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Resilience of benthic ecosystem C-cycling to future changes in dissolved oxygen availability

Carol M. White[1], Clare Woulds[1*], Greg L. Cowie[2], Andrew Stott[3], Hiroshi Kitazato[4,5]

[1]School of Geography, University of Leeds, Leeds, UK, LS2 9JT

[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK

[3]Centre for Ecology and Hydrology Lancaster, Lancaster, UK

[4]Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Japan

[5]School of Marine Resources and Environment, Tokyo University of Marine Science and Technology, Tokyo, Japan

c.woulds@leeds.ac.uk

Dr.Greg.Cowie@ed.ac.uk

astott@ceh.ac.uk

kitazatoh@jamstec.go.jp

hkitaz0@kaiyodai.ac.jp

[*]Corresponding author.

Abstract

In marine sediments, the availability, cycling and burial of organic carbon (OC), the size and composition of the faunal community, and the availability of dissolved oxygen (DO) are closely coupled. In light of expected expansions in marine hypoxia and of oxygen minimum zones (OMZs) in particular, it is now necessary to de-convolve DO from the frequently co-varying factors OC concentration and faunal biomass, in order to

understand the effect of changing dissolved oxygen (DO) concentrations on the magnitude and pattern of biological processing of organic carbon (OC). This is especially important on the continental slope, a significant location for C cycling and burial.

In this study, stable isotope tracer experiments were conducted at three sites with contrasting ambient DO concentrations of 0.5, 2.8 and 21.2 μM (at depths of 530 m, 812 m and 1140 m respectively) on the Indian continental margin. Experiments were conducted both at ambient DO concentrations, and also, for the first time, under manipulated DO concentrations both 5% above and below ambient. The ^{13}C label was added as algal detritus, and traced through the processes of respiration, and uptake into bacterial biomass, and into metazoans and foraminifera.

Total C biological processing under ambient DO conditions was similar across all three sites, suggesting that benthic communities are well adapted to local conditions, such that OC processing is optimised even at severely hypoxic sites.

DO manipulation produced changes in the pattern of OC processing by the benthic community. Oxygen manipulations in both directions resulted in decreases in total community respiration, except at the most hypoxic site. Bacterial uptake, in contrast, increased in response to all DO manipulations. Faunal ^{13}C uptake tended to increase with increased DO. At the most hypoxic site (0.5 μM) this was attributable to increased foraminiferal activity, whereas at the most oxygenated site (21.2 μM) it was the metazoans that showed increased biomass-specific ^{13}C uptake. Similarly, decreases in DO tended to reduce faunal ^{13}C uptake, with metazoans disproportionately affected where they were already living at the lower end of their DO tolerance (i.e. 2.8 μM). Thus, the taxa most affected by DO manipulation depended on antecedent DO conditions. The total capacity of the benthic community to process freshly deposited OC (i.e. respiration plus uptake by bacterial and different fauna) increased following upwards manipulation of DO at the 0.5 μM site, but was not adversely affected by downwards manipulation of DO. Thus, results suggest that benthic communities possess some functional resilience, and that future expansion of marine hypoxia, while impacting benthic ecosystem structure, may not have as marked an effect on biological C processing.

Keywords: Isotope tracing experiment, benthic fauna, oxygen minimum zone, dissolved oxygen, manipulation

1. Introduction

Understanding the cycling and burial of organic carbon (OC) in marine sediments is crucial, to facilitate accurate modelling of the C-cycle both under current, and expected future conditions. Extensive research into the factors controlling OC burial efficiency in marine sediments has identified dissolved oxygen (DO) availability and exposure time, OC source and reactivity, hydrodynamics, and organic-mineral interactions as being particularly important (e.g. Canfield,1994; Cowie et al., 1999; Hedges and Keil, 1995; Mayer, 1994). However, some of these factors are difficult to quantify, they are often difficult to deconvolve, and their relative influences vary between environments. Thus a full mechanistic understanding of OC cycling and burial at the seafloor has not yet been reached (Arndt et al., 2013). Moreover, multiple interdependent variables relevant to OC cycling and fate are projected to change in the future. These include changes both to the amount and quality of OM exported to the seafloor (Sweetman et al., 2017). In particular, a key result of climate warming will be the increasing occurrence of marine hypoxia (Helly and Levin, 2004; Sweetman et al., 2017), and this is highly likely to alter benthic OC cycling and burial.

The least well understood aspect of OC cycling in marine sediments is the role of benthic biological communities. Both DO concentration and OC availability are known to heavily influence the abundance, biomass and diversity of benthic faunal communities (e.g.Levin et al., 2000; Levin, 2003; Gooday et al., 2009). In turn, benthic organisms can exert a control on the concentration and composition of sedimentary OC (e.g. Aller, 1982; Bianchi et al., 1988; Sun, 2000; Sun et al., 1993), through ingestion and digestion(e.g. Thomas and Blair, 2002; Woulds et al., 2014), bioturbation and bioirrigation (Levin et al., 1997;Aller and Aller, 1998;Sun et al., 1999; Sun et al., 2002), respiration (Aberle and Witte, 2003; Witte et al., 2003b), and microbial stimulation (Aller, 1982; Levin et al., 1997; Sun et al., 1999). Thus, dynamic relationships exist between benthic faunal community structure, oxygen availability, and OC cycling, and the responses of benthic communities and OM cycling to projected change remain uncertain.

Research into the impact of hypoxia on benthic faunal communities has mainly focused on impacts of longer-term hypoxia on community metrics such as abundance and diversity. Seasonal hypoxia is acknowledged to favour organisms with opportunistic life histories, and that are shorter lived with smaller body sizes. Hypoxia has a range of

effects on different timescales. In the medium-long term it compresses habitats, forces migration, and reduces bioturbation and bioirrigation, and is expected to divert C-cycling into more microbial pathways (Diaz and Rosenborg 2008; Middelburg and Levin, 2009). Shorter term responses include shallower burrowing and, contrary to longer term response, increased bioirrigation rates (Forster et al., 1995; Middelburg and Levin, 2009). Multiple studies of the impacts of hypoxia on benthic communities have concluded that changes in faunal communities will have an impact on sediment biogeochemical processes, but these effects themselves have been poorly studied (Middelburg and Levin, 2009). Efforts have tended to focus on impacts on benthic nutrient fluxes. For example, Gammal et al., (2017) found the oxygen-dependent abundance of macrofauna to be an important controlling factor on benthic nutrient fluxes along an oxygen gradient in the Baltic Sea. Further study is required to understand the impacts of hypoxia on benthic cycling of OC.

Few studies have investigated the impact of changing DO availability on the extent and pathways of OC cycling by benthic communities, and even fewer have involved experimental manipulation of DO. In a series of experiments across the Pakistan margin of the Arabian Sea, low oxygen concentrations were observed to inhibit respiration (Andersson et al., 2008), and to determine the types of organisms responsible for OC uptake (Woulds et al., 2007). Foraminifera dominated faunal uptake of OC at the lowest DO concentrations, while macrofauna dominated at higher DO concentrations. In addition, at a shelf site that showed a major monsoon-induced reduction in bottom-water O_2 concentration, OC uptake switched from being dominated by metazoan macrofaunal, to being dominated by foraminifera and bacteria, leading to an hypothesis that O_2 exerts a threshold type effect on the pathway of biological OC uptake. In contrast, a study on the Murray Ridge of the Arabian Sea in which DO was manipulated at sites within and below the oxygen minimum zone (OMZ) observed a lack of impact on benthic respiration and bacterial uptake of OC, and suggested that in some cases an oxygen threshold may be considerably lower than previously suggested (Moodley et al., 2011; Pozzato et al., 2013).

Due to the small number of experiments that have been conducted in low oxygen settings, the influence of hypoxia on biological OC processing by benthic communities remains uncertain. In particular, in light of expected expansion in marine hypoxia in general, and of OMZs in particular (Helly and Levin, 2004; Stramma et al., 2008), including increased incidence of shelf and coastal short-term hypoxic events, the impact of

reductions in DO availability on OC cycling requires investigation. In addition, the oxygen threshold hypothesis requires testing. An OMZ provides sites which are naturally exposed to different DO concentrations, and host different biological communities, and therefore is a natural laboratory in which to investigate the role of DO in controlling the biological processing of OC over several days following deposition.

In this study, we examined the short-term biological processing of OC at sites with contrasting DO concentrations across the Indian continental margin, and, in one of the first such experiments, in response to experimental DO manipulation. We addressed the following hypotheses:

1) Faunal ^{13}C uptake will be driven by biomass, therefore variation in benthic community structure will play a key role in determining short-term OC processing patterns.
2) Overall OC processing rates will be inhibited by the natural presence of lower DO concentrations.
3) At naturally low DO sites, small reductions in DO concentration will result in marked shifts towards smaller faunal classes in the routing of OC through biomass, in line with the oxygen threshold hypothesis (Woulds et al., 2007).

2. Methods

2.1 Study sites

The Arabian Sea oxygen minimum zone is one of the largest volumes of depleted water in the world (Helly and Levin, 2004), impinging on the western Indian continental margin between ~150 and 1500 m water depth. OMZ formation in the Arabian Sea results from monsoon-driven upwelling of nutrient-rich waters fuelling intense productivity, and thus rapidoxygen consumption in mid-water depths as OC sinks. In addition, freshwater inputs increase stratification and reduce ventilation, and the presence of a landmass to the north inhibits the exchange of intermediate water(Levin et al., 2009; Naqvi et al., 2009).

In September-November 2008, a pair of cruises was conducted with the R/V Yokosuka to the Indian margin of the Arabian Sea. Experiments were repeated across 3 sites with bottom water DO concentrations of 0.5 μM, 2.8 μM, and 21.2 μM, (at depths of 530 m, 812 m, and 1140 m respectively, Table 1; Cowie et al., 2014). Thus all sites were hypoxic, and there was a 10-fold increase in DO concentration with each increase in depth.

2.2 Isotope tracing experiments

Duplicate push cores (i.d. 8 cm) were collected using the manned submersible Shinkai 6500, and submerged in tanks containing stirred, filtered seawater in a shipboard laboratory in which dissolved DO was automatically maintained at a chosen level using the OXY-REG system (Loligo Systems), and maintained at in situ temperature using refrigerated incubators.

At each site a pair of replicate cores was incubated at each of three DO concentrations; 'normal', which was the ambient DO concentration, 'low', which was 5% saturation below ambient, and 'high', which was 5% saturation above ambient. The exception was the 0.5 μM site, where the ambient concentration was so low that a downwards manipulation (i.e. the 'low' treatment) would not have been measurable.

Experiments were initiated by the addition of ^{13}C and ^{15}N enriched labelled algae (Chlorella, Cambridge Isotope Laboratories) at a concentration of 650 mg C m^{-2} to cores (equal to 0.3-0.6 % of existing organic C in the surface 1 cm of sediment), which was allowed to settle onto the sediment surface. Following incubation for 5 days, cores were sectioned at intervals of 0-1, 1-2, 2-3, 3-5, 5-7 and 7-10 cm, and sampled for pore waters by centrifugation. Each section was halved. One half was centrifuged to extract

porewaters which were preserved in capped vials with $HgCl_2$. The remaining solid was freeze dried. The other half was preserved in 10% buffered formalin for later faunal extraction.

It is recognised that the experiments are limited to two replicates, and that 8 cm cores are fairly small. These features were imposed by equipment and sample availability, and the considerable analytical burden involved. Therefore the data are interpreted with these limitations in mind. In particular, they limit the extent to which patterns in the data can be supported using statistical testing, and mean that uncertainty will have been introduced by small scale patchiness. However, the approach is consistent with other similar experiments (e.g. Woulds et al., 2009, and references therein), and such an approach has been shown to provide useful insights regarding benthic biogeochemical processes.

2.3 Analyses

Porewater samples were analysed for DIC by transferring to exetainers containing He, and acidifying with concentrated H_3PO_4. The resulting CO_2 was focused twice in loops cooled with liquid N_2 prior to analysis on a Sercon 20-20 isotope ratio mass spectrometer.Sediments preserved in formalinwere washed and sieved at 300 µm before microscopic inspection. At each depth interval (0-1, 1-2 and 2-3 cm), fauna in the >300 µm fraction, were picked, photographed and placed in pre-weighed silver capsules. Individuals were often pooled so that each sample contained sufficient C for analysis. Samples were air dried, de-carbonated by addition of 1N HCl (soft-bodied taxa) or 6N HCl (foraminifera and molluscs), and dried once again. Samples were analysed in dual isotope mode (C+N from the same sample) using a Eurovector elemental analyser coupled to an Isoprime isotope ratio mass spectrometer (Elementar UK Ltd, Stockport, Cheshire), and standards calibrated against the National Institute of Standards and Technology (NIST) certified reference materials Sucrose-ANU (NIST no. 8542) for $\delta^{13}C$, and IAEA-N1 ammonium sulphate (NIST no. 8547) for $\delta^{15}N$. Thus all $\delta^{13}C$ results are expressed relative to the international standard of Pee Dee Belemnite and all $\delta^{15}N$ results are relative to the international standard of atmospheric air. In-house standards of isotopically enriched glucose(~199‰), REFCEN, for $\delta^{13}C$, and isotopically enriched urea (~235‰), REF 310B for $\delta^{15}N$, yielded analytical precisions of 10.76‰ and 1.50‰ respectively.

From one replicate per treatment freeze dried sediments (the solid residue following centrifugation) were analysed for isotopic composition of bacterial phospholipid fatty

acids (PLFAs). PLFAs were extracted using an adapted Bligh and Dyer method (Bligh and Dyer, 1959). Lipids were extracted in a chloroform: methanol: citrate buffer (1:2:0.8 v-v:v) mixture.Lipids were fractionated using6 ml ISOLUTE SI SPE columns, preconditioned with 5 ml chloroform, and the polar fraction was eluted in methanol, and dried under N_2.Samples were taken up in a 1:1 (v:v) mixture of methanol and toluene, and following addition of nonadecanoate internal standard, the polar fraction was derivatisedin0.2 M KOH in methanol at 37 °C for 15 mins. After cooling, isohexane:chloroform (4:1 v:v), acetic acid and deionised water were added, and the organic phase was extracted and dried under N_2.

Extracts were taken up in isohexane, and analysed for the concentration and isotopic composition of PLFAs on a Trace Ultra gas chromatograph connected with a Combustion III to a Delta V Advantage isotope ratio mass spectrometer (Thermo Finnegan, Bremen). Delta ^{13}C values were measured with respect to a reference gas traceable to IAEA reference material NBS 19 TS-Limestone, and are reported standardised to the Vienna Pee Dee Belemnite. Replicate measurement of reference material gave a precision of ± 0.31 ‰. PLFAs were quantified using the combined peak areas of all masses (m/z 44, 45 and 46), compared to the same of the internal C19:0 standard (Thornton et al., 2011).

2.4 Data treatment

The amount of ^{13}C incorporated by fauna (I_{FAUNA}) in the experiments was calculated as the product of excess ^{13}C *(E)* and faunal carbon biomass (C_{FAUNA}) following equation 1:

$$I_{FAUNA} = E_{13C} \times C_{FAUNA}$$

Equation 1

Excess ^{13}C (E_{13C}) is defined as the difference between the ^{13}C signature *(F)* of the control and the sample following equations 2-4:

$$E_{13C} = F_{SAMPLE} - F_{CONTROL}$$

Equation 2

where:

$$F = \frac{^{13}C}{^{13}C + {}^{12}C} = \frac{R}{R + 1}$$

Equation 3

and

$$R = \frac{^{13}C}{1000 + 1} \times R_{VPDB}$$

Equation 4

R_{VPDB} is the $^{13}C/^{12}C$ ratio of the reference material (Vienna PDB; 0.0112372). The amount of ^{15}N incorporated by fauna in the experiments was calculated in the same manner, but R_{AIR} is the $^{15}N/^{14}N$ ratio of the reference material (atmospheric air; 0.0036765). As natural faunal isotopic signatures were not obtained directly in this study, $F_{CONTROL}$ was calculated using the literature of previously published studies (Supplement A). Studies from nearby or similar margins, with similar fauna, were chosen. Small uncertainties in the background signatures will not have affected data processing to a measurable extent, due to the high levels or isotopic enrichment.

Respiration was quantified following modelling of labelled DIC flux out of the sediment based on porewater profiles. Assuming steady state, diffusive benthic DIC fluxes, Fick's First Law was applied to estimate the porewater fluxes (Q) from the sediments into the overlying water column as in equation 5 (Berner, 1980):

$$Q_{DIC} = -\phi D_{sed} \left[\frac{\Delta C}{\Delta x}\right]$$

Equation 5

Where ϕ is the porosity of the sediments, $D_{sed}$is the sediment diffusion coefficient, and $\left[\frac{\Delta C}{\Delta x}\right]$ is the concentration gradient of the porewater profile in the surface sediments. Ideally $\left[\frac{\Delta C}{\Delta x}\right]$ would take into account the sediment-water interface concentration of DIC but this was not available so the 0-1cm interval was used. The whole sediment diffusion coefficientD_{sed} was given by equation 6:

$$D_{sed} = \frac{D_{sw}}{\theta^2}$$

Equation 6

whereD_{sw} is the diffusion coefficient of the solute in seawater ,and θ the tortuosity. D_{sw} was corrected for bottom water temperature to produce a D_{sw} of 1 x 10^{-5} cm^2 s^{-1}(Broecker and Peng, 1974; Li and Gregory, 1974). The tortuosity of the sediment was estimated from its porosity using equation 7 (Boudreau, 1997):

$$\theta^2 = 1 - \ln(\phi^2)$$

Equation 7

Bacterial biomass and uptake of ^{13}C were quantified using concentrations and ^{13}C signatures of the bacteria-specific PLFAs i14:0, i15:0, ai15:0, and i16:0 after Middelburg et al. (2000). Bacterial biomass (C_b) was calculated using the summed carbon concentrations of the bacteria-specific PLFAs ($\sum C_{PLFA-b}$: i14:0, i15:0, ai15:0, i16:0) and applying the transfer functions detailed by Middelburg et al.(2000) following equation 8:

$$C_b = \sum C_{PLFA-b}/(A \times B)$$

Equation 8

A is the average PLFA concentration in bacteria: 0.056 g of PLFA carbon per gram of carbon biomass (Brinch-Iversen and King, 1990). *B* represents the fraction of total bacterial PLFAs represented by the sub-set used here: 0.28 ± 0.04. Similarly, ^{13}C incorporation (I_b) into bacterial biomass was calculated from the sum of incorporated label in these bacteria-specific PLFAs ($\sum I_{PLFA-b}$), and transfer functions*A* and *B*were applied as described in equation 9:

$$I_b = \sum I_{PLFA-b}/(A \times B)$$

Equation 9

3. Results

3.1 Benthic community biomass

Metazoan macrofauna and foraminifera were present at all sites, with biomasses ranging from 3.5±4.9-26.0±18.1 mg C m^{-2} and 79.6±19.2-181±41 mg C m^{-2} respectively (Table 1). Foraminifera tended to dominate the faunal biomass, accounting for 75-98 %. They showed the greatest dominance under the lowest oxygen conditions, at the 0.5 μM site (Table 1).Metazoan macrofaunal biomass, predominantly comprised of polychaetes, was maximal at the 2.8 μM site, where they accounted for 25 % of the faunal biomass. Bacterial biomass ranged between 375±143 and 1241±428 mg C m^{-2}, and was maximal at the 0.5 μM site (Table 1). It should be noted that these biomass data are averages across all experimental cores at each site, and are provided as important context for interpretation of ^{13}C processing patterns, representing as they do the communities that were present in the experiments. They are not intended to be a formal survey of the benthic faunal community, as sample volume and replication was not sufficient for that purpose.

3.2 Respiration

Across all sites and treatments the total amount of added C that was respired varied between 28.3 and 131.4 mg C m^{-2}, with the highest value at the 0.5 μM site following upwards DO manipulation, and the lowest value at the 2.8 μM site following upwards DO manipulation (Table 2; Fig. 2). Under ambient oxygen conditions, the amount of respired ^{13}C was greatest at the 21.2 μM site (93.5 mg C m^{-2}), and smallest at the at the 2.8 μM site (51.0 mg C m^{-2}). at the 0.5 μM site the upwards DO manipulation resulted in a greater amount of respired ^{13}C (131.4 mg C m^{-2}) compared to the ambient treatment (73.6 mg C m^{-2}). In contrast, at the 2.8 μM and 21.2 μM m sites, both upwards and downwards DO manipulations appeared to result in decreased respiration rates (Fig. 2). However, this pattern must be treated with caution, as it was only clear for the upwards manipulation at the 2.8 μM site, and in other cases is to some extent equalled by variability between replicates.

3.3 Bacterial uptake

Bacterial uptake of the added ^{13}C varied between 0.48 mg C m^{-2} at the 21.2 μM site under ambient DO, and 1.80 mg C m^{-2} at the 0.5 μM site under elevated DO (Table 2; Fig. 3).

Under ambient DO, bacterial ^{13}C uptake decreased with increasing DO (Table 2; Fig. 3). Following upwards manipulation of DO, bacterial ^{13}C uptake increased by 45%, 48% and 28% at the 0.5 μM, 2.8 μM, and 21.2 μM sites respectively. Following downwards manipulation of DO, bacterial ^{13}C uptake increased by 45% and 209 % at the 2.8 μM, and 21.2 μM sites respectively.

3.4 Faunal uptake

Under ambient DO, uptake of ^{13}C into the fauna (foraminifera plus metazoans) varied between 23 mg C m^{-2} at the 2.8 μM site, and 31 mg C m^{-2} at the 0.5 μM site. Manipulated DO generally resulted in reduced faunal ^{13}C uptake when DO was reduced (minimum was 8.5 mg C m^{-2} at the 2.8 μM site), and enhanced faunal ^{13}C uptake when DO was increased (maximum was 59 mg C m^{-2}, also at the 2.8 μM site; Table 2; Fig. 4).

In most cases faunal ^{13}C uptake was dominated by the foraminifera, which accounted for between 68 % and 100 % across all sites and treatments. The exception to this was the 2.8 μM site under ambient DO, where foraminifera accounted for only 41 % of total faunal ^{13}C uptake. Manipulated DO conditions had different effects on the different faunal groups at different sites. At the 2.8 μM site, both downwards and upwards DO manipulations resulted in an increase in the extent to which foraminifera dominated ^{13}C uptake (taking it to 78% and 70% respectively). However this pattern was driven differently in each case. Following the decrease in DO, metazoan ^{13}C uptake was markedly reduced, while the upwards DO manipulation did not result in a marked response by metazoans, but foraminiferal ^{13}C uptake showed a substantial increase (Table 2; Fig. 4). At the 21.2 μM site, both downwards and upwards DO manipulations resulted in a reduction in the dominance of faunal ^{13}C uptake by foraminifera (from 87% to 73% and 68% respectively). Following the reduction in DO, foraminiferal ^{13}C uptake was reduced while metazoan ^{13}C uptake remained similar, whereas in response to the experimental increase in DO, metazoan ^{13}C uptake increased markedly while foraminiferal ^{13}C uptake was relatively unchanged (Table 2; Fig. 4).

3.5 Biomass-specific uptake

Biomass-specific uptake for each group (bacteria, foraminifera and metazoans) was calculated by normalising ^{13}C uptake to the biomass of the biotic group concerned (Fig. 5). At all sites, bacterial biomass-specific uptake was smaller than the biomass-specific uptake of both metazoans and foraminifera.At the 0.5 μM site, the biomass-specific

uptake by foraminifera was greater than that for metazoans. Conversely, at the 2.8 μM and 21.2 μM sites, biomass-specific uptake by metazoans exceeded that of foraminifera, with the exception of the downwards DO manipulation at the 2.8 μM site. Under manipulated oxygen conditions at the 2.8 μM site, foraminiferal and metazoan biomass-specific ^{13}C uptake decreased, and little change was seen in the bacterial biomass-specific ^{13}C uptake.Conversely, elevated oxygen concentrations at the 21.2 μM site corresponded to an increase in both bacterial and metazoan biomass-specific^{13}C uptake, while only a bacterial biomass-specific ^{13}C uptake altered under decreased DO (Fig. 5).

4. Discussion

4.1 Respiration

Manipulations of DO appeared to impact the amount of added C that was respired. At 0.5 μM, artificially elevated DO led to increased respiration of added OC (Fig. 2), in line with expectations that increased availability of oxygen would facilitate more rapid respiration. However, at the 2.8 μM and 21.2 μM sites, both upwards and downwards manipulations in DO resulted in reductions in the total amount of added C that was respired (Fig. 2). This suggests that at the more oxic sites the benthic community is well adapted to the ambient DO, such that upwards as well as downwards DO manipulations reduce the capacity of the community to process OC. This result, observed at 2 out of 3 sites are supported by Pozzato et al. (2013) who conducted oxygen manipulations at 2 sites on the Murray Ridge in the Arabian Sea. Although they did not observe a systematic effect of oxygen manipulation on respiration rates (Moodlet et al., 2011; Pozzato et al., 2013), they did conclude that benthic communities process OC most efficiently under ambient oxygen conditions.

Comparisons between sites shows that the amount of added C respired under ambient conditions did not vary systematically with ambient DO. This is in line with previous research in which low ambient DO has been observed to cause only minor reductions in rates of production of labelled DIC in isotope tracer experiments (Andersson et al., 2008). Further, while the presence or absence of oxygen can affect OC degradation rates, in studies considering degradation of fresh OC (such as was used here), the presence or absence of oxygen is often relatively unimportant (Burdige, 2007). Thus our study adds to a body of evidence suggesting that oxygen availability is not a main factor driving remineralisation of relatively fresh OC.

It should be noted that the respiration rates reported here are conservative estimates, as the vertical resolution of porewater sampling was relatively coarse, and they account for only the diffusive flux of ^{13}C DIC, and exclude the portion associated with bioirrigation and other infaunal activity. Nonetheless, they are in the same range as those previously reported from similar experiments (e.g. Woulds et al., 2016), however direct comparisons are not appropriate.

4.2 Bacterial Uptake

Bacterial ^{13}C uptake under ambient conditions was greatest at the site with lowest DO concentration (0.5 μM), and tended to decrease with increasing DO (Fig. 3). This

corresponds with greater bacterial biomass at the 0.5 μM site, which may be driven and supported by the higher concentration of sedimentary organic carbon (%C_{org}, Table 1). The 0.5 μM with the highest bacterial ^{13}C uptake was also the site with the lowest metazoan mcrofaunal biomass (Table 1). Across the same sites, Hunter et al. (2012) observed a significant negative relationship between bacterial ^{13}Cuptake and macrofaunal biomass. They hypothesised that metazoans may suppress formation / persistence of bacterial biomass through either competition for the added C (Van Nugteren et al., 2009), and / or grazing, and release from these pressures allows more uptake of added C into bacterial biomass. Therefore, bacterial uptake of ^{13}C under ambient conditions could have been determined by OC availability and bacterial biomass, but interactions with metazoan macrofaunal may also have played a role.

Bacterial uptake rates were similar to those previously observed at similar depths in the Arabian Sea (Woulds et al., 2007; Pozzato et al., 2013), and also at other sites showing considerably different environmental conditions, such as a shallow sub-tidal site in the Gulf of Gdansk (Evrard et al., 2012), and the 4800 m deep Porcupine Abyssal Plain (Aberle and Witte, 2003). The similarities may be due to the presence of similar bacterial biomass (in the range 0.5-1.5 g C m^{-2}, see Table 2 and Woulds et al., 2016 for values), which is in line with an overall correspondence in this study between bacterial ^{13}C uptake and bacterial biomass.

At all sites, both upwards and downwards manipulation of DO resulted in increases in bacterial ^{13}C uptake (Fig. 3). Similarly, with the exception of the 0.5 μM site, biomass-specific ^{13}C uptake also increased following both increases and decreases in DO (Fig. 5). Thus, bacteria appeared to respond to the stress imposed by abnormal oxygen availability by increasing production of biomass. This is in contrast to results of oxygen manipulation experiments on the Murray Ridge, in which manipulated oxygen conditions appeared to reduce ^{13}C incorporation into bacterial biomass, however the authors concluded that there was no measurable effect due to high variability (Moodley et al., 2011; Pozzato et al., 2013). Together with the decreases in total community respiration observed in response to DO manipulation at the 2.8 μM and 21.2 μM sites, and an assumption that most respiration will have been bacterial, this suggests an increase in bacterial growth efficiency (BGE) in response to DO manipulation. Although controls on BGE are not entirely clear, it is generally thought to be maximised in conditions which are especially suitable for growth, in particular where organic substrate and nutrient limitation are not present (Del Giorgio and Cole, 1998). In this context it is surprising to

observe that DO induced stress appears to increase BGE. However, BGE is also thought to be maximised when a greater fraction of bacterial cells are active as opposed to being dormant (or dead), therefore a potential explanation for the apparent increase in BGE in response to DO manipulation may be that variation in DO initiated activity in additional fractions of the bacterial community.

4.3 Faunal Uptake

Under ambient conditions, inter-site differences in faunal ^{13}C uptake appear to be driven by faunal biomass, and not DO concentration. Faunal ^{13}C uptake was greatest at the most hypoxic, 0.5 μM site, which also showed the highest foraminiferal biomass, as well as the highest organic C concentration, and least degraded OC composition (Table 1; Fig. 4; Cowie et al., 2014). This suggests that maximal ^{13}C uptake at this site was attributable to the presence of a faunal community accustomed to a high quality food supply, and thus primed for responding to the added OC pulse. Furthermore, total faunal ^{13}C uptake under ambient DO did not vary between the 2.8 μM and 21.2 μM sites, despite a 10-fold difference in DO, and this is consistent with their similar faunal (metazoans plus foraminifera) biomass (Table 1). Previous studies which have also observed this correlation between faunal biomass and ^{13}C uptake, and have noted a greater influence of OC availability than oxygen on the ability of faunal communities to respond to an OM pulse under normal conditions (e.g. Woulds et al., 2007; Levin et al., 2000).

Foraminifera (as opposed to metazoans) dominated faunal carbon uptake at all sites, which was unsurprising given that they are better able to tolerate hypoxia than larger metazoan macrofauna (Josefson and Widbom, 1988; Moodley et al., 1997) and are common in faunal communities in oxygen deficient settings, including the Arabian Sea OMZ (Sen Gupta and Machain-Castillo, 1993; Levin et al., 2002; Larkin and Gooday, 2009).

The dominance by foraminifera of ^{13}C uptake at the 0.5 μM site is due to foraminiferal dominance of the biomass (Table 1), suggesting, in support of hypothesis 1, that more abundant and larger taxa play a larger role in OC processing. This is supported by previous observations that uptake of ^{13}C-labelled algae by faunal groups occurs in direct proportion to group biomass in a variety of benthic environments, including estuarine (Middelburg et al., 2000), shelf (Buhring et al., 2006; Kamp and Witte, 2005), and deep-sea (Woulds et al., 2007) settings. Only at the 2.8 μM site under ambient DO concentration did metazoans dominate faunal ^{13}C uptake. This may be due to a peak in metazoan macrofaunal abundance around this depth. This biomass peak is known as an

'edge-effect' (Mullins et al., 1985), and results from the interplay of OC rich sediment and just-sufficient DO which occurs especially at the lower boundaries of oxygen minimum zones. Larger organisms have larger guts and are more motile than foraminifera, and are therefore capable of ingesting more added C (Fauchald and Jumars, 1979; Levin et al., 1997; Nomaki et al., 2005), and for these reasons have sometimes been observed to be responsible for a greater proportion of ^{13}C uptake than their biomass would suggest (Witte et al., 2003a, b).

Changes in the magnitude and pattern of faunal uptake were observed under manipulated DO conditions, indicating, in line with hypothesis 3, that relatively subtle shifts in oxygen concentrations do impact benthic faunal carbon uptake. In general, increases in DO released fauna from oxygen stress and allowed increases in faunal ^{13}C uptake, while decreases tended to reduce faunal uptake, however there was variation in the response of different faunal classes, as discussed below.

On the Pakistan margin of the Arabian Sea, Woulds et al. (2007) observed a shift from metazoan domination of ^{13}C uptake to it domination by foraminifera in response to a seasonal decrease in DO. By comparison with experiments at other OMZ sites they hypothesised that this shift could occur in response to a relatively small alteration in DO, and hence proposed that DO can exert a threshold type control on faunal OC uptake. The DO manipulations in this study were relatively subtle (5% saturation), and were designed to test this hypothesis.

At the 0.5 μM site, the upwards manipulation of DO did not result in an increase in faunal ^{13}C uptake, however, there was an increase in biomass-specific ^{13}C uptake (Fig. 5). Therefore, at the most hypoxic site additional DO availability did appear to lead to an increase in foramniferal feeding. In contrast, at the most oxic, 21.2 μM site, the increase in faunal ^{13}C uptake under high DO was principally due to increased metazoan biomass-specific ^{13}C uptake. On the other hand, at the intermediate DO site (2.8 μM), upwards DO manipulation did not result in increases in either absolute or biomass-specific metazoan ^{13}C uptake. Thus, it was only at the site with the highest ambient DO that the metazoans were able to take advantage of an increase in DO, whereas foraminifera, which are better suited to low DO concentrations (e.g. Levin et al., 2000; Levin, 2003; Gooday et al., 2000) benefitted from the upwards manipulation only at the most hypoxic site The suggestion that small organisms such as foraminifera are best placed to respond to additional DO is supported by an oxygen manipulation conducted on the Murray Ridge by Pozzato et al. (2013), in which meiofaunal foraminifera showed increased ^{13}C uptake in response to

addition of oxygen, but hypoxia-specialised polychaetes did not. At the two more oxic sites, competition and/or predation by metazoans may have prevented the foraminifera from benefiting from upwards DO manipulation.

Downwards manipulation of DO resulted in reduced faunal ^{13}C uptake at both the 2.8 μM and 21.2 μM sites (Fig. 4). At the 2.8 μM site, the decrease under low DO was dominantly attributable to reduced metazoan ^{13}C uptake (Fig. 4), although biomass-specific uptake was reduced for both metazoans and foraminifera (Fig. 5). Thus, at this hypoxic site when DO was manipulated downwards the larger organisms suffered disproportionately from the additional oxygen stress. This downward DO manipulation at the 2.8 μM site was the only case where the hypothesised oxygen threshold effect was observed, with a shift from metazoan to foraminiferal dominance of ^{13}C uptake in response to a small reduction in DO. These observations are consistent with a general recognition that hypoxic conditions favour organisms with smaller body sizes, partly due to the advantages of a high surface area to volume ratio (Diaz and Rosenberg, 2008; Middelburg and Levin, 2009). In addition, the ability of foraminifera to function and survive under very low DO concentrations may be facilitated by the ability of some taxa to either conduct denitrification (Risgaard-Petersen et al., 2006; Glock et al., 2013), or to enter a state of dormancy (LeKieffre et al., 2017).

At 21.2 μM site, the reduced faunal ^{13}C uptake under reduced DO was driven by lower foraminferal ^{13}C uptake. This could have been driven by lower biomass, as foraminiferal biomass-specific uptake was unchanged (as was metazoan biomass-specific uptake, Fig. 5).

Thus the oxygen threshold hypothesis was supported at only one site, which implies that it only operates in particular low oxygen settings where the ^{13}C uptake of metazoans versus foraminifera is finely balanced. We therefore further suggest that it is just one part of a complex response by benthic communities to variations in DO. Pozzato et al. (2013) also considered whether their oxygen manipulation results supported the oxygen threshold hypothesis. They observed continued functioning of metazoan macrofauna at lower DO concentrations than the originally proposed threshold of 5-7 mM, and suggested that for some fauna it could be as low as 2 mM, and dependant of antecedent DO conditions. This, together with the results shown at different sites in this study illustrates that the response of the benthic faunal community depends not only on the size and direction of DO change, but also on faunal community composition, and the pre-existing DO conditions to which they are adapted. Considering this study together with

the two previous studies which have discussed it (Woulds et al., 2007; Pozzato et al., 2013), we propose a broadening of the oxygen threshold hypothesis. We suggest that at severely hypoxic sites foraminifera (small organisms) are able to increase feeding activity in response to additional oxygen availability, while metazoans are only able to utilise such additional DO at sites where they are already adapted to higher DO concentrations. Reductions in DO tend to reduce feeding activity of all types of fauna. The larger organisms are disproportionately affected, especially at the lower end of their DO tolerance, and in some cases this gives rise to a shift in dominance of C uptake from metazoans to foraminifera (i.e. the oxygen threshold effect, Woulds et al., 2007). The exact DO concentrations at which these effects occur are likely to vary between sites. It should also be noted that the experiments on which the oxygen threshold hypothesis is based could not include epibenthic macrofauna or megafauna. Such organisms can be very abundant at oxygen minimum zone lower boundaries (e.g. Gooday et al., 2009; Mosch et al., 2012), and their inclusion in future studies would be beneficial.

4.4 Effect of DO manipulations on short-term OC processing capacity and pattern

Total biological OC processing (the sum of respiration, bacterial uptake and faunal uptake) appeared to increase from low DO, through ambient DO, to the high DO treatment at each site, except for the high DO treatment at 21.2 μM (Fig. 6). This suggests that the potential of the benthic community to cycle OC was enhanced by increased availability of oxygen. However, it should be noted that only at the 0.5 μM was the effect greater than the variability amongst replicates. Further, counter to hypothesis 2, there was no systematic variation in total biological OC processing under ambient DO between sites, therefore the adaptation of each benthic community to the DO conditions it typically experienced had resulted in very similar OC processing capacities. This is supported by a previous oxygen manipulation on the Murray Ridge of the Arabian Sea, which led Moodley et al. (2011) to conclude that overall benthic functioning was not impacted by experimental hypoxia. Therefore we suggest that benthic communities possess some functional resilience, and that future expansion of marine hypoxia, while impacting benthic ecosystem structure, may not have as marked an effect on biological C processing.

Conclusions

- The overall capacity of the benthic community to cycle the added OC did not show a clear response to DO (only one site showed a clear increase with upwards

manipulations of DO), therefore benthic communities showed functional resilience to reduced DO.

- Overall, faunal ^{13}C uptake was maximised by upwards manipulation of DO, however the taxa most affected by DO manipulation was controlled by antecedent conditions. Foraminifera responded to additional DO at the most hypoxic site, while metazoans responded at the least hypoxic site. Metazoans were disproportionately by reduced DO where they were already living at the lower end of their DO tolerance.
- The oxygen threshold hypothesis was supported at one site. We propose a broadening of the oxygen threshold hypothesis, and suggest that at severely hypoxic sites, small organisms are able to increase feeding activity in response to additional oxygen availability, while metazoans are only able to utilise additional DO at sites where they are already adapted to higher DO concentrations. Reductions in DO tend to reduce feeding activity of all types of fauna, with larger organisms disproportionately affected when living at the lower end of their DO tolerance.
- In general, respiration by the entire benthic community was maximal under ambient DO conditions, and was reduced by DO manipulation. The exception to this was at the most hypoxic site, where addition of oxygen resulted in more respiration of the added ^{13}C.
- Bacterial ^{13}C uptake was maximal at the most hypoxic site, and increased with both upwards and downwards DO manipulations at all sites. This suggested an increase in bacterial growth efficiency in response to DO manipulation.

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References

Aberle, N., Witte, U., 2003. Deep-sea macrofauna exposed to a simulated sedimentation event in the abyssal NE Atlantic: in situ pulse-chase experiments using C-13-labelled phytodetritus. Marine Ecology-Progress Series 251, 37-47.

Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. Pleum, New York.

Aller, R.C., Aller, J.Y., 1998. The effect of biogenic irrigation intenstiy and solute exchange on diagenetic reaction rates in marine sediments. Journal of Marine Research 56, 905-936.

Andersson, J.H., Woulds, C., Schwartz, M., Cowie, G.L., Levin, L.A., Soetaert, K., Middelburg, J.J., 2008. Short-term fate of phytodetritus in sediments across the arabian sea oxygen minimum zone. Biogeosciences 5, 43-53.

Arndt, S., Jorgensen, B.B., LaRowe, D.E., Middelburg, J.J., Pancost, R.D., Regnier, P., 2013. Quantifying the degradation of organic matter in marine sediments: A review and synthesis. Earth-Science Reviews 123, 53-86.

Bianchi, T.S., Dawson, R., Sawangwong, P., 1988. The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments. Journal of Experimental Marine Biology and Ecology 122, 243-255.

Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37, 911-917.

Boudreau, B.P., 1997. Diagenetic Models And Their Implementation : Modelling Transport And Reactions In Aquatic Sediments. Springer, Berlin.

Brinchiversen, J., King, G.M., 1990. Effects of substrate concentration, growth-state, and oxygen availability on relationships among bacterial carbon, nitrogen and phospholipid phosphorus-content. Fems Microbiology Ecology 74, 345-355.

Buhring, S.I., Ehrenhauss, S., Kamp, A., Moodley, L., Witte, U., 2006a. Enhanced benthic activity in sandy sublittoral sediments: Evidence from ^{13}C tracer experiments. Marine Biology Research 2, 120-129.

Burdige, D.J., 2007. Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? Chemical Reviews 107, 467-485.

Canfield, D.E., 1994. Factors influencing organic carbon preservation in marine sediments. Chemical Geology 114, 315-329.

Cowie, G., Mowbray, S., Kurian, S., Sarkar, A., White, C., Anderson, A., Vergnaud, B., Johnstone, G., Brear, S., Woulds, C., Naqvi, S.W.A., Kitazato, H., 2014. Comparative organic geochemistry of Indian margin (Arabian Sea) sediments: estuary to continental slope. Biogeosciences 11, 6683-6696.

Cowie, G.L., Calvert, S.E., Pedersen, T.F., Schulz, H., Von Rad, U., 1999. Organic content and preservational controls in surficial shelf and slope sediments from the Arabian Sea (Pakistan margin). Marine Geology 161, 23-38.

del Giorgio, P.A., Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. Annual Review of Ecology and Systematics 29, 503-541.

Diaz, R.J., Rosenborg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926-929.

Evrard, V., Huettel, M., Cook, P.L.M., Soetaert, K., Heip, C.H.R., Middelburg, J.J., 2012. Importance of phytodetritus and microphytobenthos for heterotrophs in a shallow subtidal sandy sediment. Marine Ecology Progress Series 455, 13-31.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: A study of polychaete feeding guilds. Oceanography and Marine Biology 17, 193-284.

Forster, S., Graf, G., Kitlar, J., Powilleit, M., 1995. Effects of bioturbation in oxic and hypoxic conditions - a microcosm experiment with a North-Sea sediment community. Marine Ecology Progress Series 116, 153-161.

Gammal, J., Norkko, J., Pilditch, C.A., Norkko, A., 2017. Coastal Hypoxia and the Importance of Benthic Macrofauna Communities for Ecosystem Functioning. Estuaries and Coasts 40, 457-468.

Glock, N., Schonfeld, J., Eisenhauer, A., Hensen, C., Mallon, J., Sommer, S., 2013. The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone. Biogeosciences 10, 4767-4783.

Gooday, A.J., Bernhard, J.M., Levin, L.A., Suhr, S.B., 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. Deep-Sea Research Part Ii-Topical Studies in Oceanography 47, 25-54.

Gooday, A.J., Levin, L.A., Aranda da Silva, A., Bett, B.J., Cowie, G.L., Dissard, D., Gage, J.D., Hughes, D.J., Jeffreys, R., Lamont, P.A., Larkin, K.E., Murty, S.J., Schumacher, S., Whitcraft, C., Woulds, C., 2009. Faunal responses to oxygen gradients on the Pakistan margin: A comparison of foraminiferans, macrofauna and megafauna. Deep Sea Research Part II: Topical Studies in Oceanography 56, 488-502.

Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assesment and speculative synthesis. Marine Chemistry 49, 81-115.

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

Josefson, A.B., Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the gullmar-fjord basin. Marine Biology 100, 31-40.

Kamp, A., Witte, U., 2005. Processing of C-13-labelled phytoplankton in a fine-grained sandy-shelf sediment (North Sea): relative importance of different macrofauna species. Marine Ecology-Progress Series 297, 61-70.

Larkin, K.E., Gooday, A.J., 2009. Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300 m water depth in the NE Arabian Sea. Deep Sea Research Part II: Topical Studies in Oceanography 56, 403-421.

LeKieffre, C., Spangenberg, J.E., Mabilleau, G., Escrig, S., Meibom, A., Geslin, E., 2017. Surviving anoxia in marine sediments: The metabolic response of ubiquitous benthic foraminifera (Ammonia tepida). Plos One 12.

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

Levin, L.A., 2003. Oxygen minimum zone benthos: Adaptation and community response to hypoxia. Oceanography and Marine Biology 41, 1-45.

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

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

Levin, L.A., Whitcraft, C.R., Mendoza, G.F., Gonzalez, J.P., Cowie, G., 2009. Oxygen and organic matter thresholds for benthic faunal activity on the Pakistan margin oxygen minimum zone (700-1100 m). Deep Sea Research Part II: Topical Studies in Oceanography 56, 449-471.

Mayer, L.M., 1994. Surface area control of organic carbon accumulation in continental shelf sediments. Geochemica et Cosmochemica Acta 58, 1271-1284.

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos carbon: An in situ ^{13}C-labeling study. Limnology and Oceanography 45, 1224-1234.

Middelburg, J.J., Levin, L.A., 2009. Coastal hypoxia and sediment biogeochemistry. Biogeosciences 6, 1273-1293.

Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M., Heip, C.H.R., 2002. Bacteria and foraminifera: Key players in a short-term deep-sea benthic response to phytodetritus. Marine Ecology Progress Series 236, 23-29.

Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M., Heip, C.H.R., 2005. Similar rapid response to phytodetritus deposition on shallow and deep-sea sediments. Journal of Marine Research 63, 457-469.

Moodley, L., Nigam, R., Ingole, B., Babu, C.P., Panchang, R., Nanajkar, M., Sivadas, S., van Breugel, P., van Ijzerloo, L., Rutgers, R., Heip, C.H.R., Soetaert, K., Middelburg, J.J., 2011. Oxygen minimum seafloor ecological (mal) functioning. Journal of Experimental Marine Biology and Ecology 398, 91-100.

Moodley, L., vanderZwaan, G.J., Herman, P.M.J., Kempers, L., vanBreugel, P., 1997. Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina). Marine Ecology Progress Series 158, 151-163.

Mosch, T., Sommer, S., Dengler, M., Noffke, A., Bohlen, L., Pfannkuche, O., Volker, L., Wallman, K., 2012. Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone. Deep Sea Research Part I 68, 123-135.

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

Naqvi, S.W.A., Naik, H., Pratihary, A.K., Narvenkar, G., Roy, R., Thorat, B.R., Kurian, S., Gauns, M., Narvekar, P.V., 2009. Intensification of seasonal oxygen-deficient zone over the western Indian shelf. Geochimica Et Cosmochimica Acta 73, A930-A930.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005b. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments. Limnology and Oceanography 50, 134-146.

Pozzato, L., van Oevelen, D., Moodley, L., Soetaert, K., Middelburg, J.J., 2013. Carbon processing at the deep-sea floor of the Arabian Sea oxygen minimum zone: A tracer approach. Journal of Sea Research 78, 45-58.

Risgaard-Petersen, N., Langezaal, A.M., Ingvardsen, S., Schmid, M.C., Jetten, M.S.M., Op den Camp, H.J.M., Derksen, J.W.M., Pina-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., van der Zwaan, G.J., 2006. Evidence for complete denitrification in a benthic foraminifer. Nature 443, 93-96.

Sen Gupta, B.K., Machain-Castillo, M.L., 1993. Benthic foraminifera in oxygen-poor habitats. Marine Micropaleontology 20, 183-201.

Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655-658.

Sun, M.Y., 2000. Mass spectrometric characterisation of ^{13}C-labelled lipid tracers and their decomposition products in microcosm sediments. Organic Geochemistry 31, 199-209.

Sun, M.Y., Aller, R.C., Lee, C., Wakeham, S.G., 1999. Enhanced degradation of algal lipids by benthic macrofaunal activity: Effect of Yolida Limatula. Journal of Marine Research 57, 775-804.

Sun, M.Y., Cai, W.J., Joye, S.B., Ding, H., Dai, J., Hollinbaugh, J.T., 2002. Degradation of algal lipids in microcosm sediments with different mixing regimes. Organic Geochemistry 33, 445-459.

Sun, M.Y., Lee, C., Aller, R.C., 1993. Laboratory studies of oxic and anoxic degradation of chlorophyll-a in Long Island Sound sediments. Geochemica et Cosmochemica Acta 57.

Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.L., Gooday, A.J., Jones, D.O.B., Rex, M.A., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Wurzberg, L., Baco, A.R., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.-A., Roberts, M., 2017. Major impacts of climate change on deep-sea benthic ecosystems. Elementa: Science of the Anthropocene 5.

Sweetman, A.K., Witte, U., 2008. Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. Deep-Sea Research Part I-Oceanographic Research Papers 55, 1503-1514.

Thomas, C.J., Blair, N.E., 2002. Transport and digestive alteration of uniformly ^{13}C-labelled diatoms in mudflat sediments. Journal of Marine Research 60, 517-535.

Thornton, B., Zhang, Z.L., Mayes, R.W., Hogberg, M.N., Midwood, A.J., 2011. Can gas chromatography combustion isotope ratio mass spectrometry be used to quantify

organic compound abundance? Rapid Communications in Mass Spectrometry 25, 2433-2438.

van Nugteren, P., Moodley, L., Brummer, G.J., Heip, C.H.R., Herman, P.M.J., Middelburg, J.J., 2009. Seafloor ecosystem functioning: the importance of organic matter priming. Marine Biology 156, 2277-2287.

Witte, U., Aberle, N., Sand, M., Wenzhofer, F., 2003 a. Rapid response of a deep-sea benthic community to POM enrichment: an *in situ* experimental study. Marine Ecology Progress Series 251, 27-36.

Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.-R., Jorgensen, B.B., Pfannkuche, O., 2003 b. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424, 763-766.

Woulds, C., Andersson, J.H., Cowie, G.L., Middelburg, J.J., Levin, L.A., 2009. The short-term fate of organic carbon in marine sediments: Comparing the Pakistan margin to other regions. Deep Sea Research Part II: Topical Studies in Oceanography 56, 393-402.

Woulds, C., Bouillon, S., Cowie, G., Drake, E., Middelburg, J.J., Witte, U., 2016. Patterns of carbon processing at the seafloor: the role of faunal and microbial communities in moderating carbon flows. Biogeosciences 13, 1-15.

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

Woulds, C., Middelburg, J.J., Cowie, G.L., 2014. Alteration of organic matter during infaunal polychaete gut passage and links to sediment organic geochemistry. Part II: Fatty acids and aldoses. Geochimica Et Cosmochimica Acta 136, 38-59.

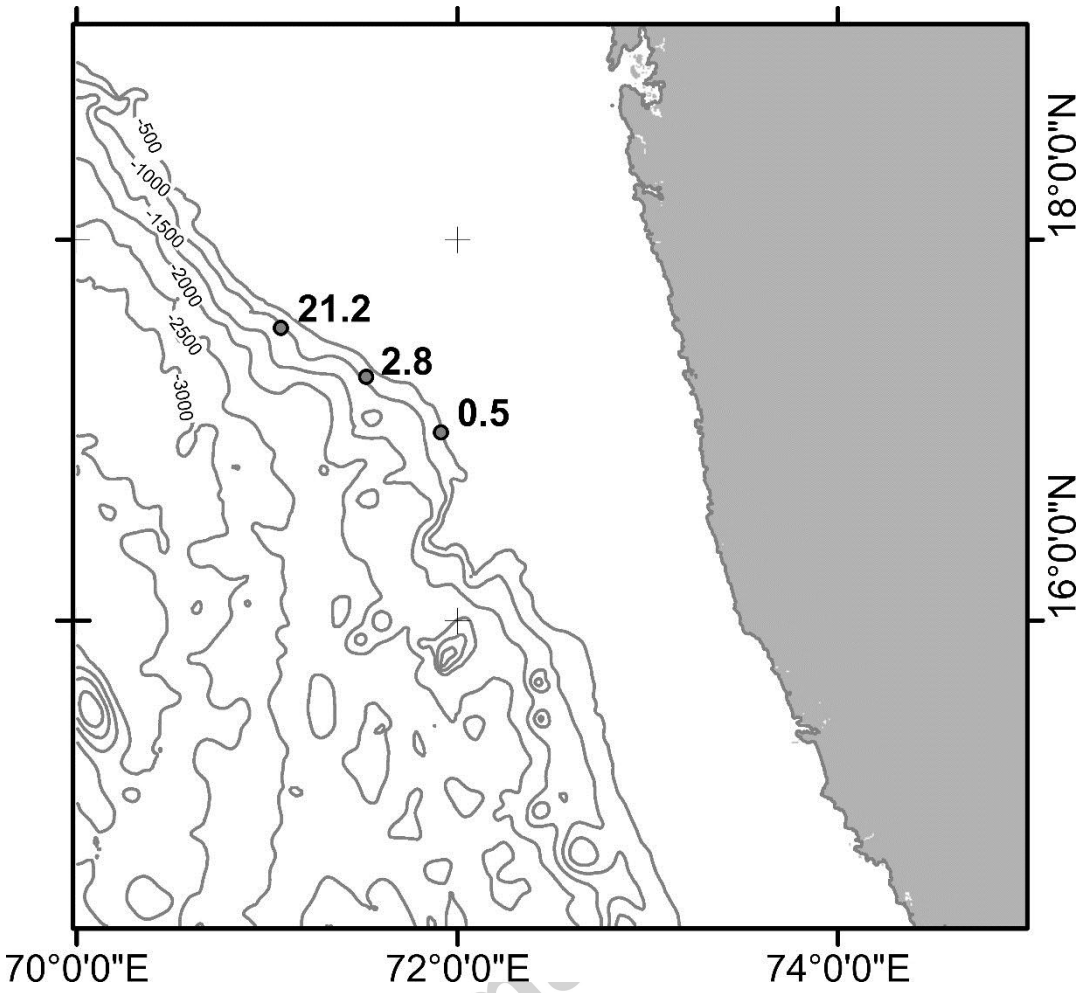


Fig 1. A bathymetric map of the Indian margin of the Arabian Sea showing the location of the sample sites as multiple red diamonds.

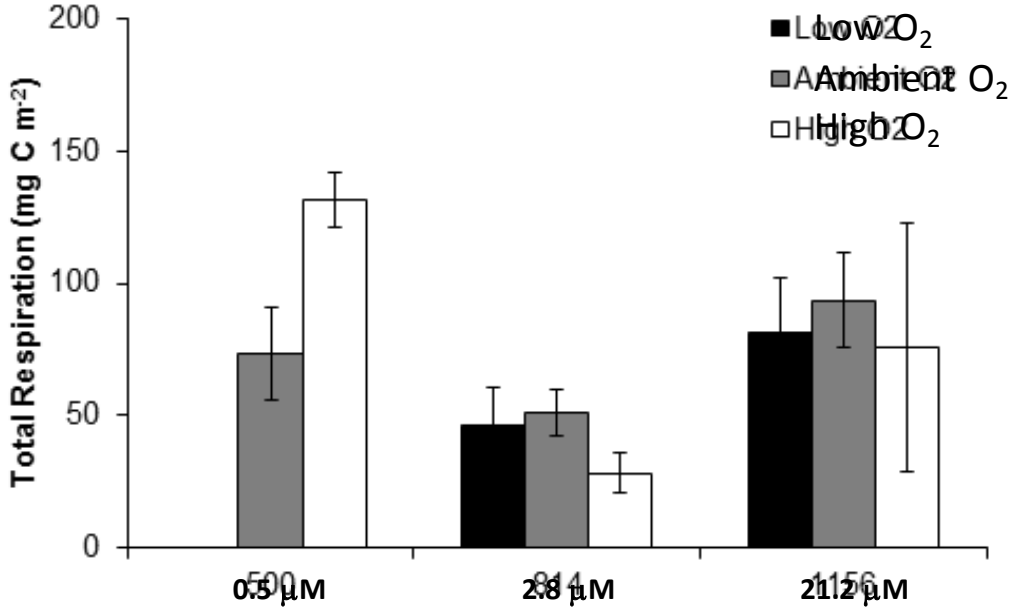


Fig 2. Total respiration of added C during each experiment.

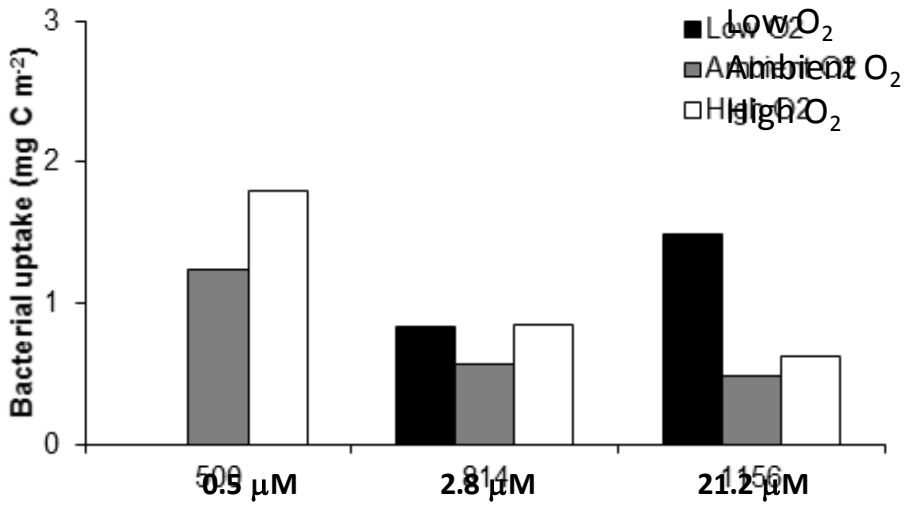


Fig 3. Bacterial uptake at all sites and in all treatments.

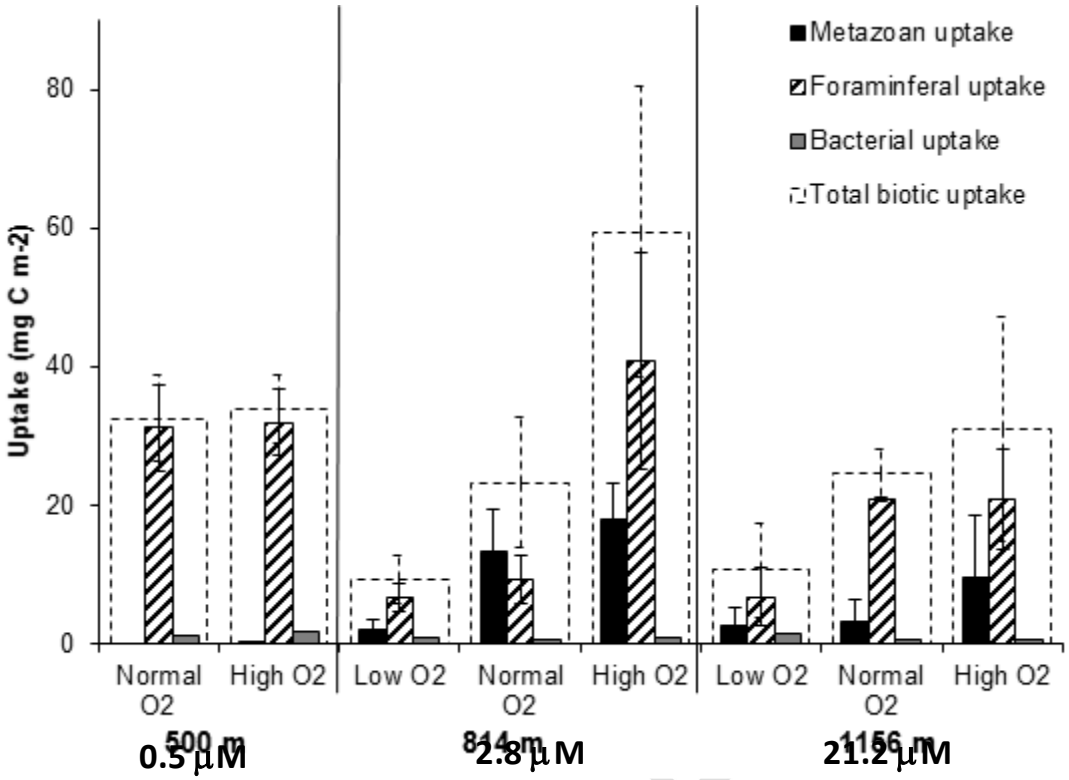
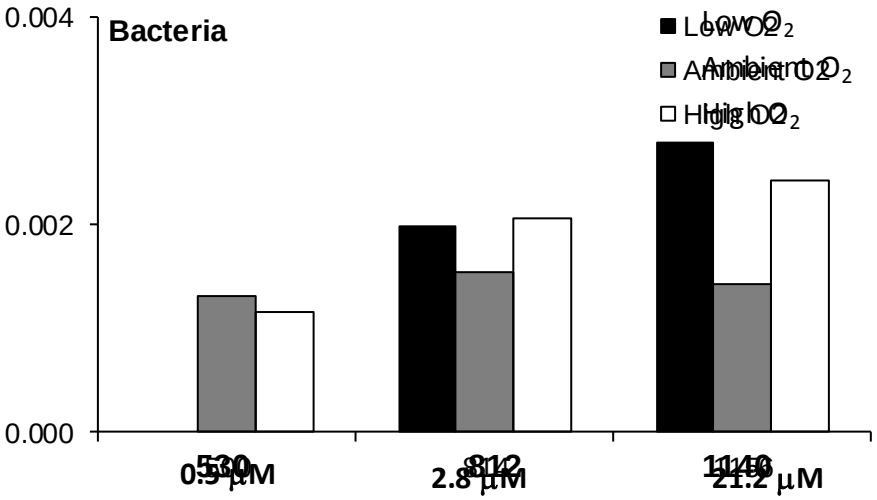
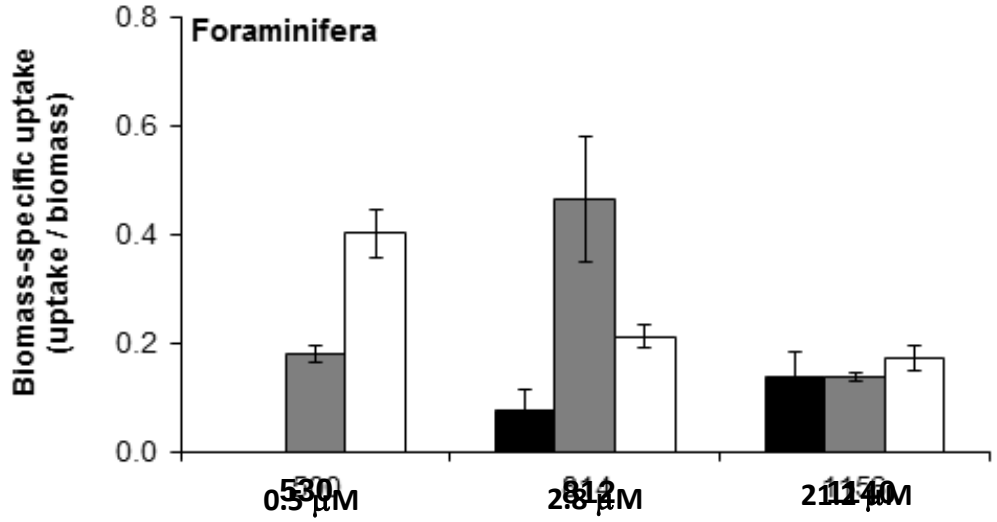


Fig 4. Uptake of added C into biomass at different sites and in different treatments.



A



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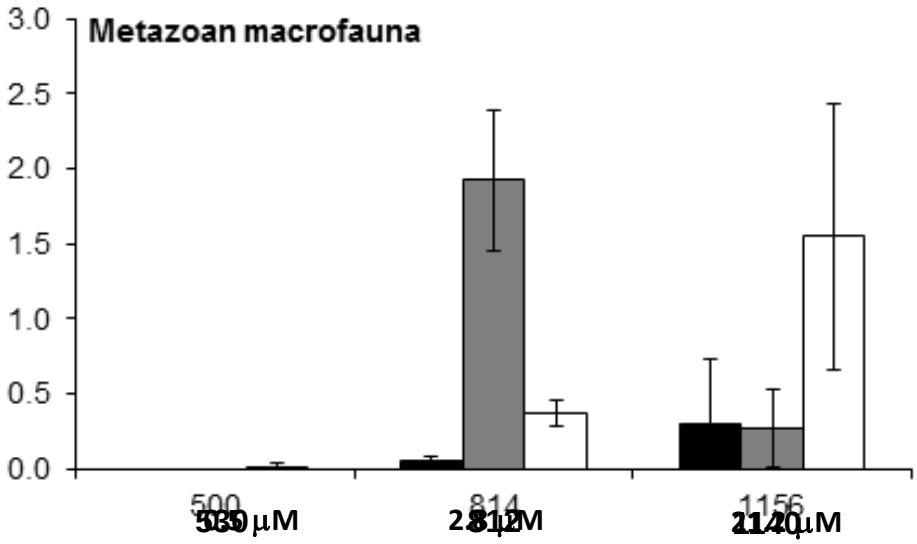

C

Fig 5. Biomass specific uptake by a) bacteria; b) foraminifera, and c) metazoan macrofauna in response to oxygen manipulation.

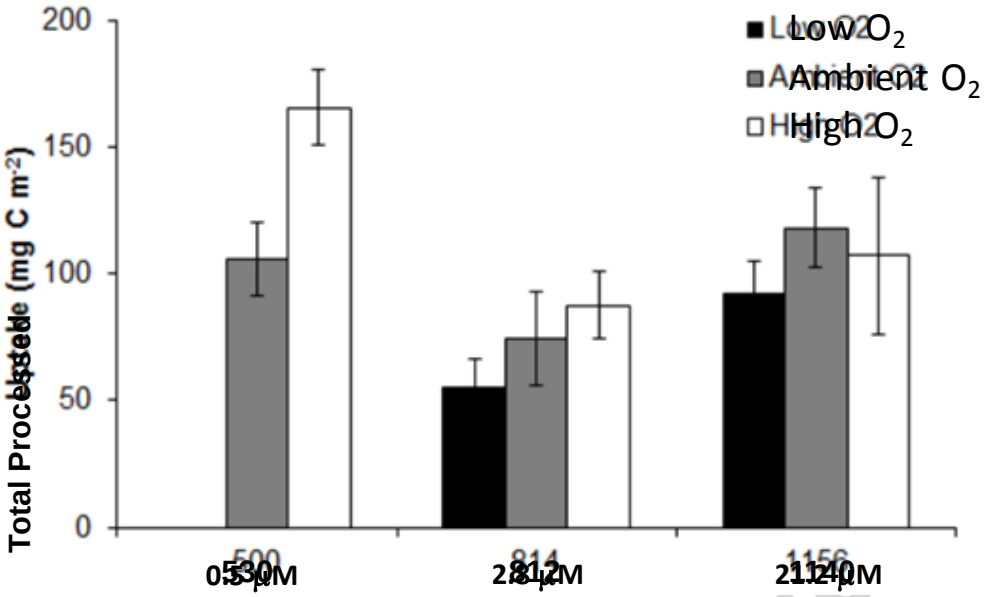

Fig 6. Total amount of added C processed by the benthic community (sum of respiration, bacterial uptake, and faunal uptake).

Table 1. Site depths, locations, and conditions, after Cowie et al. (2014). Biomass values are for the surface 1 cm, and are averaged across treatments.

Site DO (µM)	Lat. N	Long. E	Depth (m)	$\%C_{org}$	Temperature (°C)	Metazoan biomass (mg C m^{-2})	Foraminiferal biomass (mg C m^{-2})	Bacterial biomass (mg C m^{-2})
0.5	16.9804°	71.9217°	530	6.9	12.3	3.5±4.9	181±41	1241±428
2.8	17.5249°	71°1704°	812	4.3	10	26.0±18.1	79.6±19.2	401±27
21.2	17.5275°	71.0806°	1140	4.6	7	6.8±2.8	106±53	375±143

Table 2. Total amounts of added C subject to each biological process over the duration of the experiments. Values given are means from 2 replicates, ± standard deviation.

Site	Treatment	Total respiration (mg C m^{-2})	Bacterial uptake (mg C m^{-2})	Metazoan macrofaunal uptake (mg C m^{-2})	Foraminiferal uptake (mg C m^{-2})	Total (mg C m^{-2})
0.5 µM	Normal DO	73.6 (±17.6)	1.24	-	31.2 (±6.2)	106 ± 14
	High DO	131.4 (±10.1)	1.80	0.1 (±0.2)	31.9 (±4.8)	165 ± 15
2.8 µM	Normal DO	51.0 (±8.9)	0.57	13.4 (±5.9)	9.2 (±3.5)	74 ± 18
	Low DO	46.2 (±14.5)	0.83	1.9 (±1.5)	6.6 (±2.0)	56 ± 11
	High DO	28.3 (±7.8)	0.85	17.9 (±5.3)	40.7 (±15.6)	88 ± 13
1140 m	Normal DO	93.5 (±17.8)	0.48	3.1 (±3.4)	20.9 (±1.3)	118 ± 16
	Low DO	81.1 (±20.9)	1.49	2.5 (±3.6)	6.7 (±4.2)	92 ± 13
	High DO	76.1 (±47.0)	0.62	9.6 (±8.9)	20.8 (±7.3)	107 ± 31