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Benthic processes in the deep Arabian Sea: introduction and overview

John D. Gage[a,*], Lisa A. Levin[b], George A. Wolff[c]

[a]*Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, P.O. Box 3, Oban, PA34 4AD, Scotland, UK*

[b]*Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA*

[c]*Environmental Organic Chemistry and Geochemistry Group, Oceanography Laboratories, Department of Earth Sciences, University of Liverpool, Liverpool L69 3BX, UK*

1. Introduction and historical context

The Arabian Sea in the north-western Indian Ocean is a relatively small but biogeochemically active area of the world ocean. As a result of the monsoon dynamics and consequent high material flows the region has been thought to have global significance in terms of biogeochemical fluxes (Law and Owens, 1991; Owens et al., 1991). The seasonal reversal of winds leads to strong seasonal upwelling of nutrient-rich water from the depths along the narrow continental shelf resulting in high surface productivity and high export particle flux from the euphotic zone (Quasim, 1982; Sen Gupta and Naqvi, 1984; Nair et al., 1989).

However, our understanding of the biological oceanography of the Arabian Sea, particularly its benthic biology, has developed rather intermittently because the region has been far away from the areas of main research emphasis. Benthic fauna in deep water was collected in the Arabian Sea during the voyages of the Indian Marine Survey vessels "Investigator I" and "Investigator II" between 1885 and 1925. The discovery of what was considered a more or less azoic zone on the sea bed between about 100–1200 m depth along the continental margin of Arabia is associated with the trawling and dredging work of the Egyptian research vessel "Mabahiss" during the John Murray Expedition of 1933–1934 (Sewell, 1934a,b). Taxonomic studies of the fauna collected underlined the taxonomic and zoogeographic importance of the area. But the realisation of the connection between the sediment samples smelling strongly of hydrogen sulphide, along with the apparent absence of megabenthos and the

* Corresponding author. Fax: + 44-(0)-1631-565518.
E-mail address: jdg@dml.ac.uk (J.D. Gage)

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development of the oxygen minimum layer had to await the detailed oceanographic studies during the International Indian Ocean Expedition of 1959–1965. This was because detailed oxygen profiles obtained by the "Mabahiss" were never published, even though Mohamed (1940) emphasised the link between his low pH values and low dissolved oxygen (see Deacon and Rice, 1984).

Russian studies after World War II and during the International Indian Ocean Expedition focused on productivity and quantitative benthic sampling using standardised sampling techniques. This work found an abundant benthic biomass in the deep Arabian Sea, with a standing crop at 3,000 m of 1.92 g wet weight m^{-2} and more (Neyman et al., 1973), a value unusually high for the low-latitude deep sea. The reason for this was suggested to be not only the pattern of seasonal upwelling and non-stationary eddies causing replenishment of nutrients from depth, but also the well-developed oxygen minimum zone. The high organic production and limited sources of water replacement results in over-consumption of oxygen and development of an intense and unusually deep oxygen minimum layer. This depresses mid-water recycling of the organic matter allowing much more detrital material to sink to great depths without being recycled by mid-water consumers (Angel, 1984), resulting in an enhanced flux of labile organic material to the deep-sea benthic boundary.

High, and intensely seasonal variable, particle flux to the deep ocean has since been confirmed in long time-series sediment trapping undertaken in Indian and German programmes. Furthermore, the presence of the OMZ, and possibly even of free H_2S in the upper part of the this layer down to 600 m (Ivanenkov and Rozanov, 1961), was observed also to have a direct effect on the distribution of bottom-living organisms. A minimal biomass measured in areas on elevated sea bed that lie within the OMZ and the benthic fauna was sparse, or absent, in layers exposed to free H_2S. As would be expected with low mid-water re-mineralisation of particulate organic material, organic carbon and nitrogen content is relatively high, with well-developed reducing conditions, evidenced by negative or low positive values of redox potential and the sediment oxygenated layer being either absent or of insignificant thickness. In deeper, mid-oceanic abyssal areas, sediment organic carbon remains high, but the bottom water is much less depleted in oxygen and a well-developed and diverse benthic fauna is present (Parulekar et al., 1982).

Despite the fascinating novelty in the benthic environment uncovered by these studies the deep-water benthic biology continued to suffer neglect, even if valuable studies have been undertaken using foraminiferans as palaeo-indicators of oceanic hypoxia (e.g. Hermelin and Shimmield, 1990; Cannariato et al., 1999). Elsewhere the powerful effect on the deep-sea benthos of oxygen minima impinging on the continental margin was first noted in the benchmark investigations of deep-sea benthic community structure in the Atlantic by Sanders and his colleagues at the Woods Hole Oceanographic Institution in the 1960s. In a transect off Walvis Bay, south-western Africa, Sanders (1969) noted the ultimate controlling influence of oxygen concentration on benthic populations responding to the very high input to the bottom of labile food. The influence of hypoxia on both the composition, community structure and vertical distribution of the benthic and mid-water zooplankton community has since been investigated elsewhere, particularly in studies in the eastern Pacific where sea mounts penetrate the oxygen minimum zone (e.g. Levin et al., 1991; Wishner et al., 1990,1995).

The benthic system has an important role in the biogeochemical fluxes at the continental margin (Walsh, 1991). This has been addressed in several large research programmes at the ocean margins, such as SEEP-1 and SEEP-II and related studies in the north-western Atlantic (Walsh et al., 1988; Biscaye et al., 1994; Blake and Diaz, 1994), OMEX (Van Weering et al., 1998) and ECOMARGE (Monaco et al., 1990) in the north-eastern Atlantic and Mediterranean, respectively. However, the potential influence of the oxygen minimum on benthic biogeochemical fluxes at the continental margin remains poorly understood. In the Arabian Sea research in various national programmes under the international umbrella of the Joint Global Oceanographic Flux Study, JGOFS, has had a distinct emphasis on upper-ocean processes. With a few exceptions, limited resourcing generally has not allowed these programmes to concurrently study benthic processes. This is despite a recognition that coupling of the deep-sea benthic system with the upper ocean may be at least as intimate as that which has been revealed from intensive oceanographic studies by deep-sea biologists in the North Atlantic and Pacific oceans (e.g. Graf, 1989; Smith et al., 1994; Pfannkuche et al., 1999).

This volume with its research emphasis on the continental margin and the oxygen minimum zone, along with the results of a large-scale German study, BIGSET, in the abyssal Arabian Sea (to be published in a forthcoming volume of Deep-Sea Research Part II), aim to help balance this situation. As such the work reported on here is not any formal part of an international programme, nor does it solely address biogeochemical cycling. Rather it is a compilation of work with relevance to benthic processes, particularly in relation to the oxygen minimum zone and high flux of organic carbon to the bottom. It is hoped that results in this volume will influence thinking on the importance of the benthic system as part of the overall biogeochemical cycling in the Arabian Sea.

With its emphasis on the impingement of the OMZ on the benthic environment, a large part of the work reported on in this volume focuses on the continental margin off southern Oman and the adjacent Owen Basin, rather the abyssal basins further offshore. This work was undertaken during one 5-week cruise (Gage, 1995, R.R.S. "*Discovery*" cruise 211) in October/November 1994. This formed part of a suite of cruises by this British research ship that included the two cruises in the ARABESQUE study led by the Plymouth Marine Laboratory in the U.K. (see Deep-Sea Research Part II Volume 46 No. 3–4) that addressed the upper-ocean biogeochemical processes of the Arabian Sea during 1994/95.

2. Overview of contributions to volume

Papers within this volume take a very broad look at the biogeochemical, ecological, genetic and evolutionary consequences of the presence of an oxygen minimum zone. Studies range from those conducted at the level of the individual, to population-, community- and ecosystem-wide phenomena. These papers consider protistans both large and small, as well as metazoan meiofauna, macrofauna and megafauna. Never before has such a diverse cross-section of benthic organisms and processes been examined in this geochemically important setting, the oxygen minimum zone.

Lamont and Gage document morphological adaptation by spionid polychaetes to low oxygen within the Arabian Sea OMZ. This adaptation consists of enlarged respiratory surface area. Interesting questions are raised about whether observed adaptations reflect phenotypic plasticity, or are produced by selection and are genetic in nature.

Gooday et al., take another look at the foraminiferan community associated with organically enriched and oxygen depleted environments, but, in contrast to earlier studies, includes the complete assemblage, including the poorly known soft-shelled forms such as allogromiids and saccamminids. Similarities are revealed to community patterns in oxygen-depleted settings elsewhere. Although foraminiferans often well outnumber metazoans in bathyal oxygen-depleted areas they show similar trends in abundance and diversity in relation to degree of hypoxia. Interesting differences in size–class related responses of foraminiferans compared to metazoans are uncovered, with the smaller sizes most abundant within the OMZ.

In another paper Gooday et al. describe the systematics and ecology of a strange, new species of giant protozoan from the Oman margin beneath the OMZ. Although gromids are conspicuous and widespread in shallow water settings, this golf-ball-size organism (*Gromia sphaerica* sp. nov.) is the first gromid ever reported from the deep sea. It occurs clustered at high densities near the lower OMZ boundary and the authors speculate that it may play an important role in the degradation of organic matter at the sediment-water interface.

Small size classes are also addressed by Cook et al. who test a previous finding from the Pacific that nematode abudance is not influenced by oxygen concentration. They find support for this hypothesis in food quality (measured as hydrogen ion index) rather than oxygen as the major predictor of nematode abundance, which is also positively correlated with abundance of total macrofauna.

Creasey et al. examine aspects of the population biology, parasite pressure and population genetics of galatheid crabs (*Munidopsis scobina*) living in the lower part of the Arabian Sea OMZ. They document a size-dependent response to hypoxia and genetic differentiation, but conclude conspecificity of populations.

Rogers takes a more general look at shifts in the distribution of OMZs over geological time. He considers OMZ roles as genetic barriers, as agents selecting for habitat specialisation, and in allopatric speciation of benthic fauna. This paper suggests that, historically, long-term shifts in the extent of oxygen minima will have led to isolation of populations providing many opportunities for allopatric speciation on the slope, while on a smaller scale strong selective gradients at the lower reaches of the OMZ will also increase rates of speciation.

A number of contributions examine deeper regions of the Arabian Sea floor. Two papers address deep-water sites studied during recent German cruises. Boetius and

Lochte used phospholipid concentrations to measure microbial biomass at sites between 2300 and 4400 m water depth. They found a positive correlation of microbial biomass with sedimentation rates, suggesting that the standing stock of benthic micro-organisms is controlled by particle sedimentation. Koppelmann et al. examine the role of the mesozooplankton community in relation to heterotrophic activity and calcium carbonate flux in the bathypelagic zone. In comparing calculated metabolic requirement to carbon input measured in sediment traps, both spatial and strongly seasonal variability is detected in the zone between 1050 and 3000 m depth, but not at greater depths. The authors conclude that flux data estimated from net sampling yield a sufficiently high spatial and temporal resolution to provide a proxy for particle flux measurements.

Levin et al. investigated the relationship between environmental conditions and macrofaunal assemblages and lifestyles across the OMZ at the Oman Margin. Interestingly, an abundance maximum of macrofauna was not observed at the lower boundary of the OMZ as originally hypothesised, but rather reflects a potential oxygen threshold (0.15–0.2 ml l^{-1}) above which macrofauna can utilise organic material. They also note an interesting relationship between pigment preservation and species diversity which may reflect long-term oxygenation conditions. Overall, the OMZ was associated with taxonomic dominance by polychaetes, reduced spatial heterogeneity and reduced species diversity of macrofauna.

Smith et al. examine bioturbation properties across the OMZ of the Oman Margin from depths of 400–3400 m. Mixed layer sediment depths did not vary significantly. However, mean values in the OMZ are substantially less ($\times 2$) than at oxygenated margins, which probably reflects the oxygen stress at the Oman Margin, and the preponderance of surface-deposit feeders and tube builders in the Oman sediments. It was also apparent that burrow diversity was strongly correlated with macrofaunal species diversity, suggesting that the former may be a good proxy for the latter in palaeo–dysaerobic assemblages.

In two related papers, Meadows et al. and Murray et al. look at interactions between bioturbation and sediment geochemistry and geotechnical parameters. Relationships between degree of anoxia and water depth are described with a distinctive pattern in the OMZ which includes the presence of subsurface sediment heterogeneity and down-core trends in sediment properties with an apparent break at 4–7.5 cm. Geotechnical measurements (using a new microscale penetrometer) of the fine structure of the sediment showed a complex pattern in relation to bioturbation, expressed as visible burrow numbers, that seems to be associated with burrowing macrofauna activity.

Papers by Rao and Veerayya and Suthof et al. are concerned with the processes controlling the burial of organic carbon or the degradation of organic matter in sediments from the west Indian and Pakistan Margins, respectively. The former have demonstrated that marginal highs along the continental slope have elevated levels of organic carbon, when compared to the continental slope at equivalent depths. They ascribe this to the differences in the sedimentology and burial rates in particular. Suthof et al. found significant differences in the organic matter distributions across the Pakistan Margin, above, within and below the OMZ. They suggest that this variability arises from ambient environmental differences at the sampling stations. Export productivity, accumulation rates and oxygen exposure times apparently have a critical role in controlling organic carbon burial.

Smallwood and Wolff measure sediment biomarkers along the D211 transect to assess the relative contributions of primary – versus secondary – producers in the water column. As expected, there was little detectable input from secondary producers except at the lower boundary of the OMZ. But there was clear but unexpected evidence of benthic re-working by detrivore megafauna within the OMZ. Biomarkers of aerobic versus anaerobic microbial activity mirror oxygen availability, but the study uncovered considerable within- and between site variability interpreted as reflecting spatial and temporal variability in surface production and particle flux.

Together these studies demonstrate not only that the benthic community is alive and well at the margin of the deep Arabian Sea, but also the powerful effects of the oxygen minimum zone on animal morphology, genetic structure, community structure, sediment reworking and organic matter preservation.

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