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Microbial bioavailability regulates organic matter preservation in marine sediments

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Abstract

Burial of organic matter (OM) plays an important role in marine sediments, linking the short-term, biological carbon cycle with the long-term, geological subsurface cycle. It is well established that low-oxygen conditions promote organic carbon burial in marine sediments. However, the mechanism remains enigmatic. Here we report biochemical quality, microbial degradability, OM preservation and accumulation along an oxygen gradient in the Indian Ocean. Our results show that more OM, and of biochemically higher quality, accumulates under low oxygen conditions. Nevertheless, microbial degradability does not correlate with the biochemical quality of OM. This decoupling of OM biochemical quality and microbial degradability, or bioavailability, violates the ruling paradigm that higher quality implies higher microbial processing. The inhibition of bacterial OM remineralisation may play an important role in the burial of organic matter in marine sediments and formation of oil source rocks.

1 Introduction

In the ocean organic matter (OM) degradation starts immediately in the water column and continues at the sediment-water interface (Hedges et al., 2000). The mechanisms involved in degradation of OM have been extensively studied and oxygen deficiency of the depositional setting has been shown to favour the formation of organic-rich deposits (Hartnett et al., 1998) and oil source rocks (Demaison and Moore, 1980; Gélinas et al., 2001). In addition, many other parameters, including enhanced primary productivity (Pedersen and Calvert, 1990), sorption to surfaces (Keil et al., 1994a) and high sediment-accumulation rate (Hedges and Keil, 1995) are typically associated with formation of OM-rich sediments.

OM remineralisation in marine sediments is mainly attributed to bacteria (Turley et al., 2000). A wide array of bacteria are required to carry out successful OM degradation, of which hydrolytic and fermentative bacteria play a key role, being able to

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breakdown (hydrolyse) complex multi-carbon compounds into smaller and more soluble and digestible ones. Therefore, their activity is often attributed as a limiting step in OM degradation rate and extent of degradation (Tyson, 1995; Arnosti, 2004). However, macrofauna has been shown to facilitate OM remineralisation rates. For example, experimental work has shown that under oxic bottom-water conditions the redistribution and transport of OM from surface sediments to deeper units makes it more available for a wider bacterial community, and thus substantially stimulates bacterial OM remineralisation (Kristensen and Mikkelsen, 2003; Van Nugteren et al., 2009). Similarly, in soils particle manipulation by animals is well known to stimulate microbial OM degradation (Brussaard et al., 1997). The potential to degrade OM differs between bacteria and macrofauna. Macrofaunal deposit feeders have a higher intensity digestion system whereas bacteria use a low intensity hydrolysis based on extracellular enzymes (Mayer et al., 2001). These different degradation pathways may lead to variations in the biochemical composition of OM (Woulds et al., 2012), and the macrofaunal digestion has been suggested to enhance the degradability of OM by microbes (Van Nugteren et al., 2009). Furthermore, macrofaunal bio-irrigation will "add" oxygen deeper into the sediment and enhance solute transport, stimulating microbial activity and net remineralisation (e.g. Aller, 1982, 1994; Aller and Aller, 1998).

From geological and oil-source rock perspective it is important to understand which fraction of the OM survives the early degradation and what is left behind in the rock record, potentially becoming a hydrocarbon source. Traditionally OM degradation (or OM bioavailablity) has been observed to co-vary with OM biochemical quality and quantity, higher biochemical quality and quantity typically leading to higher remineralisation rates (Henrichs, 1992; Cowie et al., 1995). A robust and commonly applied indirect indicator of biochemical quality of sedimentary OM are the concentrations of chlorophyll *a* (chl *a*) and other intact (or non-altered) pigments. The degradation products of chl *a*, phaeopigments (phaeo), in turn serve as indicators of more degraded OM, and the ratio of the two is a commonly applied to examine the quality of sedimentary C_{org} (e.g. Jeffrey and Vesk, 1997; Woulds and Cowie, 2009). Amino

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acid composition provides another powerful indirect tool for examination of biochemical composition of OM, certain amino acids becoming preferentially enriched (e.g. β-alanine and γ-aminobuturic acid) during degradation while others (e.g. aspartic acid and glutamic acid) are lost (e.g. Cowie and Hedges, 1992, 1994; Dauwe and Middelburg, 1998; Dauwe et al., 1999). Moreover, a quantitative degradation index (DI), based on a range of amino acids and reflecting the progressive compositional change during OM remineralisation, provides yet another tool to assess the biochemical composition of OM (Dauwe et al., 1999; Vandewiele et al., 2009).

The aim of this study is to show a comprehensive view of sedimentary OM matter quantity and biochemical quality along a bottom-water oxygen (BWO) gradient in the Arabian Sea. In addition, an experimental approach was used to independently validate the bioavailability, or the potential net microbial remineralisation, of the OM deposited along this gradient. Furthermore, biological mixing, or metazoan activity, was assessed, using downcore phaeopigment and ^{210}Pb profiles, and OM burial was estimated using ^{14}C-dating.

2 Materials and methods

The Arabian Sea is characterised by a pronounced mid-water-column OMZ, which is sustained through monsoon driven high surface water primary productivity and relatively weak bottom-water ventilation via Antarctic Intermediate Water (Wyrtki, 1973). The modern day OMZ (O2 < 22 µM after Helly and Levin, 2004) extends from ±100 to ±1400 m water depth with some spatial and seasonal variability, however, the core of the OMZ is relatively stable with the bottom-water oxygen (BWO) values falling down to 2 µM (Cowie and Levin, 2009). On geological timescales the intensity of Arabian Sea OMZ appears to fluctuate on orbital and sub-orbital timescales, minimum OMZ intensity coinciding with productivity low and high winter mixing during the climatic cooling in the North Atlantic (Reichart et al., 1998).

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In January 2009 during the PASOM (Process study on the Arabian Sea Oxygen Minimum zone) cruise in the Northeastern Arabian Sea OMZ, undisturbed surface sediments were collected with a multiple corer, along a BWO gradient, ranging from 2 µM to 80 µM from the Murray Ridge. The studied sites also lie along a depth transect ranging from 900 m to 3000 m water depth (Fig. 1, Table 1). In addition to coring, a CTD profile, including an attached oxygen sensor (Sea-Bird SBE43, accuracy 2 %), was carried out at each station to monitor the water-column properties.

2.1 Degradability potential of organic matter

To assess the potential microbial decomposition of OM under oxic conditions, we performed series of sediment incubations where CO_2 production per unit of C was quantified (Dauwe et al. 2001). Homogenized surface sediments (top 3 cm) were used to determine the bioavailability of in situ OM, and to quantify the organic carbon (C_{org}) remineralisation through CO_2 production under oxic conditions (Moodley et al., 2011). As the incubations were carried under oxic conditions, some bias in these potential availability rates may result from the adaptation of different bacterial communities. However, we believe this is unlikely to be a major concern as very similar carbon remineralisation rates were observed for surface sediments of the eastern Arabian Sea OMZ sediment, where both anoxic and oxic incubations were performed (Moodley et al., 2011).

Following the recovery the samples were stored in dark in plastic bags at 4 °C. The incubations were initiated after two months and carried out in dark, at 10 °C. At the same time sediment was sub-sampled for background analysis (C_{org}, total hydrolysable amino acids, grain size). At the end of the incubations (18 days) the sediments from duplicate bottles was combined (due to expected low concentration of polar lipid-derived fatty acids, PLFAs) for PLFA extraction used to estimate bacterial biomass (Sect. 1.3).

The OM reactivity, expressed as a half-life, was calculated as $-\ln(0.5)/k$ with k (decay constant) based on quotient of CO_2 production and C_{org} content per wet sediment (Hargrave and Phillips, 1981).

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2.2 Analytical measurements

The total hydrolysable amino acids (THAA) were measured after Vandewiele et al. (2009). The obtained THAA distribution was used to calculate the DI index, which translates subtle differences in the amino acid composition into one number indicative of the degradation state of particulate OM: −2 extensively degraded to +1 fresh algae (Dauwe et al., 1999).

The grain size measurements of the surface sediment (top 3 cm) was performed using a Malvern Particle Analyzer. The sediment was not acidified prior to analyses.

At the end of the slurry incubations, the sediment was freeze-dried and subsequently analyzed for PLFA (polar lipid-derived fatty acids) content and compound specific carbon isotope signature. The bacterial biomass was estimated from concentration of bacteria specific PLFAs (i14C:0, i15C:0, a15C:0 and i16C:0) (Middelburg et al., 2000).

Sedimentary pigments were analyzed for all ten stations. On board top 10 cm of a multicore (with 6 cm diameter) was subsampled into 10 slices: the top 2 cm every 0.5 cm, between 2–6 cm every 1 cm and between 6–10 at every 2 cm. The samples were stored at −80 °C, and freeze dried prior to pigment extraction in 10 ml of acetone: water (90 : 10). The full pigment composition was gained through application of high-performance liquid chromatography (HPLC) equipped with a C18 reverse phase column. See Barranguet et al. (1998) for the full methodological description. The calibration was based on working standards prepared from commercially available compounds (DHI, Denmark). The pigment concentrations are reported per $\mu g\,g^{-1}$ of sediment and as a depth-integrated pigment-inventory in top 10 cm of sediments.

2.3 Bioturbation and sediment mixing

Downcore ^{210}Pb profiles were measured for four stations (Pasom-2, -3, -4, -6). Samples were taken from the top 6 cm of sediment. The top 2 cm was sampled at every 0.5 cm and from there after at 1 cm intervals. The ^{210}Pb activity in 100 mg dry weight of sample was measured at Royal NIOZ by α-spectrometry of its granddaughter ^{210}Po,

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which was precipitated on silver after digestion of sample in an acid solution (Boer et al., 2006). It should be noted that in open marine sediments, like Murray Ridge, with relatively low sediment-accumulation rates (rates in few cm kyr^{-1}), the down core changes in ^{210}Pb (and phaeopigment) content are due to particle mixing (bioturbation) rather than accumulation. If the ^{210}Pb profile would represent isotope decay, and thus reflect the sedimentation rate, it should not penetrate the surficial sediments but complete decay within the first cm of sediment. The same principle applies to phaeopigments, however, at stations where the surficial pigment concentrations are very low, microbial degradation may play a role.

The ^{14}C-AMS dating was performed on carbonate from handpicked planktonic foraminiferal tests from three depth intervals (top, middle, bottom). The ^{14}C dating was carried out at each station. The ^{14}C ages were corrected using a marine reservoir age of 400 yr and calibrated using the Int09 calibration curve with CALIB software package version 6.0.1 (Stuiver and Reimer 1993).

2.4 Carbon accumulation rates

Carbon accumulation, or burial, rates were based on the organic carbon content of the top 3 cm of sediment. The surface C_{org} values in the OMZ sediments can be taken to represent the burial values, as the downcore profiles are relatively constant (Vandewiele et al., 2009; Kraal et al., 2012). In the sediment outside the OMZ, the surface values may slightly overestimate the final burial concentration. A sediment density of 2.65 g cm^{-3} was assumed in all calculations. The sedimentation rates were inferred from ^{14}C ages. If a clear linear average age depth correlation was not possible, a maximum and minimum accumulation rates (and average) were calculated. No C_{org} accumulation rate was calculated for station 6 as no clear relationship between ^{14}C-data and depth was observed.

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3 Results and discussion

3.1 Sediment characteristics: OM quantity and biochemical quality

None of our stations contained clearly laminated sediments, although stations 7–10 outside the OMZ could be argued to show some subsurface very fine scale lamina (Fig. 2). However, distinct changes in the sediment characteristics were observed along the oxygen gradient, with respect to colour (Fig. 2), organic carbon (C_{org}) content and biochemical composition (Fig. 3). The stations 1B and 2 with BWO contents of 2–3 µM were distinctly darker (dark-olive brown vs. olive brown) than sediments from the stations 3–5 (with BWO ranging 5–17 µM). With BWO increasing to 27 µM at station 6B, a colour change from light-olive-brown to more grayish sediment underneath was seen in the top 1 cm, indicating a shallow oxidation front. However, clearly bioturbated sediments with red-brownish surfaces overlying more gray sediments were not seen until station 7 with a BWO of 45 µM.

All measured parameters indicative of OM quantity in recent sediments, C_{org} (Fig. 3a), C_{org} accumulation (Fig. 3b), total pigment inventory (Fig. 3c) and total hydrolysable amino acids (Fig. 3d), showed a clear exponential decline with increasing BWO content. The exponential relationship between C_{org} content and BWO in the Arabian Sea OMZ closely corresponds to data from Slater and Kroopnick (1984).

The biochemical composition of OM changes during remineralisation due to preferential loss of reactive compounds and accumulation of other, more refractory compounds (Cowie and Hedges, 1992; Dauwe et al., 1999). Therefore, biochemical OM quality indicators, like amino acids and photosynthetic pigments, provide powerful tools to assess the extent of the OM degradation. Our biochemical OM quality indicators showed clear linear trends with the BWO content with the highest quality coinciding with the lowest oxygen concentrations in the OMZ (Fig. 3e, f). The quantitative amino-acid degradation index (DI), which is based on subtle changes in amino acids composition reflecting the progressive compositional change during OM remineralisation (Dauwe et al., 1999), ranged from −0.45 to −1.4 and correlated strongly with the

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BWO content (R^2 = 0.95). As the DI was negative at all sites (+1 represents freshly produced algal matter and −2 corresponds to extensively degraded deep-sea sediments (Dauwe et al., 1999; Vandewiele et al., 2009), the OM in the core of the OMZ was moderately degraded. However, extensive degradation (DI = −1.4) was seen at the deepest better-oxygenated site consistently with observations in the Pakistan margin (Vandewiele et al., 2009). Similarly the phytopigment OM quality indicator (the content of chlorophyll *a* (chl *a*) and other intact phytopigments over total pigments) showed a strong correlation with the BWO content (R^2 = 0.74), implying enhanced degradation with elevated bottom-water oxygenation as previously reported by Woulds and Cowie (2009). The pigment index also correlated with the DI (R^2 = 0.65). Clearly biochemical indices for OM quality consistently show preservation of high quality OM at low oxygen.

3.2 Bacterial biomass and OM (microbial) degradability

The bacterial biomass was relatively constant averaging 248 ± 67 mmol C m^{-2} and did not show a clear trend along the study transect (Fig. 3g). Our biomass data fit with the general observation that bacterial biomass is rather constant in oceanic sediments, regardless of the depositional setting (Wei et al., 2010). Despite the high quantity and high biochemical quality of OM in the OMZ sites, the potential remineralisation rates under oxic conditions were remarkably constant along our study transect, averaging 2.01 ± 0.33 mmol C m^{-2} d^{-1} (Fig. 3g). Our remineralisation rates are similar to those measured for OMZ sediments along the eastern Arabian Sea and one order of magnitude lower than those for continental shelf sediments (Moodley et al., 2011). Hence, the abundant OM of biochemically moderately high quality in OMZ sediments exhibits surprisingly poor microbial degradability, or bioavailability. The examination of the OM decay constants (k) derived from the incubation experiments, reveals the poor OM bioavailability further, showing that the OM accumulating in the OMZ is significantly less biodegradable than the OM deposited in the oxygenated zone below the OMZ (Mann-Whitney test, 1-tailed, $p < 0.005$, $n = 18$; Fig. 3h). The resulting average OM

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half-life for OMZ sediments is 35 ± 14 yr while the corresponding numbers for the zone below the OMZ is only a half of this (15 ± 2 yr; not shown). As the incubations were carried under oxic conditions, some bias may result from the adaptation of different bacterial communities. However, we believe this is unlikely to be a major concern as very similar carbon remineralisation rates were observed for surface sediments of the eastern Arabian Sea OMZ sediment, where both anoxic and oxic incubations were performed (Moodley et al., 2011). Furthermore, it should be noted that our remineralisations rates reflect the potential degradation rates under oxic conditions. Thus, the rates of moderately degraded OM inside the OMZ may be considerably lower due to near absence of oxygen (Hulthe et al., 1998; Dauwe et al., 2001).

3.3 OM bioavailability versus biochemical OM quality

The paradox between the biochemical quality and direct microbial bioavailability is intriguing and in contrast with the ruling paradigm that less degraded OM, or OM of higher quality as inferred from biochemical composition, is typically more readily degradable (Henrichs, 1992; Cowie et al., 1995; Hedges and Keil, 1995). We suggest that this retardation of OM remineralisation in OMZ sediments may be the controlling parameter for the accumulation of OM in the OMZ sediments.

Several mechanisms have been linked to the inhibition of OM remineralisation. For example, physical protection through encapsulation of reactive OM with algaenans, compounds present in algal cell walls, or other hydrolysis-resistant matrices may inhibit the remineralisation of OM of high biochemical quality (Knicker, 2004). However, we do not believe that algaenans play a major role in the protection of OM in the OMZ sediments as the relative abundance of amino acids typically found in the algal cell wall, such as of glycine and threonine, were equally abundant in the OMZ sediments (27.2 ± 0.4 %) and in sediments outside the OMZ (27.8 ± 0.7 %; data not shown). Alternatively, sedimentary OM has been shown to be commonly enriched in finely grained sediments (e.g. Bordovskiy, 1965; Premuzic et al., 1982; Keil et al., 1994b) and it has been suggested that this may be due to OM association, or sorption to mineral surface

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(e.g. Keil et al., 1994a; Mayer, 1994; Hedges and Keil, 1995). In this study no data for mineral surface area is available, nevertheless, no correlation was observed between the median grain size or clay content (Table 1) and sedimentary organic carbon content (Pearson correlation, respectively: $p = 0.513$, $n = 9$; and $p = 0.247$, $n = 9$). Moreover, Vandewiele et al. (2009) showed that sediments under Pakistan OMZ are also enriched in organic carbon when normalised to specific mineral surface area. Therefore, we believe that the mineral surface sorption is not the primary preservation agent of OM in the OMZ sediments.

The OM depolymerisation via extracellular enzymatic hydrolyses has been show to be the rate-limiting step in the OM remineralisation (e.g. Hoppe, 1991; Arnosti, 2004). Microbial remineralisation of OM of high molecular weight substrate typically begins with extracellular enzymatic hydrolysis, which produces compounds small enough to be taken up by a bacterial cell. The typical size limit for microbial uptake is around 600 Da (Weiss et al., 1991). Thus, the inhibition of OM remineralisation in the OMZ sediments may be due to presence of higher molecular weight compounds, which are not bioavailable to microbes despite their higher biochemical quality (Arnosti and Holmer, 2003). This may also be the case in our OMZ transect as the results of pyrolysis indicate relatively higher concentrations of pigment-derived, macromolecular-bound tetrapyrrole compounds in the OMZ sediments and the absence of these pigment related macromolecules outside the OMZ (Klaas Nierop, 2012).

The inhibition of OM breakdown in the OMZ may be linked to limited of macrofaunal OM processing. Macrofauna, having relatively complex digestion pathways, involving many enzymes, make the OM more accessible to microbes by increasing the surface area of particles and making nutrient-rich molecules more easily obtainable (Mayer et al., 2001). In addition, macrofauna may provide catalyzers for microbial degradation, thus simultaneously aiding in the breakdown of macromolecular compounds. The particle manipulation by fauna and associated bioturbation would also enhance the diffusion of enzymes, thus accelerating microbial degradation in agreement with the OM degradation model of Rothman and Forney (2007). Experimental work has also

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demonstrated enhanced degradation of OM in the presence of macrofauna, which can distribute and spread the OM to the wider bacterial community (Van Nugteren et al., 2009).

Only limited macrofaunal data is available for the Murray Ridge. However, the biomass estimates of Pozzato (2012) for PASOM station-1b and -7 are intriguing as they indicate higher total macrofaunal abundances in the OMZ station 1B ($\pm 1400\,mg\,C\,m^{-2}$) than outside the OMZ at station 7 ($\pm 930\,mg\,C\,m^{-2}$). Nevertheless, the diversity of the macrofaunal community is very low inside the OMZ where 65 % of the total biomass (inc. bacteria) is atributed to polycheate *Linopherus* sp. The low diversity and high dominance inside the OMZ has also been highlighted in the studies on the adjacent Pakistan margin OMZ, which show that few polychaeta taxa dominate the assemblage (Gooday et al., 2009; Hughes et al., 2009). The role of macrofauna in the organic matter processing is thus limited to very few taxa, although both Woulds et al. (2007) and Pozzato (2012) noted that *Linopherus* sp. played an important role in carbon uptake during their experiments. The general consensus is that the lower limit of oxygen tolerance of macrofauna adapted to long-term low-oxygen conditions, like OMZs, is around $0.5\,ml\,l^{-1}$, or 22 µM (Levin, 2003). Above this "threshold" the macrofaunal community becomes more diverse and at higher bottom-water oxygen concentration macrofaunal community becoming more diverse and occupying various in-sediment niches. Consistently, our ^{14}C data, which is here used to assess sediment mixing or bioturbation, does suggest limited macrofaunal mixing at very low oxygen sites and increased biological activity with increasing BWO content (Fig. 4).

At the OMZ stations 1 and 2 the bioturbation appears to be limited to very surficial sediments, as indicated by the linear ^{14}C age-depth relationship (Fig. 4). However, some recent mixing in the top sediments may be induced from the down core phaeopigment and ^{210}Pb profiles, which have half-lives of 22.2 yr and ±1–12 yr, respectively; the half-life of pheaopigmenst varying with oxygenation which in turn will influence the decay constant (Woulds and Cowie 2009). At station 3 to 5 the bioturbation horizon appears to reach down to ±4 cm depth in sediment based on pigment

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and ^{210}Pb profiles (Fig. 4). The ^{14}C-profiles suggest somewhat deeper mixing depth for stations 4 and 5 especially. Some of the discrepancy may be due to compaction of sedimentation with depth. However, it may also be related to different time frames of the mixing tracers. Thus, it is possible that at intermittent timescales bioturbation at stations 4 and 5 reaches down to 10 cm depth, as indicated by the ^{14}C data. This deep mixing may be related to activity of *Zoophycos* burrowing, which has been observed to transport old sediments to surface (Leuschner et al. 2002). At station 6B the ^{14}C dates indicate constant age with depth. This is most likely due to a mass deposit, a slump or a turbidite. However, the event does not seem to be very recent as both the ^{210}Pb and phaepigment profiles imply that hemi-pelagic sedimentation has continued since then. Based on the ^{210}Pb and phaeopigment profiles, mixed zone reaches below 4 cm. At station 7 the bioturbation zone probably reaches down to ±6–7 cm depth as indicated by the phaeopigment and deeper sediment ^{14}C-data. The offset of the intermediate and deep ^{14}C-data may be due to *Zoophycos* or other macrofaunal activity. At stations 8 to 10, the bioturbation horizon reached beyond 7 cm depth and at station 10 below 10 cm depth. The pigment profiles of stations 8 and 10 may underestimate the mixing depth. Due to the very low OM concentrations at these depths, the organic carbon consumption will be closer to the surface and the expected half-life also shorter (Woulds and Cowie, 2009).

4 Implications and conclusions

Our data support the view that the enhanced preservation of OM occurs in the OMZ sediments where the BWO content is < 22 µM. The biochemical quality of the OM (phytopigments and amino acids) also showed a negative linear relationship with BWO content. In addition, the biochemical quality indicators also correlated well with each other, thus providing robust and consistent information about the composition of OM in the Arabian Sea sediment. However, we believe that the enhanced OM preservation in the OMZ is only indirectly related to oxygenation of the environment as the microbial

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bioavailability did not reflect the biochemical quality of OM. This observation also contradicts the ruling paradigm in marine biogeochemistry that higher biochemical quality implies higher microbial bioavailability. The proposed mechanisms would also lead to preservation and burial of OM with high biochemical composition, thus proving an analogue for oil source rocks.

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Table 1. Station positions, water depth, bottom water oxygen (BWO) content, median grain size and silt content.

Station PASOM-	Lat (N)	Lat (E)	Depth (m)	BWO (µm)	Median (µm)	Silt (%)
1B	22° 32.9′	64° 02.4′	885	2.1	35.4	70.4
2	22° 33.9′	64° 03.8′	1013	2.6	41.2	63.3
3	22° 19.9′	63° 36.0′	1172	5.1	38.6	65.2
4	22° 18.0′	63° 36.0′	1306	13.8	29.6	71.4
5	22° 09.3′	63° 12.8′	1379	16.8	74.7	46.5
6	22° 04.7′	63° 04.5′	1495	26.8	27.4	73.8
7	22° 18.5′	63° 24.5′	1791	45.2	16.6	92.2
8	22° 08.7′	63° 01.1′	1970	56.9	15.2	91.8
9	22° 06.3′	62° 53.7′	2470	66.3	No data	No data
10	21° 55.6′	63° 10.6′	3010	76.9	14.8	94.7

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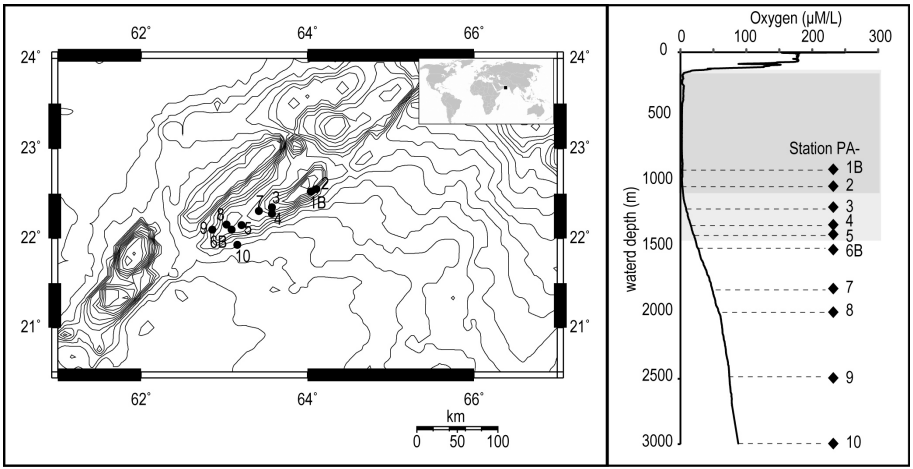

Fig. 1. Left: Map of Murray Ridge, Arabian Sea, showing the station locations with an annex of the world map with the Murray Ridge indicated with a square. Right: Water column profile of dissolved oxygen in the study area. Water depth and BWO content of each station shown. Dark gray shaded area = core of the OMZ, BWO content < 5 µM; light gray shaded area = OMZ, BWO content < 22 µM (or 0.5 ml l^{-1}).

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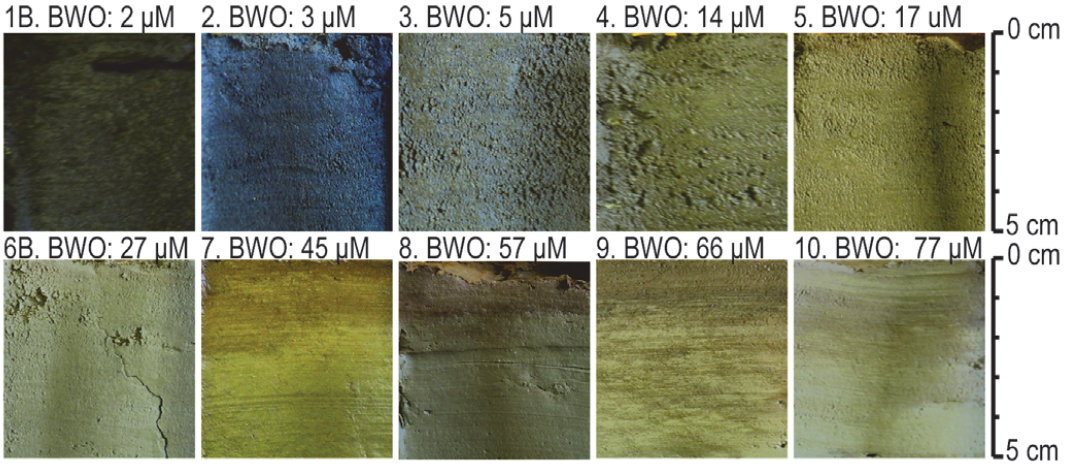

Fig. 2. Images of surface sediments from the studied oxygen transect. First row: stations 1B-5, located in the OMZ where bottom water oxygen (BWO) is less than 22 µM. Second row: stations 6B-10 located below the OMZ. BWO ranges from 27 µM to 77 µM.

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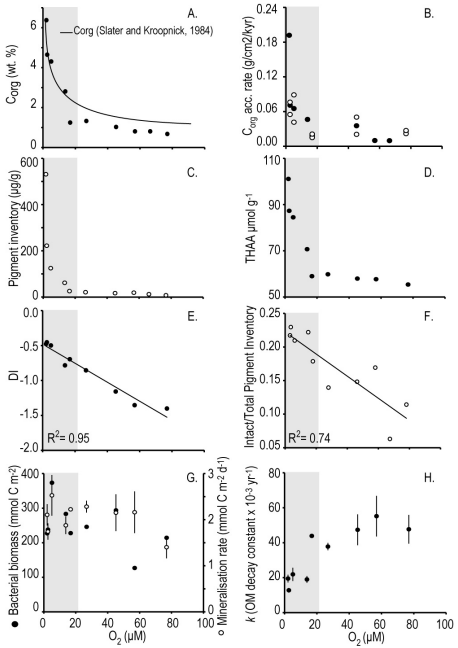

Fig. 3. Organic matter quantity, organic carbon accumulation and biochemical quality indices versus bottom water oxygen content. **(A)** Organic carbon with a trend line of Slater and Kroopnick (1984); **(B)** organic carbon accumulation rate; **(C)** total pigment inventory; **(D)** total hydrolysable amino acid content (THAA); **(E)** DI, the amino acid degradation index; **(F)** intact/total pigment inventory; **(G)** bacterial biomass and mineralization rate; **(H)** OM decay constant versus bottom water oxygen content along the studies transect. The area shaded in gray represents the zone where BWO content is $< 22\,\mu M$ and invertebrate fauna are accordingly affected by the low O_2 concentrations (Levin, 2003). The solids circles in plot B indicate the values based on average sedimentation rates where are the open circles indicate the maximin and minimum accumulation rates. The error bars in plots G and H represent the standard deviation of two replicate incubations. No error bars are available for bacterial biomass **(G)**.

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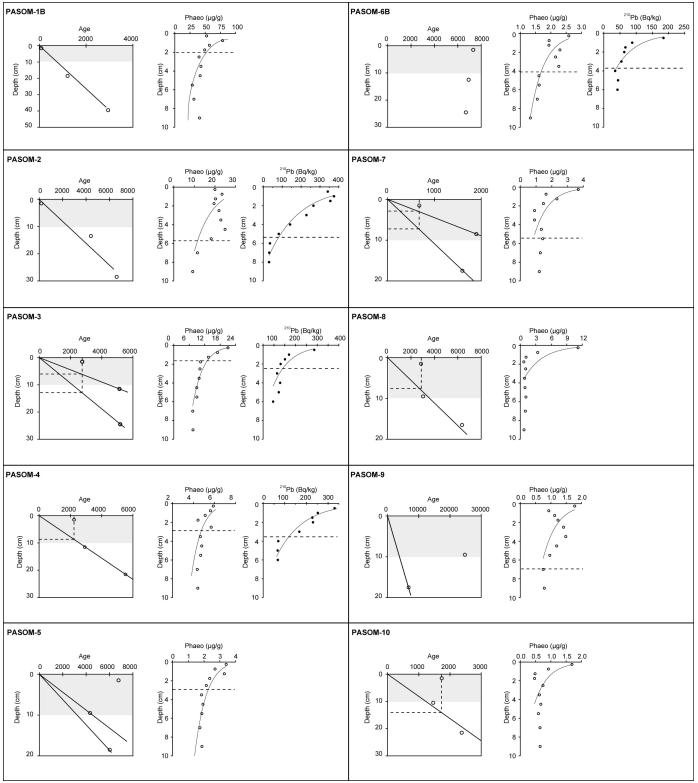

Fig. 4. Sediment mixing or bioturbation indicators used in this study. Stations 1B–5 located in the OMZ and stations 6B–10 located outside the OMZ. Three mixing indicators used: ^{14}C data to give age of sediment in absolute years, and down core phaeopigment ^{210}Pb data. Due to various half-lives of the mixing indicators, long term and short-term mixing can be examined independently, see main body of text for more detail. Light gray shading in the ^{14}C age plots indicates the top 10 cm of sediment, which is also shown in phaeopigment and ^{210}Pb profiles. Horizontal, dashed lines indicate the inferred mixing/bioturbation zone.

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