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A multiproxy approach to understanding the “enhanced” flux of organic matter through the oxygen deficient waters of the Arabian Sea

R. G. Keil, J. Neibauer, C. Biladeau, K. van der Elst, and A. H. Devol

School of Oceanography, Box 355351, University of Washington, Seattle, Washington 98195, USA

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Correspondence to: R. G. Keil (rickkeil@uw.edu)

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Abstract

Free-drifting sediment net traps were deployed 14 times at depths between 80 and 500 m for 1–3 days each during the late monsoon/intermonsoon transition in the central Arabian Sea. Two locations (19.5 and 15.5° N) were within the permanently oxygen deficient zone, and a third (11° N) had a shallow and thin oxygen minimum. The secondary nitrite maximum, which serves as a tracer of the oxygen deficient zone (ODZ) zone, thinned from ~ 250 m thick at stations 19.5 and 15.5° N to ~ 50 m thick at station 11° N. Overall, organic carbon fluxes ranged from 13.2 gm²yr⁻¹ at 80 m to a minimum of 1.1 gm²yr⁻¹ at 500 m. Fluxes at the more oxygenated 11° N station attenuate faster than within the permanent ODZ. Martin curve attenuation coefficients for 19.5 and 15.5° N are 0.59 and 0.63 and for 11° N it is 0.98. At least six potential mechanisms might explain why sinking particles sinking through the ODZ are more effectively transferred to depth; (M1) oxygen effects, (M2) microbial loop efficiencies and chemoautotrophy, (M3) changes in zooplankton dynamics, (M4) additions of ballast that might sorb and protect organic matter from decay, (M5) inputs of refractory organic matter, and (M6) changes in sinking speeds. These mechanisms are intertwined, and were explored using a combination of mineral (XPS) and organic matter characterizations of the sinking material and ship-board incubation experiments. Evidence was found supporting an oxygen effect and/or changes in the efficiency of the microbial loop including the addition of chemoautotrophic carbon to the sinking flux in the upper 500 m. Less evidence was found for the other potential mechanisms. A simple conceptual model consistent with our and other recent data suggests that the upper ODZ microbial community determines the initial flux attenuation, and that deeper in the water column zooplankton and sinking speed become more important. The exact interplay between the various mechanisms remains to be further evaluated.

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1 Introduction

Sinking particles are an important component of the biological pump. Once below the euphotic zone, organic matter and nutrients in sinking particles are removed from the biogeochemical processes of the upper ocean; the time scale of this sequestration depending on the depth to which the material sinks or is remineralized (Buesseler and Boyd, 2009). For sediment trap data, this is typically quantitated using either a power decay function (Martin et al., 1987) or by relating organic matter fluxes to ballast mineral flux (Armstrong et al., 2002). Using either approach, the decay function within Oxygen Deficient Zones (ODZ; waters with zero or unmeasurable oxygen; Jensen et al., 2011) is different – less decay – from that of the oxic portions of the ocean (Hartnett and Devol, 2003; Roullier et al., 2014; Van Mooy et al., 2002). That is, the flux of organic matter through ODZs is proportionally higher than that for oxic waters. There are many possible reasons for this, and currently they are poorly evaluated.

Potential mechanisms (M) that might cause organic carbon fluxes through ODZ waters to be less attenuated include those that are directly related to ODZs themselves; (M1) the possibility that anoxic degradation is sufficiently slower or less comprehensive relative to oxic carbon remineralization, (M2) the possibility that the microbial consortia in ODZ regions have a higher growth efficiency and incorporate chemoautotrophy might add carbon to the flux, and (M3) zooplankton dynamics in ODZ regions might alter the flux attenuation in a variety of ways.

Mechanisms that are not necessarily specific to ODZ regions, but might simply be coincident, include (M4) mineral protection where differences in bio and lithogenic mineral inputs control the remineralization profile of sinking organic matter in the ocean, (M5) inputs of recalcitrant organic matter could alter the flux attenuation, and (M6) changes in the sinking speed of particles. Sinking speed impacts attenuation because higher sinking speeds move particles deeper per unit time. Each of these potential mechanisms for enhanced flux through ODZ regions has merit, and are briefly introduced below.

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While the long-term (decade to millennia) importance of (M1) oxygen effects on organic matter preservation are well established (Arnarson and Keil, 2007; Hedges and Keil, 1995), the importance of oxygen over short time periods or during early diagenesis has been an extremely hard issue to address (Cowie and Hedges, 1992b). There seems to be an effect; Harnett et al. (1998) suggested that the diminished oxygen exposure of ODZ sinking particles increases the efficiency with which they are transferred to deeper waters, and Van Mooy et al. (2002) observed direct oxygen effects in incubations of ODZ water from the Eastern Tropical North Pacific.

The microbial loop within an ODZ can influence the flux in a number of ways. If the community grows with a higher growth efficiency than oxic communities (M2a), then ODZ communities could more biomass per unit respiration. For example, if a dark aerobic community has a growth efficiency of 10 % and a suboxic ODZ community has a growth efficiency of 20 %, then for every unit respiration twice as much new biomass will result, and this will manifest itself as a change in the attenuation coefficient. This concept has been loosely explored by W. Naqvi (personal communication, 2014). The long held assumption that heterotrophic respiration is the only significant biogeochemical process in the mesopelagic has been overturned by the discovery of abundant chemoautotrophic microorganisms (Dalsgaard et al., 2003; Kuypers et al., 2003). Thus, a subcomponent of M2 could be the (M2b) chemoautotrophic production of new organic matter in ODZs, which if it sinks would add to the flux (Close et al., 2014; Roland et al., 2008).

Zooplankton dynamics within the ODZ are complex and could alter the sinking flux in a variety of ways. When they migrate into the ODZ, they (M3a) deliver dissolved nutrients supporting chemoautotrophy and (M3b) create pulses of defecated material that is not subject to remineralization in shallower waters (Cavan et al., 2015). Both these thing would enhance the flux. However, the ODZ is a harsh environment for a eukaryotic obligate aerobe, and if the ODZ hosts fewer zooplankton than an aerobic water column (Levin et al., 2015; Wishner et al., 2013) then it is logical to hypothesize

that (M3c) the overall effect of zooplankton respiration will be less, which might in-and-of itself be enough to result in enhanced fluxes through the upper watercolumn.

Minerals are a strong determinant on organic matter burial in sediments (Keil and Cowie, 1999; Keil et al., 1997). How this impact is felt in the water column remains largely unconstrained. Inorganic material acts as a catalyst for particle formation, altering the flux of organic carbon (Lee et al., 2009). A possible mechanism linking mineral and enhanced flux would be that minerals can provide abundant points of interaction with organic matter, promoting aggregation and sorption (e.g., Passow and De La Rocha, 2006). (M4) Organic-mineral interactions might then protect the organic matter from remineralization, at least on the short time scale of sinking particles (Arnarson and Keil, 2005). Overall organic carbon export might be enhanced both by increasing sinking rates and slowing degradation. Whether this mechanism could explain ODZ enhanced fluxes has not been explored.

Lithogenic minerals might also impact sinking carbon by (M5) bringing refractory terrestrial organic matter with them (Burdige, 2005; Keil et al., 2004). To date, analyses of terrestrial carbon in sinking fluxes has largely been constrained to oxic water columns very close to land where the inputs are significant (Hedges et al., 1988).

Finally, another potential factor linking carbon fluxes and mineral material is (M6) sinking speed. In both the Martin equation and the ballast model, sinking speed and remineralization rate combine to control the flux. If for some reason, ODZ regions have particles with enhanced sinking speeds, then lower attenuation per unit depth would result. Changes in sinking speed could result from changes in species composition or from changes in dust inputs, or the efficiency with which zooplankton and other community members package material into sinking particles (Cavan et al., 2015).

We evaluated these possible mechanisms using a combination of sediment trap and incubation studies, and by evaluating for a variety of mineral and organic markers. Mineral components were evaluated for their surface area and surface-associated elemental compounds (using X-ray photoelectron spectroscopy). Organic matter was evaluated for its quantity and bulk ^{13}C and ^{15}N isotopic composition, and total amino

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and tethered to the surface using polydac line, a string of surface floats, and a surface spar with radio transmitter and light beacon. The net traps were deployed open, and then closed using the messenger immediately prior to recovery. Each trap sample was analysed in duplicate.

Four additional samples were collected at depths > 1000 m by deploying the net traps as vertical nets and raising them through a prescribed portion of the water column at 2 m min⁻¹ before closing the nets using messengers (Table 1). These samples were not used to evaluate fluxes but were analysed for their organic components.

The 500 mL–2 L samples from sediment trap collection cups were transferred to polypropylene bottles, frozen and transported to the lab at the University of Washington. No poisons were used. In the lab samples were thawed, spun at 15 000 × *g* in ~ 200 mL aliquots and the resultant pellets were separated from the liquid, weighed wet, freeze dried, and weighed again. After a small salt correction the dry weight was used to calculate the mass flux.

2.2 Elemental, XPS, amino acid and lignin analyses

Elemental analyses for carbon, nitrogen quantities and ¹³C and ¹⁵N isotopic compositions were carried out at the U.C. Davis Stable Isotope Facility (<http://stableisotopefacility.ucdavis.edu>) on both raw and acidified samples. Acidification was achieved via direct application of 1 M HCl using the technique described in Kennedy et al. (2005).

XPS surface characterizations were done at the University of Washington's Surface Analysis Recharge Center (<http://www.nb.engr.washington.edu/content/surface-analysis-recharge-center-sarc>) with Surface Science Instruments (SSI) S- and M-probes as described in Arnarson and Keil (2001). Analyses were made in duplicate with an average spot size of ~ 200 μm and a theoretical average scanning depth into the sample matrix of ~ 20 nm. The measured atom percent of each detected element was multiplied by its molecular weight and then weight percentages were calculated. We assume that hydrogen has a negligible contribution on a weight basis (hydrogen is

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the only element that the XPS cannot see; the detection limits for most other elements are ~ 1 atom percent; Arnarson and Keil, 2001).

Amino acids were liberated via acid digestion (Cowie and Hedges, 1992a) and quantified by liquid chromatography – triple quadruple mass spectrometry using an isotope pairing technique similar to that of Piraud et al. (2005). Briefly, samples were hydrolysed in 6 M HCl via programmed microwave assistance in a MARS 5 microwave system (CEM Corp), brought to dryness in a CentriVap system (LabConCo), resuspended in MilliQ water and filtered through a 13 mm 0.2 µm nylon membrane (Acrodisc, PALL Life Sciences). Isotopically-labeled amino acids (Cambridge Isotopes) were then added. Samples were run on an Agilent Poroshell 120 SB-C18 column (100 mm) with solvents of (a) Milli-Q containing 0.05 % Heptafluorobutyric acid (*v/v*) and (b) acetonitrile containing 0.05 % Heptafluorobutyric acid (*v/v*). A six-point standard curve plus blanks was run each day, and the NIST Amino Acid standard mixture with added isotopically labelled amino acids was run with every set of samples (e.g. every day) as a test the accuracy of the LCMS. The multiple reaction monitoring parameters used for identification are shown in Supplement Table S1.

Lignin phenols were analyzed by microwave-assisted cupric oxide oxidation (Goni and Montgomery, 2000) followed by trimethylsilyl derivatization and capillary gas chromatography – mass spectrometry (Keil et al., 2011). Yields of cinnamyl “C”, syringyl “S” and vanillyl “V” phenols were used to evaluate vascular plant sources of the sedimentary organic bulk mixture. These phenol yields are conventionally represented as lambda (Λ8; mg per 100 mg of organic carbon) and Σ8 (the sum of the eight major phenols normalized to 10 g of bulk sample).

2.3 Targeted peptidomics

Peptides specifically diagnostic to proteins of interest were identified using a targeted peptidomics approach (Bertrand et al., 2013). Briefly, peptides were extracted as per Bridoux et al. (2015) where samples were suspended in a lysis buffer (7 M urea, 2 M thiourea, carrier ampholytes (2% *v/v*, pH 3–10), dithiothreitol (DTT, 1% *w/v*), and

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Total carbon on the surfaces of the particles, as measured by XPS, is highest (60–72 atom percent) in the 80 m samples and decreases to ~ 50 % in the particles collected deeper (Fig. 4a). The only other elements detected by XPS were oxygen, silicon, calcium and nitrogen. As opposed to carbon, the proportions of oxygen, silicon and calcium are enriched with depth (Fig. 4b–d). Combining the bulk elemental data with that collected by XPS allows for evaluation of the organic carbon “placement” within the sinking particles via the $OC_{\text{on the surface}} : OC_{\text{bulk}}$ ratio (Arnarson and Keil, 2001). Values of this ratio are between 2–3 in the surface waters and rise to 4–6 with depth (Fig. 4e). The ratio is higher for the deeper samples at station 3 than at the other two stations (Fig. 4).

Using the Redfield ratio for organic matter, as modified by Hedges et al. (2002), the amount of inorganic mass was calculated as the difference between the mass flux and the total organic matter flux (Table 1). Settling particles range from 55–84 % inorganic matter. The inorganic matter flux ranges from 9–39 $g\ m^{-2}\ yr^{-1}$ and decreases with depth (Fig. 2a). Station 2 has the largest inorganic mass flux, coincident with the highest chlorophyll levels.

Amino acid abundances and compositions change as a function of depth, but show little variation with station (Fig. 5). The mole percent non-protein amino acids, which is an indicator of the diagenetic state of the amino acid pool (Cowie and Hedges, 1994), are less than 1 at the surface and less than 3 in the deeper samples (Fig. 5a). The amino acid degradation index (DI), as calculated using the formulation of Dauwe and Middelburg (1999), ranges from 0.25–1.0 and represents relatively “fresh” organic matter (Table A4). At stations 2 and 3 the DI decreases with depth (Fig. 5b).

For the sediment trap samples, the CuOxide yield of lignin phenols is $< 2\ mg\ g\ dw^{-1}$ (Table A5) and is less at the deeper samples relative to the 80 m samples (Fig. 5c). When normalized to the total amount of organic carbon present, there is an enhancement of lignin at station 1 relative to the other two stations (Fig. 5d). There was not enough sample material in the deep net tows for lignin analyses.

The attenuation coefficients for the ODZ regions averaged 0.59 ± 0.24 whereas the oxygenated values averaged 0.89 ± 0.06 . The authors did not focus on the causes of this regional variability.

In the ETNP, Van Mooy et al. (2002) observed low particle attenuation in ODZ at a station north of Martin's and calculated an attenuation coefficient of 0.40. Using benthic lander data, flux attenuation along the Washington and Mexican margins are thought to differ, with the ODZ waters off Mexico having an average attenuation coefficient of 0.36 while the oxic Washington margin has an attenuation coefficient of 0.93 (Devol et al., 1995; Devol and Hartnett, 2001; Hartnett and Devol, 2003).

In the ETSP, systematic evaluations beyond the single Martin evaluation (1987) are few. Levin et al. (2002) evaluated benthic system ecology and energy flow at 30° S over a two-year period and suggested that oxygenation events were strongly associated with more carbon remineralization of the sinking flux (which they did not directly evaluate). That is, they found indirect evidence that the attenuation parameter was higher under the more oxic conditions. Using benthic data in a manner similar to that of Devol and Hartnett (2002), Dale et al. (2015) suggested that the attenuation in the ETSP was only slightly attenuated (Martin coefficient of 0.54) and that the impact on the sediment was greater than that in the water column. Deep sediment traps show variation suggestive of changes in fluxes of lithogenic material (Hebbeln et al., 2000; Marchant et al., 2004) but the data are not complete enough to evaluate attenuation.

In the Arabian Sea there is much flux data. Along the western margin, (Lee et al., 1998) combined sediment trap, primary production and ^{234}Th data to evaluate particle fluxes. They did not fit their data to a Martin curve, but all the information needed is available. Their attenuation values range from 0.10 to 0.49 within in the ODZ and was 0.96 at their oxygenated 10° N site. Roullier et al. (2014) used a visual profiler to evaluate sinking particles and calculated an attenuation coefficient of 0.22, suggesting little attenuation within the ODZ. Similar results have been observed in many other studies and for a variety of specific organic compounds (e.g. Haake et al., 1992). Our data are in accord; the attenuation of the organic matter flux (e.g. Fig. 2) is different

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between the three stations, with the one that is most oxic and furthest south (station 3) having the most attenuated flux.

Thus it appears to be a truism that ODZ regions “allow” proportionally more organic material to transit to the deep sea relative to oxygenated systems. The mechanisms that might cause this remain poorly evaluated and potentially include many different components, such as (M1) the possibility that anoxic degradation is sufficiently slower or less comprehensive relative to oxic carbon remineralization (Van Mooy et al., 2002), (M2) chemoautotrophy and a highly efficient microbial loop within the ODZ might add carbon to the flux (Close et al., 2014; Roullier et al., 2014), (M3) zooplankton migration into ODZ regions might enhance chemoautotrophy by providing dissolved nutrients, might result in defecation and “enhanced” fluxes within the upper ODZ (Wishner et al., 2013) or might reduce remineralization if populations sizes are small, (M4) mineral protection where differences in bio and lithogenic mineral inputs control the remineralization profile of sinking organic matter in the ocean (Arnarson and Keil, 2005; Howard et al., 2006), (M5) terrestrial inputs of recalcitrant organic carbon (Goni et al., 2009), and (M6) changes in the sinking speed of sinking particles, where sinking speed and remineralization rate both control the apparent attenuation through the water column and where changes in sinking speed can be driven by a variety of processes (Berelson, 2002; Roullier et al., 2014).

Although our data set cannot directly evaluate each of these potential mechanisms, the multiple proxy approach we employed, combined with our ship-board incubation experiments, can be used to develop a heuristic model of the particle flux in the Arabian Sea ODZ.

4.1 M1: Carbon remineralization in ODZ regions is relatively ineffectual

In sediments there is a well-established “oxygen effect” where organic carbon remineralization is more extensive under oxic rather than reducing conditions, especially over time scales of months to millennia (Arnarson and Keil, 2007; Cowie et al., 1995; Hedges et al., 1999). Little is known, however, about how effective this mechanism is

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over short time periods or for organic material in the water column. Hartnett et al. (1998) invoked an oxygen effect to explain consistencies between sediments and sinking particles, but others including Lee (1992) have found little or no direct evidence of such an effect over time periods of days. A particle with a sinking speed between 10–300 m d⁻¹ (Riley et al., 2012) will spend 1–50 days in a typical ODZ, suggesting that for this mechanism to be important, it must operate over relatively short time periods. Our data allow evaluation of this hypothesis via incubation experiments conducted at different oxygen concentrations, and by evaluating proxies that might suggest an oxygen effect in samples collected by the net traps.

The deck-board incubation studies (Fig. 7) strongly suggest an oxygen effect, with a threshold of about 20 μM under our conditions. This is consistent with previous work of Ploug et al. (2001, 2008) who suggested that microbial communities on sinking particles would begin switching from aerobic to anaerobic respiratory pathways at approximately these same concentrations. The detection of an “oxygen effect” in the incubations is suggestive, but given that particles and associated microbial communities were concentrated and subjected to abrupt changes in oxygen tension prior to beginning the experiments, these types of incubation studies need to be taken with a grain of salt. If the results are to be generalized to the sinking particles under more native conditions, either experiments need to be conducted under more realistic conditions, or geochemical measurements that allow evaluation of an oxygen effect need to be evaluated on the sinking particles themselves.

Two amino acid indicators are commonly used in sediments to evaluate degradation; the mole percentage of non-protein amino acids (higher = more degraded) and the Dauwe-Middelburg index (Dauwe et al., 1999) (lower = more degraded). When measured on the sinking particles, both these indicators suggest a difference between the ODZ stations and the more oxygenated station 3 where the sinking particles at station 3 have undergone more extensive degradation (Fig. 5).

Another possible hint to an oxygen effect is the attenuation of the histone protein marker in the samples. Histones are insoluble alkaline proteins that package DNA into

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structural units (nucleosomes) (Kornberg, 1974). Histones are found only in eukaryote nuclei, not in bacteria or archaea. We targeted the general diatom histone H4, which may be a good tracer for the transfer of diatom protein to the ocean interior. If there is an oxygen effect, we'd expect histones traveling through the ODZ be less effectively degraded relative to the oxic station 3, but we do not observe this. Instead, our histone values show no discerning trends with depth or oxygen content, suggesting that for these proteins there is no clear oxygen effect. Thus the targeted peptidomics data are inconsistent with the overall total amino acid data, suggesting that histones do not degrade in the same way the bulk amino acid pool does. How these different measures relate and whether one is a better marker for a degradative effect remains unknown.

Finally, measuring the amount of carbon on mineral surfaces relative to the total organic carbon content of a sample can be a useful tool for evaluating the relative “degradative state” of organic matter in sediments (Arnarson and Keil, 2001; Arnarson and Keil, 2007). Fresh particles are typically rich in organic matter (low $C_{\text{surf}} : C_{\text{bulk}}$) whereas particles that have undergone degradation usually have their remaining carbon associated with mineral surfaces (high $C_{\text{surf}} : C_{\text{bulk}}$). Extending this concept to the sinking particles, if an oxygen effect is the dominant reason for enhance fluxes, we might expect the ODZ particles to have lower $C_{\text{surf}} : C_{\text{bulk}}$ ratios relative to the more oxic samples (Fig. 4e). Indeed, we observe that $C_{\text{surf}} : C_{\text{bulk}}$ values at station 3 are higher than for the two ODZ stations.

Thus, the majority of indicators we measured are at least partially consistent with an oxygen effect, but the evidence to date is somewhat circumstantial and certainly not definitive. It is known that addition of fresh organic matter to incubations stimulates denitrification (Babbin et al., 2014; Chang et al., 2014), suggesting that denitrification is responsive to additions of carbon, but what is not known is whether in situ denitrification rates would match those of aerobic respiration under similar conditions.

4.2 M2: Community growth efficiency and chemoautotrophy

Because ODZ regions host a wide range of chemoautotrophic organisms, there is the possibility that chemoautotrophy adds carbon to the sinking flux (Close et al., 2014). This has been termed “substrate injection”, and if this is common in the Arabian Sea ODZ there should be bulk isotopic and biomarker measurements supporting this added material. Of the things we measured, the bulk stable ^{13}C isotopic composition of the sinking material might be the best indicator of chemoautotrophy. Lipids from ODZ chemoautotrophic organisms can be isotopically enriched (Close et al., 2014) suggesting that the bulk material, if it contains significant chemoautotrophic-derived carbon, might be similarly enriched. Our data (Fig. 3) show enrichment of the ^{13}C of the bulk sinking material at station 2 relative to station 3. This indicates that the sinking particles may contain a significant chemoautotrophic input. Because the endmember isotopic values are not known, a mixing model of euphotic zone and ODZ sources cannot be made. None-the-less, the observation that the ODZ compositions are all enriched relative to the samples from Station 3 suggest measurable inputs of material produced within the ODZ.

What material might this be? Quantifications of peptides associated with the chemoautotrophic process anammox suggest that anammox proteins are present but do not contribute substantially to the sinking flux (Fig. 6). The two anammox peptide biomarkers were rarely detected (< 50 % of the samples contained measurable amounts of the markers) and their abundance per unit mass was only 1–20 % of that N_2O reductase, the peptide marker for the heterotrophic denitrification. We interpret this as evidence that heterotrophic proteins responsible for denitrification dominate in particles over chemoautotrophic processes that also result in the formation of nitrogen gas. This is consistent with the work of Fuchsman et al. (2011, 2012) who suggested that anammox is primarily a water column process (free-living bacteria), and also consistent with other work conducted during our cruise suggesting a dominance of denitrification over anammox at the time of our sampling (Ward et al., 2009).

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How do we reconcile two biomarkers that appear to advocate opposite interpretations? The observations are not necessarily at odds. As early as 1994 Azam et al. (1994) proposed a complex microbial loop within the Arabian Sea ODZ comprising of active free-living and particle-attached bacteria working together to effectively transfer material between the dissolved, suspended and sinking pools. Close et al. (2014) suggested a similar thing based on their lipid data, and Roullier et al. (2014) suggested that the attenuated flux in the Arabian Sea was partly the result of an efficient microbial loop that effectively reconstituted and utilized the energy of the sinking flux. This is a compelling hypothesis that requires further research. What are the growth efficiencies of heterotrophic communities in oxygenated waters relative to those of the heterotrophic-autotrophic community in an ODZ? If the ODZ community growth with less respiratory loss, this might account for the appearance of chemoautotrophic carbon in the sinking particles and might also be the mechanism leading to the “enhanced flux”.

It is worth noting that the (M1) Oxygen Effect and (M2) Efficiencies and Chemoautotrophy mechanisms are not easily dissected and discerned from each other. For example, since the ship-board incubations measured the accumulation of DIC, a change in the growth efficiency of the microbial community as a function of oxygen content would result in the same observation (less DIC accumulation) as a true oxygen effect would. Similarly, since we did not develop a peptide marker for aerobic respiration, we cannot compare the abundance of the denitrification peptide marker against an oxic counterpart. Thus we cannot say whether there is relatively less protein associated with denitrification in the ODZ relative to aerobic respiratory proteins in the oxygenated waters.

Our bacterial ABC transporter protein data provide clues pertinent to this issue. ABC transporter proteins are ATP-requiring enzymes used to transport compounds across membranes. They are among the most commonly detected proteins in the ocean (Tanoue et al., 1995; Wang et al., 2011) and are critical for the heterotrophic function of acquiring organic compounds from the environment. Thus, they are a good

marker for heterotrophic processing. The ATP transporter peptide we evaluated was quite abundant at all stations (150–250 fg mgdw⁻¹) but in general there was more of this peptide at the oxic station 3 relative to the two stations within the ODZ (Fig. 6). This is suggestive that oxic station 3 might have more active heterotrophic communities on the particles than at the ODZ sites (though concentrations do not equate directly to rates). Thus, the ABC transporter protein data are consistent with more heterotrophy at station 3, but they do not preclude an efficient microbial loop at the ODZ stations, where energy transfer can be achieved using solutes such as nitrite and ammonium (e.g. the anammox process) that do not require ABC transporters. Thus, both the (M1) Oxygen Effect and (M2) Chemoautotrophy mechanisms are viable given our data.

4.3 M3: Zooplankton

One of the more intriguing mechanisms that might influence the flux is the presence and activity of zooplankton. Their actions may alter the flux in a variety of ways. Migration into the ODZ followed by subsequent defecation might result in deliver of packaged particles that sink without having to pass the upper portions of the ODZ where remineralization is fastest (Cavan et al., 2015; Wishner et al., 2013). Arguments against this are two-fold; if it occurs within the ODZ it should also occur within oxic water columns (e.g. Cavan et al., 2015), and the abundance of zooplankton in ODZ waters is generally lower than that within oxygenated water thus suggesting that the effect might be smaller not larger. Countering these criticisms is the possibility is that in addition to providing fecal material, zooplankton deliver dissolved materials (ammonium) that can promote chemoautotrophy (anammox), thus indirectly leading to “enhanced” fluxes. Our data set is very limited in its ability to address the role of zooplankton. Even though many sediment traps were deployed, our vertical resolution is too low to evaluate whether there is a “spike” in the flux at the depth that the zooplankton migrate to. We also have no zooplankton-specific biomarker to help evaluate whether their fecal material is a more important component of the sinking flux within the ODZ.

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In a recent study, Roullier et al. (2014) used an underwater vision profiler (UVP) to collect high resolution data of the particle flux within the Arabian Sea ODZ. They observed increases in the sinking flux that were associated with zooplankton assemblages living at the deeper boundaries of the ODZ, and suggest that zooplankton-derived injections of sinking particles are an important component controlling the deep flux. This data was collected deeper than our sediment traps and thus while their data clearly support a zooplankton contribution to the issue, they do not help explain why we (and others) observe attenuated fluxes above the zone where the zooplankton aggregated, within the heart of the ODZ.

4.4 M4: Mineral protection

Similarly to an oxygen effect, there is abundant evidence that mineral protection is an important mechanism promoting organic matter survival and burial in long-term sediment records (Keil and Mayer, 2014; Kennedy and Wagner, 2011; Mayer, 1994). A variety of experimental approaches have also shown mineral protection occurs for some fresh material sorbed to mineral surfaces (for example; Arnarson and Keil, 2005; Le Moigne et al., 2013). In the water column, a mineral protection mechanism would rely either on biominerals created by plankton, or the delivery of lithogenic minerals from land. Aeolian dusts from Africa deliver mineral (and pollutants; Dachs et al., 1999) to the Arabian Sea where they are thought to sensitively influence the dynamics of sinking particles (Barkmann et al., 2010). We evaluated the potential effects of dust inputs by adding dust to shipboard incubations at a variety of oxygen contents (Fig. 7) and observed immediate reduction in DIC accumulation rates. This suggests that aeolian sources of mineral to the Arabian Sea ODZ may directly influence the rate at which organic matter is remineralized, thus enhancing the flux. Our experiments were conducted by adding large quantities of dust ($\sim 4\times$ greater) relative to the maximal seasonal input (Barkmann et al., 2010), suggesting that we may have observed the maximal effect.

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To seek corroboration between the incubations and the sediment trap samples, we analysed the sediment trap material by XPS. Interestingly, no aluminium was detected in any sample, suggesting that terrestrial inputs of lithogenic material were minimal during the time of our sampling. Silica and calcium were both detected at 5–10 wt% of the surface material. The only differences observed for the biogenic markers was that the calcium content at station 2 (ODZ) was lower than at stations 1 or 3. This suggests that the sinking particles at station 2 were slightly richer in Si-rich diatom material relative carbonate compared to the other two stations.

Overall, our data are inconclusive about the effect of mineral on the remineralization rate of the organic matter; incubations suggest a strong effect, but direct measurements of the sinking particles suggest relatively minor contributions of biogenic mineral and no detectable Aeolian dust. These results do not exclude this as an important mechanism, and other modelling and data analysis efforts have suggested that it must be important in the Arabian Sea (Armstrong et al., 2002; Barkmann et al., 2010; Howard et al., 2006; Klaas and Archer, 2002). It may simply be that our sampling period (transition to the inter-monsoon) was the incorrect period to observe a strong effect.

4.5 M5: Addition of recalcitrant organic material

One poorly evaluated possibility is that ODZ regions, for whatever reason, are prone to having refractory material within them, thus providing sinking particles with material that is naturally resistant to degradation. We assessed this by measuring terrestrial lignin phenols in the trap material. Our assumption was that the lignin would be highly refractory and that if this mechanism was important we would detect more lignin at the ODZ stations relative to station 3 further south. This is somewhat logical, as (a) the lignin found in the open in the ocean is generally thought to be refractory (Goni et al., 2009; Meyersschulte and Hedges, 1986), (b) station 1 is closest to the Indus River – a known and important source of lignin to the Arabian Sea (Cowie, 2005; Cowie et al., 1999; Vandewiele et al., 2009), and (c) station 2 is in a region where the dust deposition is roughly 2–3x that of station 3 (Grand et al., 2015). However, the lignin

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yield was quite low, comparable to that found in the dissolved pool of the equatorial Pacific (Meyersschulte and Hedges, 1986) and we did not observe any differences in the quantities or compositions of the minimal lignin contribution to the sinking particles at the three stations and the contribution of lignin to the total organic matter was far less than 0.1 %, implying that refractory organic material from land was not an important component controlling the flux.

An additional component that we did not evaluate is the possibility that the phytoplankton community above the ODZ waters natively create “selectively preserved” organic matter that is strongly resistant to remineralization such as algeans (Gelin et al., 1996, 1999). However, visualizations of the sinking material using a dissecting scope aboard ship did not result in any note of differences between the various stations in the physical structure or composition of the sinking material.

4.6 M6: Changes in sinking speed

Mineral inputs can potentially control more than just the reactivity of whatever organic material is sorbed to it, the abundance of mineral in the sinking particles plays a large role controlling the sinking speed (Burd et al., 2010; Jackson and Burd, 2002). Given a single and constant degradation rate, any change in sinking speed will change how long the particle spends in the ODZ and thus influence how much it is remineralized there. Complicating matters is the fact that the ocean contains many different types of particles that aggregate and disaggregate and sink at different speeds. Riley et al. (2012) has suggested that fast sinking particles can typically account for the carbon demand of the deep sea, and that more slowly sinking particles are effectually remineralized within the water column. Use of the Martin attenuation coefficient does not help in this regard because it combined the two terms, but the Ballast model allows some insight (Armstrong et al., 2002; Klaas and Archer, 2002; Le Moigne et al., 2012). If ballasting is an important control on sinking speed, and sinking speed controls the flux attenuation in the ODZ, then samples from the ODZ should have proportionally more mineral compared to station 3. Our data show the opposite trend; samples from

station 3 (more oxygenated) have higher percentages of inorganic material (Fig. 3). This is inconsistent with ballast-driven sinking speeds being the primary driver of the reduced attenuation in the ODZ. However, as with everything else we measured, the data have the caveat that we did not measure sinking speeds directly, nor did we separate the material into pools with different sinking rates. In other studies where that has been done, the deep flux has been attributed to ballasted organic matter with fast sinking speeds (Le Moigne et al., 2012) or to fast-sinking materials derived from zooplankton (Cavan et al., 2015).

4.7 A heuristic model for organic matter cycling in an ODZ

No single parameter we measured or mechanism explored seems to singularly control the flux through the Arabian Sea ODZ, but the mechanisms (M1) Oxygen Effect and (M2) Growth Efficiency and Chemoautotrophy have the strongest support within our data set and based on literature. The effect of (M3) Zooplankton and of mineral ballast (which occurs as part of several mechanisms) appears to be most important deeper within the ODZ (deeper than our sediment traps were deployed; Roullier et al., 2014), and the role of (M6) Sinking Speed remains unclear. The role of (M4) Mineral Protection seems plausible and is supported by model efforts (Barkmann et al., 2010; Howard et al., 2006) but since no lithogenic minerals were detected by XPS in our samples, mineral protection remains to be further evaluated and might likely only be important under certain circumstances. The only mechanism that we can rule out appears to be that of (M5) Refractory terrestrial inputs, but we note that we did not evaluate algeans.

A conceptual model for how an ODZ system might funnel carbon to the deep sea thus starts with the upper ODZ being a region of intense microbial activity where respiratory reactions are either slowed by the lack of oxygen (M1 Oxygen Effect) or are highly efficient at retaining energy within the system (high growth efficiency; M2). Disentangling these two possibilities is of importance if we are to better understand the forces controlling carbon fluxes in a changing ocean, and also important for understanding the role of the changing oxygen content of the oceans (Stramma et al., 2010).

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Bacterial growth efficiencies are known to vary widely from $< 5\%$ to $\sim 60\%$ (del Gior-
gio and Cole, 1998) and this is thought to be controlled by a combination of factors
including source materials and maintenance energy costs. To our knowledge, these
things have not been evaluated in ODZ regions and comparisons between oxic wa-
5 ters and ODZs have thus not been made. As a thought exercise, assuming an aerobic
growth efficiency of 10% , to half the attenuation and double export out of a hypothetical
ODZ with similar inputs, the microbial efficiency of the bacterial community in the ODZ
need only to double to 20% . Similarly, the oxygen effect need not be large; a halving
of the degradation rate would result in a doubling of the flux. Both these terms (growth
10 efficiency and remineralization rate) are very poorly explored for ODZ systems.

Assuming a higher growth efficiency relative to oxic waters, the ODZ microbial
community could then funnel energy to its chemoautotrophic community. The major
chemoautotrophs in ODZ regions are thought to be slow growing anammox bacteria
(Lam and Kuypers, 2011) which might grow slowly but also keep biomass within the
ODZ until they are grazed or otherwise transferred into the sinking pool. This com-
15 bination of reduced respiration, increased efficiency and chemoautotrophy probably
explains most observations of upper ODZ regions including the presence of relatively
high amounts of non-sinking loosely aggregated material (Roullier et al., 2014). The
factors controlling how this material is transferred (or not) to the sinking pool remain
20 to be explored. The inputs of dust is likely to enhance the flux by sorbing and protect-
ing dissolved organic matter (Burdige, 2007) and could also change sinking speeds by
providing ballast, but again, this remains to be directly demonstrated.

Deeper within the ODZ two processes appear likely to be important; the presence
of a deep zooplankton population (Roullier et al., 2014; Wishner et al., 2008) likely
repackages suspended material and adds to the sinking flux, and the remineralization
of slowly sinking organic matter results in sinking rates that increase as a function of
25 depth (Berelson, 2002). The overall observation of “enhanced” fluxes is thus the result
of a complex series of processes, each of which may dominate at any given time or
depth.

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ecosystems in the 21st century: projections with CMIP5 models, *Biogeosciences*, 10, 6225–6245, doi:10.5194/bg-10-6225-2013, 2013.

Bridoux, M. C., Neibauer, J., Ingalls, A. E., Nunn, B. L., and Keil, R. G.: Suspended marine particulate proteins in coastal and oligotrophic waters, *J. Marine Syst.*, 143, 39–48, 2015.

Buesseler, K. O. and Boyd, P. W.: Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean, *Limnol. Oceanogr.*, 54, 1210–1232, 2009.

Bulow, S. E., Rich, J. J., Naik, H. S., Pratihary, A. K., and Ward, B. B.: Denitrification exceeds anammox as a nitrogen loss pathway in the Arabian Sea oxygen minimum zone, *Deep-Sea Res. Pt. I*, 57, 384–393, 2010.

Burd, A. B., Hansell, D. A., Steinberg, D. K., Anderson, T. R., Aristegui, J., Baltar, F., Beupre, S. R., Buesseler, K. O., DeHairs, F., Jackson, G. A., Kadko, D. C., Koppelman, R., Lampitt, R. S., Nagata, T., Reinthaler, T., Robinson, C., Robison, B. H., Tamburini, C., and Tanaka, T.: Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: what the @\$#! is wrong with present calculations of carbon budgets?, *Deep-Sea Res. Pt. II*, 57, 1557–1571, 2010.

Burdige, D. J.: Burial of terrestrial organic matter in marine sediments: a re-assessment, *Global Biogeochem. Cy.*, 19, 7, 2005.

Burdige, D. J.: Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets?, *Chem. Rev.*, 107, 467–485, 2007.

Cavan, E. L., Le Moigne, F. A. C., Poulton, A. J., Tarling, G. A., Ward, P., Daniels, C. J., Fragoso, G. M., and Sanders, R. J.: Attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean, is controlled by zooplankton fecal pellets, *Geophys. Res. Lett.*, 42, 821–830, 2015.

Chang, B. X., Rich, J. R., Jayakumar, A., Naik, H., Pratihary, A. K., Keil, R. G., Ward, B. B., and Devol, A. H.: The effect of organic carbon on fixed nitrogen loss in the eastern tropical South Pacific and Arabian Sea oxygen deficient zones, *Limnol. Oceanogr.*, 59, 1267–1274, 2014.

Close, H. G., Wakeham, S. G., and Pearson, A.: Lipid and C-13 signatures of submicron and suspended particulate organic matter in the Eastern Tropical North Pacific: Implications for the contribution of Bacteria, *Deep-Sea Res. Pt. I*, 85, 15–34, 2014.

Cowie, G.: The biogeochemistry of Arabian Sea surficial sediments: A review of recent studies, *Prog. Oceanogr.*, 65, 260–289, 2005.

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- Cowie, G. L. and Hedges, J. I.: Improved amino acid quantification in environmental samples – charge matched recovery standards and reduced analysis time, *Mar. Chem.*, 37, 223–238, 1992a.
- Cowie, G. L. and Hedges, J. I.: The role of anoxia in organic matter preservation in coastal sediments – relative stabilities of the major biochemicals under oxic and anoxic depositional conditions, *Org. Geochem.*, 19, 229–234, 1992b.
- Cowie, G. L. and Hedges, J. I.: Biochemical indicators of diagenetic alteration in natural organic matter mixtures, *Nature*, 369, 304–307, 1994.
- Cowie, G. L., Hedges, J. I., Prah, F. G., and Delange, G. J.: Elemental and major biochemical changes across an oxidation front in a relict turbidite – an oxygen effect, *Geochim. Cosmochim. Ac.*, 59, 33–46, 1995.
- Cowie, G. L., Calvert, S. E., Pedersen, T. F., Schulz, H., and von Rad, U.: Organic content and preservational controls in surficial shelf and slope sediments from the Arabian Sea (Pakistan margin), *Mar. Geol.*, 161, 23–38, 1999.
- Dachs, J., Bayona, J. M., Ittekkot, V., and Albaiges, J.: Monsoon-driven vertical fluxes of organic pollutants in the western Arabian Sea, *Environ. Sci. Technol.*, 33, 3949–3956, 1999.
- Dalsgaard, T., Canfield, D. E., Petersen, J., Thamdrup, B., and Acuna-Gonzalez, J.: N₂ production by the anammox reaction in the anoxic water column of Golfo Dulce, Costa Rica, *Nature*, 422, 606–608, 2003.
- Dale, A. W., Sommer, S., Lomnitz, U., Montes, I., Treude, T., Liebetrau, V., Gier, J., Hensen, C., Dengler, M., Stolpovsky, K., Bryant, L. D., and Wallmann, K.: Organic carbon production, mineralisation and preservation on the Peruvian margin, *Biogeosciences*, 12, 1537–1559, doi:10.5194/bg-12-1537-2015, 2015.
- Dauwe, B., Middelburg, J. J., Herman, P. M. J., and Heip, C. H. R.: Linking diagenetic alteration of amino acids and bulk organic matter reactivity, *Limnol. Oceanogr.*, 44, 1809–1814, 1999.
- del Giorgio, P. A. and Cole, J. J.: Bacterial growth efficiency in natural aquatic systems, *Annu. Rev. Ecol. Syst.*, 29, 503–541, 1998.
- Deutsch, C., Brix, H., Ito, T., Frenzel, H., and Thompson, L.: Climate-forced variability of ocean hypoxia, *Science*, 333, 336–339, 2011.
- Devol, A. H. and Hartnett, H. E.: Role of the oxygen-deficient zone in transfer of organic carbon to the deep ocean, *Limnol. Oceanogr.*, 46, 1684–1690, 2001.
- DeVries, T., Deutsch, C., Primeau, F., Chang, B., and Devol, A.: Global rates of water-column denitrification derived from nitrogen gas measurements, *Nat. Geosci.*, 5, 547–550, 2012.

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- Fuchsman, C. A., Kirkpatrick, J. B., Brazelton, W. J., Murray, J. W., and Staley, J. T.: Metabolic strategies of free-living and aggregate-associated bacterial communities inferred from biologic and chemical profiles in the Black Sea suboxic zone, *FEMS Microbiol. Ecol.*, 78, 586–603, 2011.
- 5 Fuchsman, C. A., Staley, J. T., Oakley, B. B., Kirkpatrick, J. B., and Murray, J. W.: Free-living and aggregate-associated Planctomycetes in the Black Sea, *FEMS Microbiol. Ecol.*, 80, 402–416, 2012.
- Gelin, F., Boogers, I., Noordeloos, A. A. M., Damste, J. S. S., Hatcher, P. G., and deLeeuw, J. W.: Novel, resistant microalgal polyethers: An important sink of organic carbon in the marine environment?, *Geochim. Cosmochim. Ac.*, 60, 1275–1280, 1996.
- 10 Gelin, F., Volkman, J. K., Largeau, C., Derenne, S., Damste, J. S. S., and De Leeuw, J. W.: Distribution of aliphatic, nonhydrolyzable biopolymers in marine microalgae, *Org. Geochem.*, 30, 147–159, 1999.
- Goni, M. A. and Montgomery, S.: Alkaline CuO oxidation with a microwave digestion system: Lignin analyses of geochemical samples, *Anal. Chem.*, 72, 3116–3121, 2000.
- Goni, M. A., Aceves, H., Benitez-Nelson, B., Tappa, E., Thunell, R., Black, D. E., Muller-Karger, F., Astor, Y., and Varela, R.: Oceanographic and climatologic controls on the compositions and fluxes of biogenic materials in the water column and sediments of the Cariaco Basin over the Late Holocene, *Deep-Sea Res. Pt. I*, 56, 614–640, 2009.
- 20 Grand, M. M., Measures, C. I., Hatta, M., Hiscock, W. T., Buck, C. S., and Landing, W. M.: Dust deposition in the eastern Indian Ocean: The ocean perspective from Antarctica to the Bay of Bengal. *Global Biogeochem. Cy.*, 29, 357–374, 2015.
- Haake, B., Ittekkot, V., Ramaswamy, V., Nair, R. R., and Honjo, S.: Fluxes of amino acids and hexosamines to the deep Arabian Sea, *Mar. Chem.*, 40, 291–314, 1992.
- 25 Hartnett, H. E. and Devol, A. H.: Role of a strong oxygen-deficient zone in the preservation and degradation of organic matter: a carbon budget for the continental margins of northwest Mexico and Washington State, *Geochim. Cosmochim. Ac.*, 67, 247–264, 2003.
- Hartnett, H. E., Keil, R. G., Hedges, J. I., and Devol, A. H.: Influence of oxygen exposure time on organic carbon preservation in continental margin sediments, *Nature*, 391, 572–574, 1998.
- 30 Hebbeln, D., Marchant, M., and Wefer, G.: Seasonal variations of the particle flux in the Peru-Chile current at 30° S under “normal” and El Niño conditions, *Deep-Sea Res. Pt. II*, 47, 2101–2128, 2000.

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- Hedges, J. I. and Keil, R. G.: Sedimentary organic matter preservation: an assessment and speculative synthesis, *Mar. Chem.*, 49, 81–115, 1995.
- Hedges, J. I., Clark, W. A., and Cowie, G. L.: Fluxes and reactivities of organic matter in a coastal marine bay, *Limnol. Oceanogr.*, 33, 1137–1152, 1988.
- 5 Hedges, J. I., Hu, F. S., Devol, A. H., Hartnett, H. E., Tsamakis, E., and Keil, R. G.: Sedimentary organic matter preservation: a test for selective degradation under oxic conditions, *Am. J. Sci.*, 299, 529–555, 1999.
- Hedges, J. I., Baldock, J. A., Gelinas, Y., Lee, C., Peterson, M. L., and Wakeham, S. G.: The biochemical and elemental compositions of marine plankton: a NMR perspective, *Mar. Chem.*, 10 78, 47–63, 2002.
- Howard, M. T., Winguth, A. M. E., Klaas, C., and Maier-Reimer, E.: Sensitivity of ocean carbon tracer distributions to particulate organic flux parameterizations, *Global Biogeochem. Cy.*, 20, 384–393, doi:10.1029/2005GB002499, 2006.
- Jackson, G. A. and Burd, A. B.: A model for the distribution of particle flux in the mid-water column controlled by subsurface biotic interactions, *Deep-Sea Res. Pt. II*, 49, 193–217, 2002.
- Jensen, M. M., Lam, P., Revsbech, N. P., Nagel, B., Gaye, B., Jetten, M. S. M., and Kuypers, M. M. M.: Intensive nitrogen loss over the Omani Shelf due to anammox coupled with dissimilatory nitrite reduction to ammonium, *Isme J.*, 5, 1660–1670, 2011.
- 15 Keil, R. G. and Cowie, G. L.: Organic matter preservation through the oxygen-deficient zone of the NE Arabian Sea as discerned by organic carbon: mineral surface area ratios, *Mar. Geol.*, 20 161, 13–22, 1999.
- Keil, R. G. and Mayer, L. M.: 12.12 – Mineral matrices and organic matter, in: *Treatise on Geochemistry*, edited by: Turekian, H. D. H. K., 2nd Edn., Elsevier, Oxford, 337–359, 2014.
- Keil, R. G., Dickens, A. F., Arnarson, T., Nunn, B. L., and Devol, A. H.: What is the oxygen exposure time of laterally transported organic matter along the Washington margin?, *Mar. Chem.*, 25 92, 157–165, 2004.
- Kennedy, M. J. and Wagner, T.: Clay mineral continental amplifier for marine carbon sequestration in a greenhouse ocean, *P. Natl. Acad. Sci. USA*, 108, 9776–9781, 2011.
- Kennedy, P., Kennedy, H., and Papadimitriou, S.: The effect of acidification on the determination of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment, *Rapid Commun. Mass Sp.*, 19, 1063–1068, 2005.
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- Klaas, C. and Archer, D. E.: Association of sinking organic matter with various types of mineral ballast in the deep sea: implications for the rain ratio, *Global Biogeochem. Cy.*, 16, 63–77, doi:10.1029/2001GB001765, 2002.
- Kuypers, M. M. M., Sliemers, A. O., Lavik, G., Schmid, M., Jorgensen, B. B., Kuenen, J. G., Damste, J. S. S., Strous, M., and Jetten, M. S. M.: Anaerobic ammonium oxidation by anammox bacteria in the Black Sea, *Nature*, 422, 608–611, 2003.
- Lam, P. and Kuypers, M. M. M.: Microbial nitrogen cycling processes in oxygen minimum zones, edited by: Carlson, C. A. and Giovannoni, S. J., *Annu. Rev. Mar. Sci.*, 3, 317–345, 2011.
- Le Moigne, F. A. C., Sanders, R. J., Villa-Alfageme, M., Martin, A. P., Pabortsava, K., Planquette, H., Morris, P. J., and Thomalla, S. J.: On the proportion of ballast vs. non-ballast associated carbon export in the surface ocean, *Geophys. Res. Lett.*, 39, 15610–15616, doi:10.1029/2012GL052980, 2012.
- Le Moigne, F. A. C., Gallinari, M., Laurenceau, E., and De La Rocha, C. L.: Enhanced rates of particulate organic matter remineralization by microzooplankton are diminished by added ballast minerals, *Biogeosciences*, 10, 5755–5765, doi:10.5194/bg-10-5755-2013, 2013.
- Lee, C.: Controls on organic carbon preservation – the use of stratified water bodies to compare rates of decomposition in oxic and anoxic systems, *Geochim. Cosmochim. Ac.*, 56, 3323–3335, 1992.
- Lee, C., Murray, D. W., Barber, R. T., Buesseler, K. O., Dymond, J., Hedges, J. I., Honjo, S., Manganini, S. J., Marra, J., Moser, C., Peterson, M. L., Prell, W. L., Wakeham, S. G., Arabian Sea Carbon Flux G: Particulate organic carbon fluxes: compilation of results from the 1995 US JGOFS Arabian Sea Process Study, *Deep-Sea Res. Pt. II*, 45, 2489–2501, 1998.
- Lee, C., Armstrong, R. A., Cochran, J. K., Engel, A., Fowler, S. W., Goutx, M., Masque, P., Miquel, J. C., Peterson, M., Tamburini, C., and Wakeham, S.: MedFlux: investigations of particle flux in the Twilight Zone. *Deep-Sea Res. Pt. II*, 56, 1363–1368, 2009.
- Levin, L., Gutierrez, D., Rathburn, A., Neira, C., Sellanes, J., Munoz, P., Gallardo, V., and Salamanca, M.: Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño, *Prog. Oceanogr.*, 53, 1–27, 2002.
- Levin, L. A., Liu, K. K., Emeis, K. C., Breitburg, D. L., Cloern, J., Deutsch, C., Giani, M., Goffart, A., Hofmann, E. E., Lachkar, Z., Limburg, K., Liu, S. M., Montes, E., Naqvi, W., Rague-neau, O., Rabouille, C., Sarkar, S. K., Swaney, D. P., Wassman, P., and Wishner, K. F.: Comparative biogeochemistry-ecosystem-human interactions on dynamic continental margins, *J. Marine Syst.*, 141, 3–17, 2015.

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- Marchant, M., Hebbeln, D., Giglio, S., Coloma, C., and and González, H. E.: Seasonal and interannual variability in the flux of planktic foraminifera in the Humboldt Current System off central Chile (30° S), *Deep-Sea Res. Pt. II*, 51, 2441–2455, 2004.
- Martin, J. H., Knauer, G. A., Karl, D. M., and Broenkow, W. W.: VERTEX – Carbon cycling in the North East Pacific, *Deep-Sea Res. Pt. I*, 34, 267–285, 1987.
- Mayer, L. M.: Surface area control of the organic carbon accumulation in continental margin sediments, *Geochim. Cosmochim. Ac.*, 58, 1271–1284, 1994.
- McDonnell, A. M. P., Lam, P. J., Lamborg, C. H., Buesseler, K. O., Sanders, R., Riley, J. S., Marsay, C., Smith, H. E. K., Sargent, E. C., Lampitt, R. S., and Bishop, J. K. B.: The oceanographic toolbox for the collection of sinking and suspended marine particles, *Prog. Oceanogr.*, 133, 17–31, 2015.
- Meyersschulte, K. J. and Hedges, J. I.: Molecular evidence for a terrestrial component of organic matter in ocean water, *Nature*, 321, 61–63, 1986.
- Naqvi, W. A.: Geographical extend of denitrification in the Arabian Sea in relation to some physical processes, *Oceanol. Acta*, 14, 281–290, 1991.
- Newell, S. E., Babbín, A. R., Jayakumar, A., and Ward, B. B.: Ammonia oxidation rates and nitrification in the Arabian Sea. *Global Biogeochem. Cy.*, 25, 10, 2011.
- Nunn, B. L., Ting, Y. S., Malmstrom, L., Tsai, Y. S., Squier, A., Goodlett, D. R., and Harvey, H. R.: The path to preservation: using proteomics to decipher the fate of diatom proteins during microbial degradation, *Limnol. Oceanogr.*, 55, 1790–1804, 2010.
- Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, *Prog. Oceanogr.*, 80, 113–128, 2009.
- Peterson, M. L., Wakeham, S. G., Lee, C., Askea, M. A., and Miquel, J. C.: Novel techniques for collection of sinking particles in the ocean and determining their settling rates, *Limnol. Oceanogr.-Methods*, 3, 520–532, 2005.
- Piraud, M., Vianey-Saban, C., Petritis, K., Elfakir, C., Steghens, J. P., and Bouchu, D.: Ion-pairing reversed-phase liquid chromatography/electrospray ionization mass spectrometric analysis of 76 underivatized amino acids of biological interest: a new tool for the diagnosis of inherited disorders of amino acid metabolism, *Rapid Commun. Mass Sp.*, 19, 1587–1602, 2005.
- Ploug, H.: Small-scale oxygen fluxes and remineralization in sinking aggregates, *Limnol. Oceanogr.*, 46, 1624–1631, 2001.

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- Ploug, H., Iversen, M. H., and Fischer, G.: Ballast, sinking velocity, and apparent diffusivity within marine snow and zooplankton fecal pellets: implications for substrate turnover by attached bacteria, *Limnol. Oceanogr.*, 53, 1878–1886, 2008.
- Riley, J. S., Sanders, R., Marsay, C., Le Moigne, F. A. C., Achterberg, E. P., and Poulton, A. J.: The relative contribution of fast and slow sinking particles to ocean carbon export, *Global Biogeochem. Cy.*, 26, 1026–1036, doi:10.1029/2011GB004085, 2012.
- Roland, L. A., McCarthy, M. D., and Guilderson, T.: Sources of molecularly uncharacterized organic carbon in sinking particles from three ocean basins: a coupled Delta C-14 and delta C-13 approach, *Mar. Chem.*, 111, 199–213, 2008.
- Roullier, F., Berline, L., Guidi, L., Durrieu De Madron, X., Picheral, M., Sciandra, A., Pesant, S., and Stemmann, L.: Particle size distribution and estimated carbon flux across the Arabian Sea oxygen minimum zone, *Biogeosciences*, 11, 4541–4557, doi:10.5194/bg-11-4541-2014, 2014.
- Stramma, L., Schmidtko, S., Levin, L. A., and Johnson, G. C.: Ocean oxygen minima expansions and their biological impacts, *Deep-Sea Res. Pt. I*, 57, 587–595, 2010.
- Stramma, L., Prince, E. D., Schmidtko, S., Luo, J. G., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, P., and Kortzinger, A.: Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes, *Nature Climate Change*, 2, 33–37, 2012.
- Tanoue, E., Nishiyama, S., Kamo, M., and Tsugita, A.: Bacterial membranes – possible source of a major dissolved protein in seawater, *Geochim. Cosmochim. Ac.*, 59, 2643–2648, 1995.
- Thamdrup, B., Dalsgaard, T., and Revsbech, N. P.: Widespread functional anoxia in the oxygen minimum zone of the Eastern South Pacific. *Deep-Sea Res. Pt. I*, 65, 36–45, 2012.
- Tiano, L., Garcia-Robledo, E., Dalsgaard, T., Devol, A. H., Ward, B. B., Ulloa, O., Canfield, D. E., and Revsbech, N. P.: Oxygen distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen minimum zones, *Deep-Sea Res. Pt. I*, 94, 173–183, 2014.
- Ulloa, O., Canfield, D. E., DeLong, E. F., Letelier, R. M., and Stewart, F. J.: Microbial oceanography of anoxic oxygen minimum zones, *P. Natl. Acad. Sci. USA*, 109, 15996–16003, 2012.
- Van Mooy, B. A. S., Keil, R. G., and Devol, A. H.: Impact of suboxia on sinking particulate organic carbon: enhanced carbon flux and preferential degradation of amino acids via denitrification, *Geochim. Cosmochim. Ac.*, 66, 457–465, 2002.
- Vandewiele, S., Cowie, G., Soetaert, K., and Middelburg, J. J.: Amino acid biogeochemistry and organic matter degradation state across the Pakistan margin oxygen minimum zone, *Deep-Sea Res. Pt. II*, 56, 376–392, 2009.

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- Wang, D. Z., Dong, H. P., Xie, Z. X., Dai, M. H., and Hong, H. S.: Metaproteomic characterization of dissolved organic matter in the water column of the South China Sea, *Limnol. Oceanogr.*, 56, 1641–1652, 2011.
- 5 Ward, B. B., Tuit, C. B., Jayakumar, A., Rich, J. J., Moffett, J., and Naqvi, S. W. A.: Organic carbon, and not copper, controls denitrification in oxygen minimum zones of the ocean, *Deep-Sea Res. Pt. I*, 55, 1672–1683, 2008.
- Ward, B. B., Devol, A. H., Rich, J. J., Chang, B. X., Bulow, S. E., Naik, H., Pratihary, A., and Jayakumar, A.: Denitrification as the dominant nitrogen loss process in the Arabian Sea, *Nature*, 461, 78–77, 2009.
- 10 Wishner, K. F., Gelfman, C., Gowing, M. M., Outram, D. M., Rapien, M., and Williams, R. L.: Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian Sea oxygen minimum zone, *Prog. Oceanogr.*, 78, 163–191, 2008.
- Wishner, K. F., Outram, D. M., Seibel, B. A., Daly, K. L., and Williams, R. L.: Zooplankton in the eastern tropical north Pacific: boundary effects of oxygen minimum zone expansion, *Deep-Sea Res. Pt. I*, 79, 122–140, 2013.
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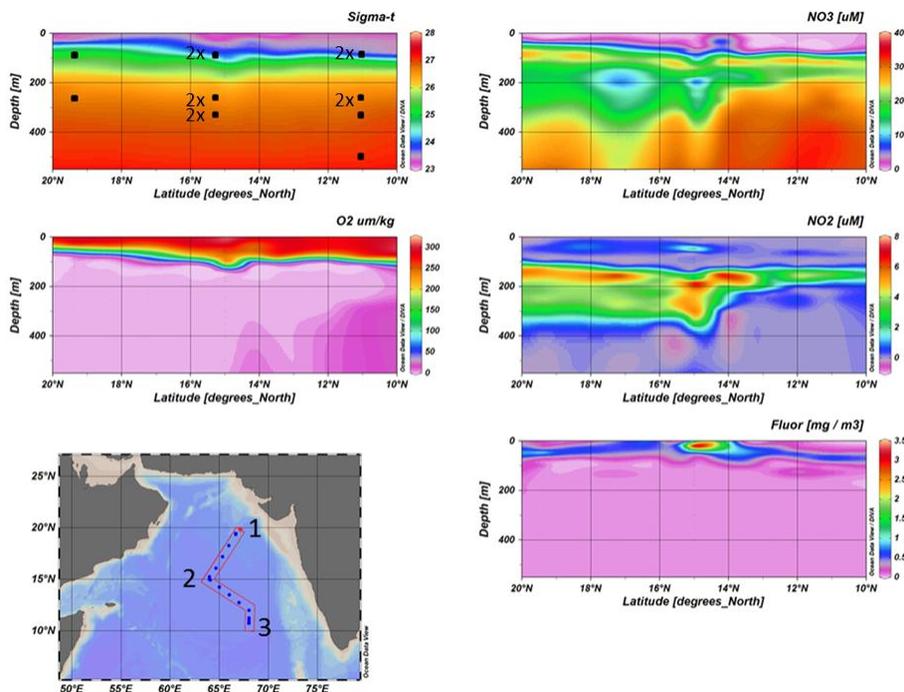


Figure 1. Spatial contours of water column parameters during the sediment trap deployments, clockwise from upper left; density, nitrate, nitrite, chlorophyll fluorescence, a map of the region including CTD stations (and with the trap deployment stations labelled 1–3), and oxygen. Squares in the upper left panel mark where sediment traps were deployed. A 2× denotes two traps deployed at these depths. Nutrient data previously reported by Bulow et al. (2009).

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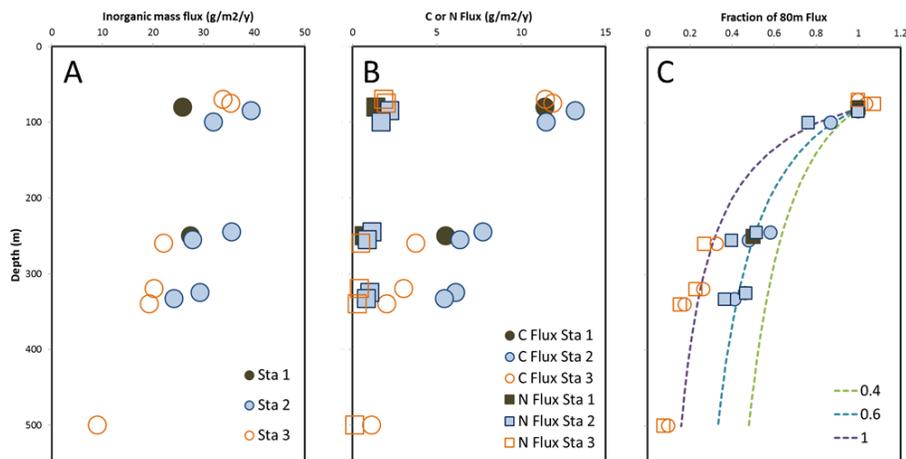


Figure 2. Sediment trap fluxes for inorganic material (a), organic C and total N (b) and the fraction of the 80 m organic C or total N flux observed in deeper traps. Dashed lines in (c) denote Martin curves with attenuation coefficients between 0.4 and 1.0.

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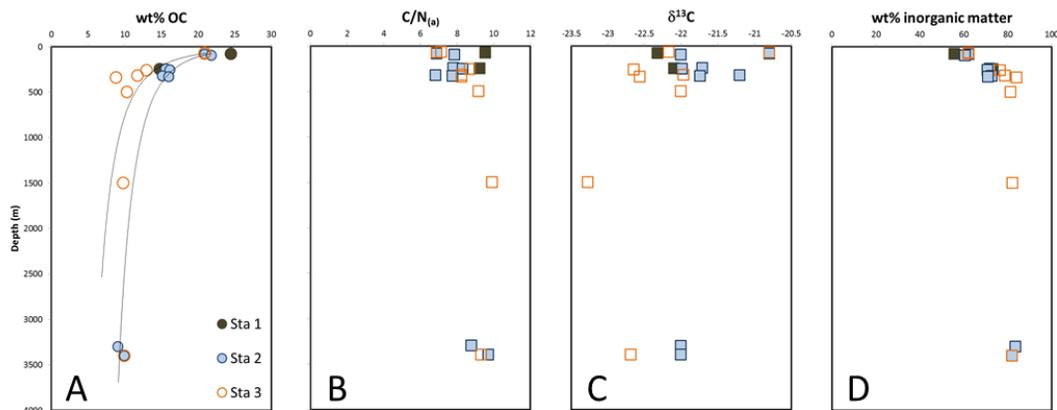


Figure 3. Weight percent organic carbon (a), atomic ratios of organic carbon to total nitrogen (b), the stable carbon isotopic composition of the bulk organic matter (c) and the percentage of inorganic material (d). Power functions in the left-most figure were added to aid the eye in discerning possible differences between the three stations. Samples from deeper than 500 m were collected via slow net haul (see methods).

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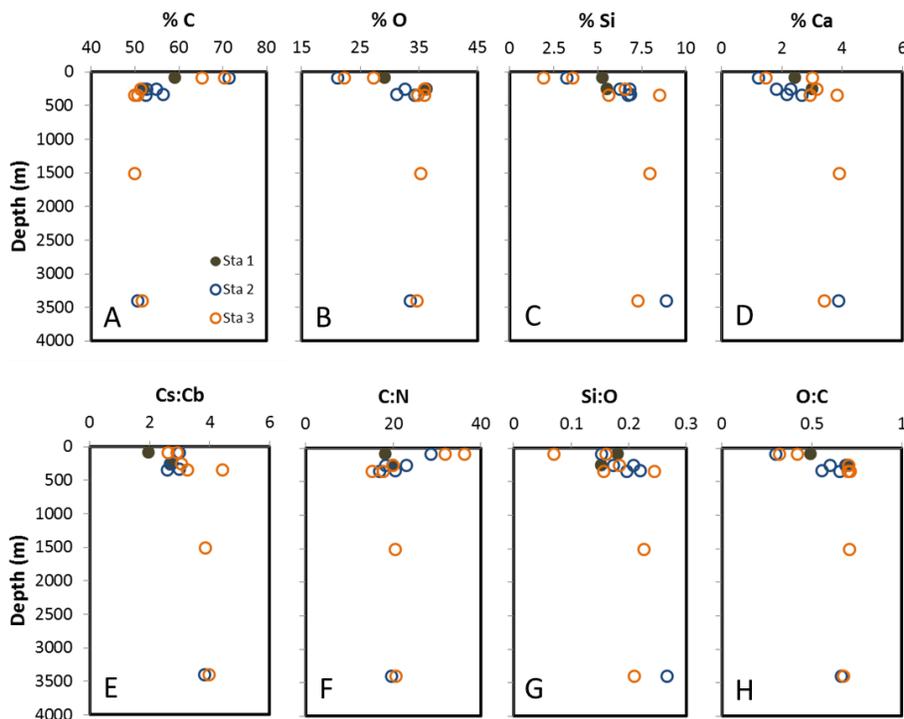


Figure 4. Atom percentages of different elements identified by XPS on the surfaces of the sinking particles; **(a)** carbon, **(b)** oxygen, **(c)** silicon, **(d)** calcium. **(e)** Weight percentage ratio of carbon on the surface of the particles to bulk carbon measured by elemental analysis, **(f)** atomic C:N ratio of carbon and nitrogen at the surface, **(g)** atomic silica: oxygen ratio, **(h)** atomic oxygen: carbon ratio. (Color scheme for symbols same as in Fig. 3.)

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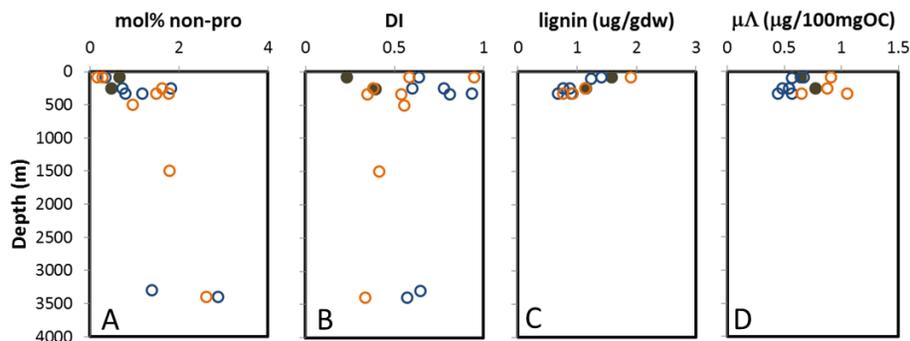


Figure 5. (a) mole percentage of non-protein amino acids, (b) amino acid degradation index, (c) lignin phenol yield per gram dry weight of sinking material, and (d) $\mu\Lambda$, the lignin yield in micrograms per 100 mg organic carbon. (Colour scheme for symbols same as in Fig. 3.)

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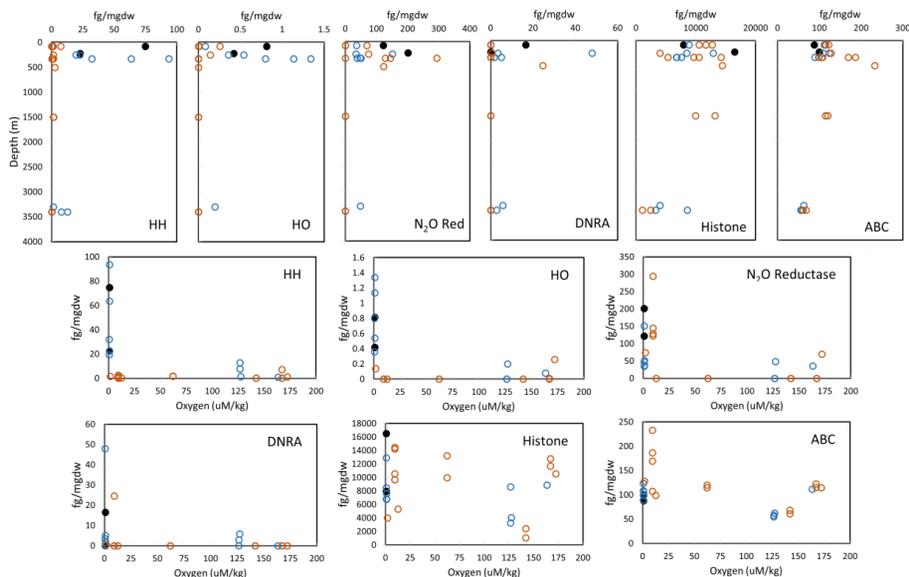


Figure 6. Target peptide quantifications. Upper row shows peptide quantifications as a function of depth, and the lower middle panels as a function of oxygen. HH combines data from 10 peptides specific to three forms of the anammox-specific enzyme Hydrazine Hydrolase; HO shows results from 4 peptides specific to the anammox enzyme Hydroxylamine/Hydrazine oxidoreductase; N_2O reductase data reflect 3 peptides specific marks the final step of denitrification; DNRA denotes 3 peptides specific to Cytochrome c nitrite reductase (*nrfA*), a key enzyme in dissimilatory nitrate reduction to ammonium. Histone identifies two peptides specific to the eukaryote-specific H4 tetramer; ABC identifies 2 peptides specific to the general class of ABC transporter proteins commonly found in active (living) bacteria. (Colour scheme for symbols same as in Fig. 3.).

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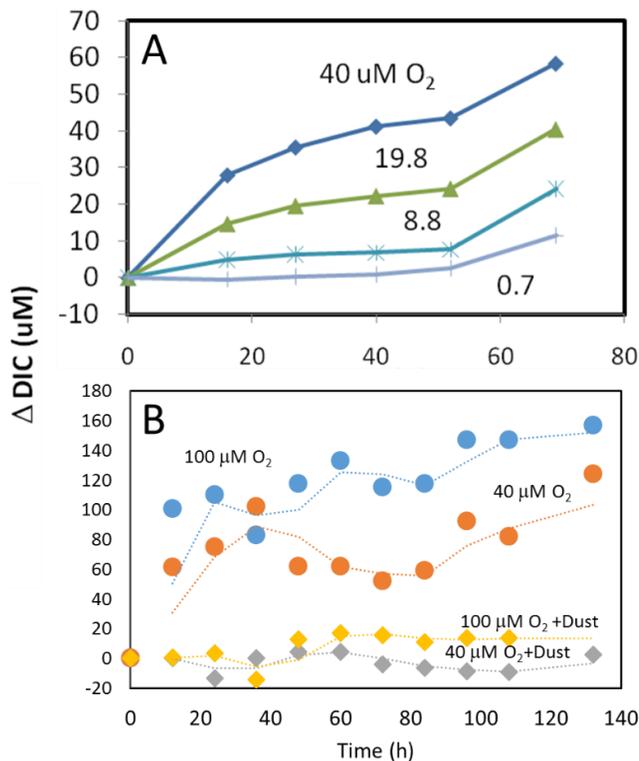


Figure 7. Incubation studies evaluating the change in DIC under different initial oxygen conditions (a) and with or without added dust from the Sahara desert (b). Sinking particles from station 3, 80 m were added to incubation bags and alkalinity, pH and nutrients were measured. DIC calculated assuming that the only changes to the alkalinity were driven by changes in nutrient concentrations (Van Mooy et al., 2002). Dashed lines denote a running average of 2 points.