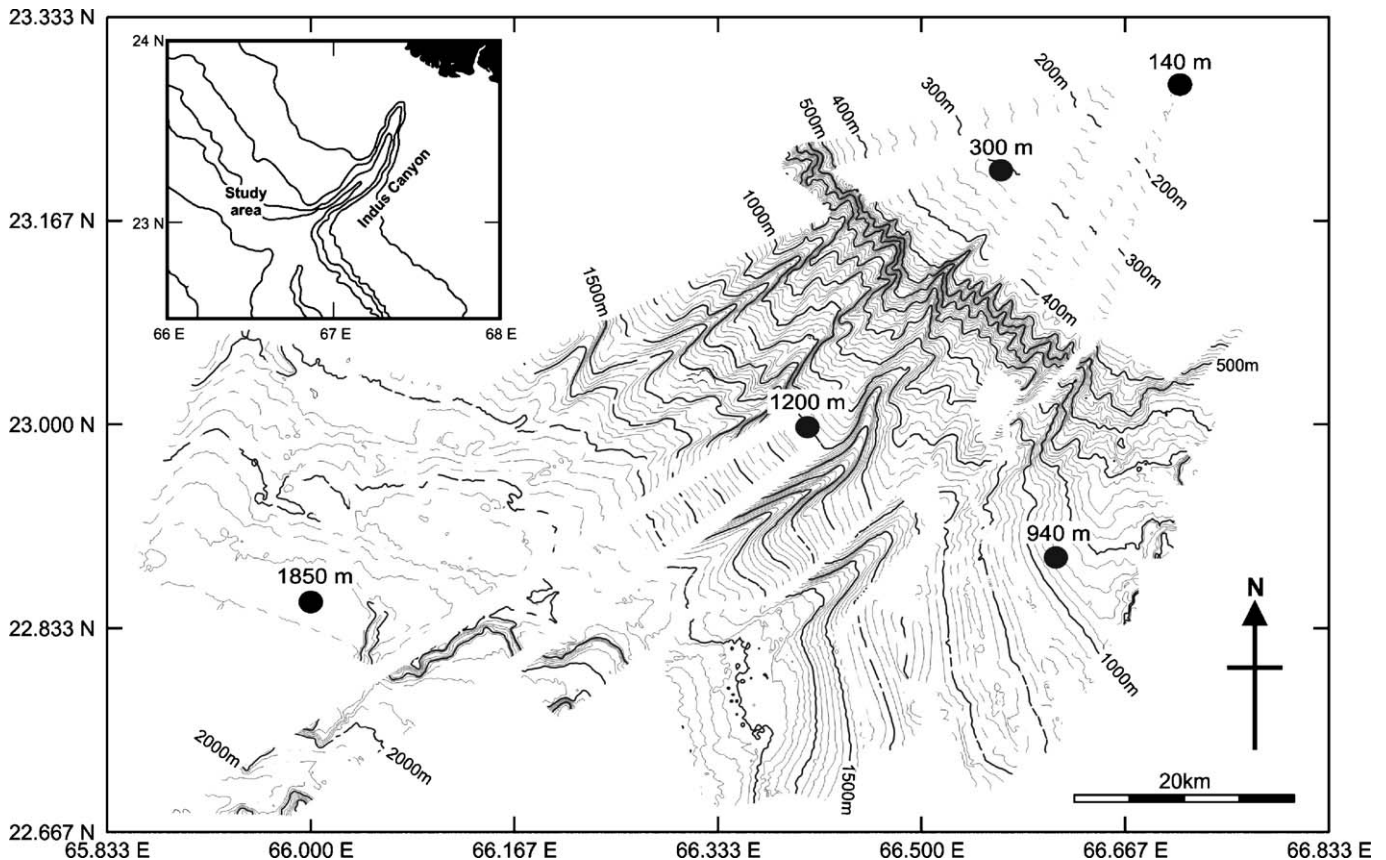


Fig. 1. Site map showing wider study area (insert), bathymetry and primary station locations off the Indus margin of the NW Arabian Sea (Pakistan). Courtesy of Gareth Knight, Liz Rourke and Brian Bett (National Oceanography Centre, Southampton, UK).

lamination in X-radiographs (Hughes et al., 2009; Levin et al., 2009). Thus, the approximate upper and lower OMZ boundaries are set at a DO concentration of 0.5 mL L^{-1} or $22 \mu\text{M}$ (Helly and Levin, 2004). The OMZ core (ca. 250–750 m) is defined by near-uniform DO concentrations of $\leq 0.1 \text{ mL L}^{-1}$ ($\sim 5 \mu\text{M}$) and laminated sediments where macrofauna were found to be rare to absent (Hughes et al., 2009). The lower OMZ transition (ca. 750–1300 m) is a depth range over which DO concentration and the numbers of macrofauna and evidence of bioturbation (numbers, size and depth of burrows) increased steeply with station depth (with a parallel decrease in evident lamination) (Levin et al., 2009). Finally, the seasonally hypoxic zone (ca. 100–250 m) is defined by the depth range over which the upper OMZ boundary shoaled between the intermonsoon and late-to-postmonsoon cruises (Fig. 2) and by the first appearance of clearly laminated sediments (at 250 m). This shoaling is associated with intensification and upward expansion of the OMZ caused by prevailing winds and increased primary production during the southwest monsoon and a northward extension of the West India Undercurrent (Brand and Griffiths, 2009). We note that the presence of some benthic infauna at all stations, and in both seasons, indicate non-zero DO concentrations at the sediment–water interface even within the core of the OMZ (consistent with estimates derived from DO data obtained with CTD profiling).

The majority of the research over all four cruises was focused at these five primary stations. Average locations and general hydrographic properties are listed in Table 1. The primary stations all fell on a single cross-margin transect (Fig. 1), with the exception of the 940-m station, which was located slightly to the southeast because bottom topography was not suitable for benthic lander deployments on the primary transect. Secondary stations were sampled by sediment coring at 50-m intervals

between 700 and 1100 m on CD 146 and 151, in an effort to capture the changing community dynamics, sediment characteristics and organic geochemical properties across DO thresholds. Additional stations also were sampled across the upper OMZ boundary (140–275 m depth) on CD 145 and 151, and at 3200 m on CD 145 (the NAST site of the German BIGSET program; Pfannkuche and Lochte, 2000). Station locations and general hydrographic details for the secondary sites are provided elsewhere in the volume (Cowie et al., 2009; Levin et al., 2009). Additional stations were visited for bottom trawls and for photographic and video surveys (Murty et al., 2009). For details of these additional sites, see individual papers in this volume.

Biological surveys were carried out with a combination of sampling devices. Megafauna were sampled with Agassiz trawls and resulting information, combined with photographic and video surveys, was used to assess surface sediment features, nekton and lebenspuren (Murty et al., 2009). Protozoan meiofauna and metazoan macrofauna were sampled using a multicorer (57 mm i.d. core tubes) and megacorer (96 mm i.d. core tubes), respectively (Larkin and Gooday, 2009; Hughes et al., 2009; Levin et al., 2009). Both corers were hydraulically damped to minimize sediment disturbance, and only cores with intact surface features were selected for sampling. X-radiography and subsequent image analysis was carried out on sediment slabs recovered from megacore barrels in order to assess sediment texture (e.g., lamination) and the nature, depth and extent of bioturbation (Hughes et al., 2009; Levin et al., 2009). As was observed in previous studies on this margin (von Rad et al., 1995; Cowie et al., 1999), sediments from the OMZ core generally showed clear and regular laminations over the entire lengths of ~ 40 -cm sediment cores, which represent annual varves (Hughes et al., 2009). At sites above and below the OMZ sediments were fully

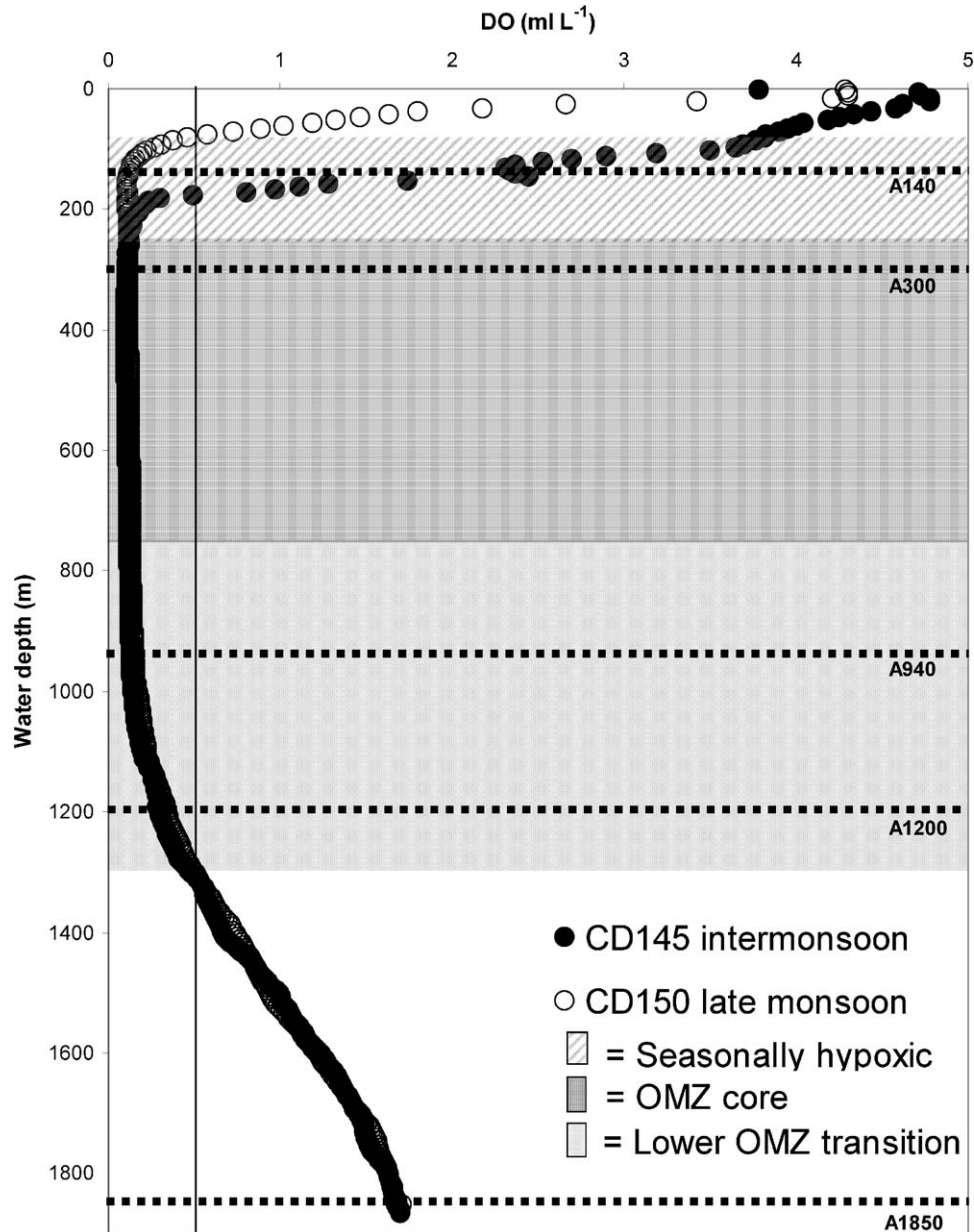


Fig. 2. Water-column dissolved oxygen (DO) concentration profiles during the intermonsoon (CD 145) and late-to-postmonsoon (CD 150) sampling periods. Vertical solid line at $\text{DO} = 0.5 \text{ ml L}^{-1}$ defines the oxygen minimum zone upper and lower boundaries. Dashed horizontal lines denote primary station depths. Shaded depth ranges denote benthic zones defined in the legend and text.

homogeneous and bioturbated, while sites across the lower OMZ transition showed a progressive increase with depth in burrow numbers, size and depth and in the degree to which laminations were mixed out (Levin et al., 2009). Notably, lower OMZ transition sites in the 700–1000 m depth range on the SE transect showed evidence of a single turbidite/mudflow event; this occurred as a discrete layer within the top 10 cm of the otherwise undisturbed records from these sites (Levin et al., 2009). Cores for X-radiography and faunal analysis were immediately sealed with overlying waters and then transferred to, and processed in, a controlled temperature laboratory set to bottom temperature at each site. Faunal samples were also analysed for stable C and N isotopic composition in order to assess food sources and trophic relationships (Jeffreys, 2006).

Replicate undisturbed megacores were also collected for geochemical analyses. The barrels were similarly sealed and then transferred to and processed in a controlled temperature

laboratory set to bottom temperature. Selected cores were sectioned in a glove bag under a N_2 atmosphere to avoid O_2 contamination of redox-sensitive parameters. Stored sediment samples were subsequently analysed to obtain depth profiles of radiochemical properties (^{230}Th , ^{210}Pb), organic geochemical composition (CN and multiple biochemical parameters; Cowie et al., 2009 and others in this volume) and inorganic geochemistry (major and minor elements; Law et al., 2009). Porewaters were extracted by refrigerated centrifugation in sealed tubes for subsequent determination of nutrients (Woulds et al., 2009a), dissolved organic and inorganic C and total dissolved N, and trace metals (Law et al., 2009).

In-situ process studies at the five primary stations were carried out on CD 146 and 151 using a UNISENSE benthic lander. In its PROFILUR mode (Glud et al., 1994), the lander was used for short deployments to collect replicated high-resolution microelectrode DO profiles across the benthic interface and into the surficial

Table 1
Average locations and hydrographic conditions at the five primary Pakistan Margin study sites.

Zone		Seasonally hypoxic	OMZ core	Lower OMZ transition	Lower OMZ transition	Below OMZ
Depth (m)		140	300	940	1200	1850
Latitude (°N)		23° 16.7'	23° 12.5'	22° 53.5'	22° 59.9'	22° 51.3'
Longitude (°E)		66° 42.7'	66° 33.9'	66° 36.6'	66° 24.4'	66° 00.0'
Bottom water						
Temperature (°C)	Intermonsoon	22.3	15.3	9.0	7.3	3.4
	Late-postmonsoon	18.2	14.9	9.3	7.3	3.7
Salinity (psu)	Intermonsoon	36.4	36.1	35.5	35.2	34.9
	Late-postmonsoon	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-postmonsoon	0.11	0.11	0.17	0.36	1.65

sediments (Breuer et al., 2009). In its ELINOR chamber mode (Glud et al., 1995), the benthic lander permitted deployment of a Teflon-lined box-core that, following post-deployment closure, served as a closed incubation chamber for enclosed sediments and overlying waters. The overlying waters were continuously stirred and periodically sampled into Teflon or glass sampling lines with pre-programmed syringes. Oxygen concentrations inside and outside the chamber were monitored by microelectrode and, at the end of the deployment, the box-core shovel was closed to permit recovery of the sediments for subsequent sectioning and analysis. Notably, to permit ambient bottom-water DO concentrations to be maintained within the chamber during incubation, the ELINOR chamber was fitted with an “oxystat” system. This consisted of a ~25-m length of gas-permeable tubing on a manifold outside of the chamber, through which chamber water was pumped, enabling DO consumed within the chamber to be replaced by diffusion from surrounding waters. The ELINOR chamber was deployed in three modes at each site:

- Short deployment (12–24 h) without oxystat*: This mode was used to monitor changes in gas concentrations that would be affected by the oxystat. This included DO concentrations for determining community O₂ consumption rates, N₂/Ar ratios for sedimentary denitrification rate determinations (Schwartz et al., 2009) and DIC.
- Long deployment (2–2.5 days) with oxystat*: This mode was used for determination of benthic fluxes of nutrients (Woulds et al., 2009a), trace metals and dissolved organic C and total dissolved N. Longer deployments were required to obtain measurable concentration changes, while the oxystat was employed to maintain ambient redox conditions and to sustain normal function of the benthic community.
- ¹³C pulse-chase tracer incubation experiments*: The ELINOR chamber was again deployed at each site for 2–2.5 days with oxystat, and with the addition of a slurry of ¹³C-enriched diatoms and kaolinite (as ballast) at the beginning of incubations. To obtain comprehensive tracking of the added ¹³C, overlying waters were monitored for ¹³C-DIC and ¹³C-DOC. Following lander recovery, sediment subcores were sectioned and sampled for solids, porewaters and fauna, which were analysed for δ¹³C signatures of sediments, and isolated meiofauna and macrofauna (Woulds et al., 2007, 2009b),

bacteria (via specific biomarkers; Andersson, 2007; Woulds et al., 2009b), and porewater DIC (Andersson, 2007; Andersson et al., 2009).

Parallel suites of conceptually identical shipboard sediment incubation studies also were carried out. These provided back-up to *in-situ* studies (which suffered various technical setbacks) and permitted greater replication and duration of experiments. They were conducted in the dark in a controlled temperature laboratory set to the bottom-water temperature at each station, and used a new incubation system developed for this project. Megacore barrels containing undisturbed sediments and overlying waters were sealed at the top and bottom, with the top cap including a built-in stirrer and ports for an O₂ microelectrode and a temperature probe, as well as ports for sampling and water replacement. Additional ports were connected to an “oxystat” system similar to that fitted to the ELINOR chamber, but in this case consisting of separate gas-permeable tubing manifolds (for each megacore) immersed in a common reservoir containing an O₂ electrode and stirred bottom water from the site. Water from each chamber was circulated through the gas-permeable tubing manifold using a multi-channel peristaltic pump. The DO concentration in this reservoir was controlled by sparging with variable proportions of N₂ and air, so as to maintain bottom-water DO concentrations within the chambers over the duration of experiments (as monitored by microelectrodes). The shipboard experiments involved the same three types of incubations that were conducted *in-situ* with ELINOR, including ¹³C-tracer studies, but all were duplicated and those with oxystats were generally extended to a 5-day duration.

A comprehensive assessment of microbial OM cycling rates was conducted by a combination of *in-situ* and shipboard determination of the rates of DO consumption (microelectrode profiles and DO fluxes; Breuer et al., 2009), sedimentary denitrification (using nutrient data, N₂/Ar fluxes, and the acetylene block method; Schwartz et al., 2009), Fe and Mn cycling (from porewater profiles and benthic fluxes; Law et al., 2009) and sulfate reduction (via the ³⁵SO₄ incubation method; Law et al., 2009). Finally, CTD profiling was carried out at selected sites on all four cruises in order to obtain water-column DO and nutrient profiles and to sample for suspended solids (Brand and Griffiths, 2009).

4. Volume contributions

The contributions to this volume represent the first project results and span the realms of hydrology, geochemistry, ecology and geobiology. Project results that relate to the cycling and burial of OM, and to trends in biogeochemical processes and faunal populations observed across the Indus margin OMZ are summarized in Fig. 3.

A summary of sediment C and N composition data (elemental and stable isotopic) from a large number of sites across the Indus Margin (Cowie et al., 2009) confirms the presence of an upslope maximum in sedimentary OM content roughly coincident with the OMZ. However, the data also show that multiple %C_{org} maxima and minima occur within the OMZ, indicating that factors other than O₂ availability also control OM distribution. Seasonal changes in sediment OM content were most apparent in the OMZ core, but were generally slight and restricted to uppermost sediment horizons, indicating that seasonal OM inputs are rapidly turned over or mixed out by bioturbation. Molar carbon-to-nitrogen ratios ([C/N]_a) reflected predominantly marine OM inputs, while heavy $\delta^{15}\text{N}$ values reflected a ¹⁴N-depleted nitrate pool created by pelagic denitrification. Neither parameter showed clear cross-margin trends, with the possible exception of shifts to lower (C/N)_a values and heavier $\delta^{15}\text{N}$ values well below the OMZ, apparently due to preferential preservation of inert inorganic N. Downcore trends in %C_{org}, (C/N)_a and $\delta^{15}\text{N}$ are comparatively

minor, suggesting limited *in-situ* OM turnover. Cross-margin and downcore trends in $\delta^{13}\text{C}_{\text{org}}$ can be explained by some combination of preferential recycling of ¹²C during OM remineralization and a ¹³C-depleted signature imparted by chemosynthetic bacteria inhabiting surficial sediments within the OMZ core.

Brand and Griffiths (2009) present a summary of water-column CTD, DO and nutrient data. The results delineate the intensity and physical extent of the OMZ, and how these varied from the intermonsoon to the late-to-postmonsoon cruises. The most notable finding was a late-to-postmonsoon upward shoaling of the upper OMZ boundary by ~80 m, and of the OMZ core (based on nitrite maxima) by ~200 m, attributed to a northward extension of the West India Undercurrent. Increased nitrite concentrations within the OMZ core were indicative of intensified denitrification, but there were not clear changes in nitrate deficits or DO concentrations (the latter already being close to detection limits). The depth of the lower OMZ boundary did not measurably change. Breuer et al. (2009) report on porewater DO concentrations (as determined by *in-situ* microelectrode profiling) as well as those in waters directly above the benthic interface. Bottom-water DO concentrations and penetration depths generally decreased slightly at all sites from the intermonsoon to the late-to-postmonsoon periods, but there was a dramatic decrease in both parameters at the 140-m site, which was engulfed by the upward expansion of the OMZ. Otherwise, cross-margin trends were from near-zero bottom-water DO and porewater penetration at 300 m,

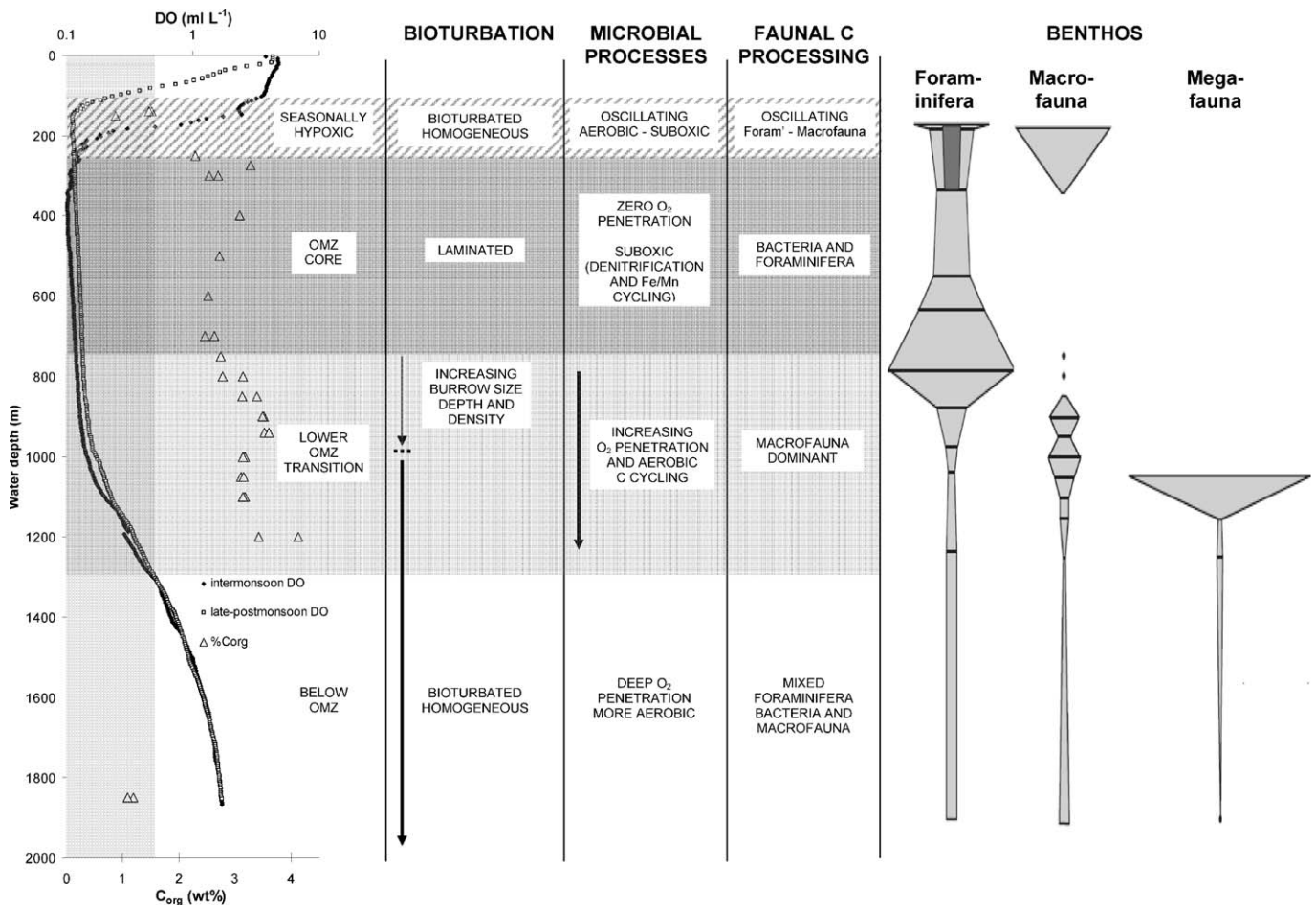


Fig. 3. A schematic summary of project results relating to organisms and processes influencing C cycling across the OMZ on the Indus margin of the Arabian Sea. Shaded zones are as defined in Fig. 2. Faunal distributions show “edge effects” at OMZ boundaries, with different depths of abundance maxima for different faunal size classes. Shaded zones are as defined in Fig. 2. Foraminifera = all stained (‘live’) individuals > 150 μm ; macrofauna = all individuals > 300 μm ; megafauna = visual. Scales for and details of faunal distributions are as described by Gooday et al. (2009).

to progressively higher values in the upper and lower OMZ transitions, and maximal values at 1850 m. Despite evidence for OMZ intensification during the monsoon, there were no consistent changes in sedimentary DO consumption rates, as determined by modelling of porewater profiles.

Woulds et al. (2009a) report on porewater nutrient profiles and *in-situ* and shipboard determinations of benthic nutrient fluxes. Porewater profiles varied across the margin in accordance with sediment OM content and redox conditions but showed little consistent seasonal change except at the 140-m site, which became hypoxic in the late-to-postmonsoon period. Variable effluxes of phosphate, silica and ammonia were observed at all depths, with no consistent seasonal variation and values that were comparable to those reported for other margin settings. However, clear nitrate consumption (i.e. influx) was observed, consistent with significant sedimentary denitrification, especially at the 300- and 940-m sites (see below).

Schwartz et al. (2009) present sedimentary denitrification rates based on nitrate consumption and N₂ efflux determinations, while Law et al. (2009) report on analyses of solid phase (CN, metals, etc.) and porewater parameters (metals, DIC, sulfate, sulfide etc.), as well as downcore ³⁵SO₄ incubation studies, which they use to determine rates of Fe and Mn cycling and sulfate reduction. Schwartz et al. (2009) show that denitrification is a significant process and OM cycling pathway across the entire OMZ, with maximal values at shallower depths in the heart of the OMZ. With the exception of the 1850-m site, rates increased from the intermonsoon to late-to-postmonsoon seasons. Law et al. (2009) demonstrate that Fe and Mn cycling were of varying significance dependent on station depth, with Mn cycling being most significant below the OMZ and Fe cycling being more significant within it. Surprisingly, sulfate reduction rates were low and sulfate reduction was at most a minor and erratic process (within the upper 40 cm) at any station depth. Neither sulfate reduction nor Fe- or Mn-cycling rates showed clear changes with season.

Papers by Woulds and Cowie (2009), Jeffreys et al. (2009) and Vandewiele et al. (2009), respectively address the pigment, lipid, and amino acid compositions of sediments from sites spanning the OMZ to assess whether OM composition and degradation state vary with respect to station depth, bottom-water DO availability and benthic communities. Jeffreys et al. (2009) find that lipid compositions were consistent with overwhelming predominance of marine OM and, surprisingly, that OM quality was generally poor (i.e. relatively advanced degradation state), across the entire margin. Seasonality was observed in the compositions of surficial sediments at three of the five primary study sites, but, in general, lipid compositions indicated heavily altered sedimentary OM below the topmost horizons at all sites. Compositional differences between sites were attributed only indirectly to DO availability, which affects benthic community structure and thus the feeding, digestion and bioturbation by different fauna that dominate at sites across the OMZ. Woulds and Cowie (2009) present pigment results that also indicate a surprisingly advanced state of OM alteration relative to other margins, even in the most OM-rich sediments at the OMZ core. However, greater total pigment yields were found at the OMZ core, apparently linked to absence of bioturbating fauna and to greater preservation of refractory pigments. Based on parameters that included total and enzymatically hydrolyzable amino acid yields and compositions, as well as mineral surface area, Vandewiele et al. (2009) likewise demonstrate that sedimentary OM at all sites was surprisingly degraded, and that OM distributions cannot be explained by variations in mineral grain size or surface area. However, sediments from the seasonally hypoxic 140-m site, as well as from the 1850-m site well below the OMZ, contained more

degraded OM than sites within the OMZ core (300 m) and the lower OMZ transition (940 and 1200 m). This is attributed to a combination of preferential preservation of cell-wall materials and differing degrees of OM alteration by bacteria and accumulation of microbial OM.

The biological papers in this volume have mixed approaches and goals, including descriptions of changes in community structure across the OMZ, examination of the sedimentary and biogeochemical consequences of those changes, exploration of community interactions with the hydrographic environment, and synthetic comparisons across taxa and with other OMZ ecosystems.

Several papers examine the abundance, composition and diversity of different faunal size classes and their biogenic structures across the margin, and assess effects of the OMZ and the SW monsoon. Murty et al. (2009), using photographic transects, document sharp zonation of megabenthos across the OMZ. Megafauna were nearly absent from the 300–900 m depth range, except for fishes and decapods. Notably, high-biomass bands of ophiuroids, cnidarians, and tunicates were present across the lower OMZ (1000–1200 m). Turning to smaller organisms and with the aid of a microscope, Hughes et al. (2009) document macrofaunal community structure at five stations, from the seasonally hypoxic OMZ upper boundary site at 140 m to below the OMZ at 1850 m, and compare patterns to those from the Oman and other low-oxygen margins. They record laminated sediments and a dearth of macrofauna at 300 m, a pattern not observed off Oman. They also document a strong numerical response to seasonal shifts in the upper OMZ boundary, and highly distinct assemblages at each of the stations. However, at the spatial scales examined, DO and OM content were found to be poor predictors of macrobenthos community structure. By sampling macrofauna and sediments at high spatial resolution and at two seasons within the lower OMZ transition, Levin et al. (2009) record abrupt transition from heavily laminated to fully bioturbated sediments as well as sharp macrofaunal gradients between 700 and 1100 m water depth. They document the existence of DO thresholds for macrofauna between 0.1 and 0.2 ml L⁻¹, and potential interactive influences of DO and OM in generating these patterns.

The protists are known to be significant contributors to deep-sea biota and processes; in this volume both the larger foraminifera and the gromiids receive attention. Aranda da Silva and Gooday (2009) present density distribution and diversity data for gromiids, a little-known group of protists whose deep-water representatives were first discovered off Oman. Gromiids are shown to be conspicuous features of the Pakistan and Oman Margin sediments below the OMZ and the authors suggest they may play key roles in C cycling and substrate provision. Larkin and Gooday (2009) examine abundance, composition and diversity responses of macrofaunal-sized foraminifera to monsoon-driven changes in O₂ and food supply on the hypoxic Pakistan upper slope. Foraminiferal abundances far exceed those of metazoan macrofauna, and appear to respond dramatically to changes in food supply, also suggesting a key role for this group in OM cycling within hypoxic regions.

Gooday et al. (2009) synthesize all of the biological information acquired for the Pakistan Margin in 2003 to compare the relative responses of the different faunal size classes to the OMZ. They show that foraminifera, macrofauna and megafauna abundances and diversity are all depressed within the OMZ, and that the lower boundary is a region of sharp changes in composition, especially for the metazoan taxa. However, each group exhibited slightly different depth-oxygen response patterns. This paper provides the most holistic, integrative view of OMZ influence on a single margin to date.

Several papers address the roles of benthic biota in biogeochemical processes. Woulds et al. (2007) have shown previously, using pulse-chase isotope tracer studies, that taxa involved in C processing change spatially and temporally across the Pakistan Margin OMZ. In Woulds et al. (2009b), these studies are placed in a broader context, identifying categories of C processing (respiration vs. uptake by metazoan macrofauna, foraminifera and bacteria). The results illustrate temperature domination of total respiration, and reduced biological mixing but enhanced macrofaunal C uptake (especially in the lower OMZ) relative to other margins. Using lipid biomarkers, Jeffreys et al. (2009) identify key roles for foraminifera in modifying polyunsaturated fatty acids at 300 m and for pennatulid cnidarians in removing labile lipids prior to OM deposition at 1200 m.

5. Overview

Taken together, the contributed papers demonstrate distinct cross-margin gradients, not only in oxygenation and sediment OM content but also in benthic communities and bioturbation, and in microbial processes (Fig. 3). They also demonstrate that benthic conditions changed significantly in response to the SW monsoon, in terms of bottom-water DO concentration and porewater DO penetration, especially at the 140-m site. However, despite this evidence of a monsoon impact, most benthic communities and process rates, as well as sedimentary OM contents and compositions, showed few clear changes from the inter- to the late-to-postmonsoon sampling periods. This may have been due to rapid processing of OM deposited at the seafloor (on timescales of days to weeks), such that the seasonal signal was largely removed by the time of the late-to-postmonsoon sampling. An exception was the pattern of phytodetrital processing at 140 m, which shifted from macrofaunal to foraminiferal dominance linked to an order-of-magnitude decrease in bottom-water DO levels.

A rough spatial correspondence between DO depletion within the OMZ and upper-slope C_{org} enrichment is reconfirmed. However, new results clearly show that sediment OM is generally quite degraded across the entire margin, that there is variability in C_{org} content within the OMZ sediments that is unrelated to DO concentration, and that differences in OM quality across the OMZ are generally subtle, despite large differences in OM content. Dramatic changes in benthic communities occur across the lower OMZ transition zone. These appear to be related to OM availability and quality as well as to DO concentrations, with different DO thresholds for different biotic size groups. Oxygen availability also exerts a threshold-type control on early faunal C processing, and biomarker and experimental data provide clear evidence that benthic fauna at sites across the margin play important and differing roles in the early cycling of sedimentary OM. These fauna also differ strongly in feeding modes and in the degrees to which they bioturbate and irrigate sediments. Consequently, variations in faunal community composition and function are also likely to determine the longer-term fate of sedimentary OM, and may be significant factors in the C_{org} distributions observed across the Pakistan Margin.

Acknowledgements

The authors thank the master, officers, engineers and crew of the R.R.S. *Charles Darwin*, as well as Andrew Louch, Colin Day and Geraint West of National Marine Facilities at the National Oceanography Centre (Southampton, UK), for their enormous help in ensuring the success of four complex cruises under particularly challenging circumstances. This paper benefited

greatly from the thorough and helpful critiques of an earlier draft by three anonymous reviewers. We also thank Profs. Andrew Gooday and George Wolff for editorial assistance with several papers in this volume, and Dr. Shahid Amjad and colleagues at the National Institute of Oceanography of Pakistan for their collaboration and for assistance in securing clearances. This project was supported by grants from the Natural Environmental Research Council of the UK (NER/A/S/2000/01280), from the Leverhulme Trust (F/00158/L), the US National Science Foundation (INT-02 27511), and the Netherlands Organization for Scientific Research (812.02.004; 833.02.2002).

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