Water column biogeochemistry of oxygen minimum zones in the eastern tropical North Atlantic and eastern tropical South Pacific Oceans

C.R. Löscher[1]*, H.W. Bange[2], R.A. Schmitz[1], C.M. Callbeck[3], A. Engel[2], H. Hauss[2], T. Kanzow[2, 4], R. Kiko[2], G. Lavik[3], A. Loginova[2], F. Melzner[2], S.C. Neulinger[1], M. Pahlow[2], U. Riebesell[2], H. Schunck[1], S. Thomsen[2], H. Wagner[2]

[1] {Institute of General Microbiology, Christian-Albrechts-University Kiel, Am Botanischen Garten 1-9, 24118 Kiel, Germany}

[2] {GEOMAR Helmholtz Center for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany}

[3] {Max Planck Institute for Marine Microbiology, Celsiusstraße 1, 28359 Bremen, Germany}

[4] {Now at AWI, Bremerhaven, Germany}

Correspondence to: cloescher@ifam.uni-kiel.de.

Table of Contents

Abstract

Recent modeling results suggest that oceanic oxygen levels will decrease significantly over the next decades to centuries in response to climate change and altered ocean circulation. Hence the future ocean may experience major shifts in nutrient cycling triggered by the expansion and intensification of tropical oxygen minimum zones (OMZs). There are numerous feedbacks among oxygen concentrations, nutrient cycling and biological productivity; however, existing knowledge is insufficient to understand physical, chemical and biological interactions in order to adequately assess past and potential future changes.

The following summarizes the current state of research on the influence of low environmental oxygen conditions on marine biota, viruses, organic matter formation and remineralization, with a particular focus on the nitrogen cycle in OMZ regions of the eastern tropical North Atlantic and eastern tropical South Pacific. The impact of sulfidic events on water column biogeochemistry, originating from a specific microbial community capable of highly efficient carbon fixation, nitrogen turnover and N_2O production is further discussed. Based on our findings, an important role of sinking particulate organic matter in controlling nutrient budgets of the water column is suggested. These particles can enhance degradation processes in OMZ waters by acting as microniches, with sharp gradients enabling different processes to happen in close vicinity, thus altering the interpretation of oxic and anoxic environments.

1 Introduction

Oxygen (O_2) plays a central role for life on Earth. Therefore, deciphering the oceanic O_2 distribution and its consequences for biogeochemical and ecological processes is one of the central aims of marine biogeochemistry. Oceanic oxygen minimum zones (OMZ) - alternatively also called oxygen deficiency zones - are defined as regions where the concentration of dissolved O_2 is significantly below the expected O_2 equilibrium concentration. The O_2 equilibrium concentration depends on seawater temperature, salinity, and the partial pressure of O_2 in the atmosphere at the time when a water mass was last in contact with the atmosphere. Significant O_2 depletion in the water column of the oceans is mainly resulting from microbial oxic respiration of organic matter. The most prominent and permanent OMZs (with midwater O_2 concentrations of less than 20 µmol kg^{-1}) are found in the eastern tropical North and South Pacific Oceans (ETNP and ETSP, respectively) as well as in the northwestern and northeastern Indian Ocean (i.e. Arabian Sea and Bay of Bengal, respectively) (see, e.g., Paulmier and Ruiz-Pinto (2009), Figure 1). The estimated volume of OMZs with O_2 concentrations <20 µmol kg^{-1} is about 1% of the global ocean volume (Lam and Kuypers, 2011). Approximately 0.05% of the global ocean volume has O_2 levels below 5 µmol kg^{-1}. This is generally considered the O_2 level where oxic respiration stops and alternative electron acceptors are used (Codispoti et al., 2001). Water masses with O_2 concentrations <20 µmol kg^{-1} are generally considered suboxic; however, no consistent definition of suboxia exists (Canfield and Thamdrup, 2009). Anoxia has been defined by the lowest measurable O_2 concentration, but because of the continued improvements in O_2 sensing this level is changing with time (Banse et al., 2014;Revsbech et al., 2009;Thamdrup et al., 2012). For the purpose of this review, we will use the terms oxic, suboxic, anoxic and sulfidic according to the definitions presented in Table 1.

Several OMZ regions are associated with wind-driven eastern boundary upwelling regions (Capone and Hutchins, 2013). Coastal upwelling supplies abundant nutrients to the surface and in turn fuels high phytoplankton productivity. The resulting increase in export production promotes a high O_2 consumption driven by respiration of organic matter in the underlying waters.

When oceanic O_2 concentrations decrease below certain (albeit not well defined and process dependent) threshold concentrations, major changes in remineralization processes and associated marine sources and sinks of important nutrient elements such as nitrogen, phosphorus and iron can occur in the water column as well as in the underlying sediments (see e.g., Wright et al. (2012)). Paleo-records give evidence for periods of dramatically reduced oceanic oxygen concentrations that had major consequences for both marine biogeochemical cycles and ecosystems (e.g., Kuypers et al. (2004)).

The effects of O_2-sensitive nutrient cycling processes occurring in these relatively small regions (Codispoti, 2010) are conveyed to the rest of the ocean (see e.g. Deutsch et al. (2007)). Hence comparatively "small" volumes of OMZs such as in the eastern tropical Pacific and NW Indian Oceans can significantly impact nutrient budgets particularly the nitrogen (N) budget, biological productivity and the overall CO_2 fixation of the ocean. For example, current estimates ascribe 30–50% of the global N loss to OMZs (Codispoti et al., 2001;Emery et al., 1955;Gruber, 2004), producing negative N* values, i.e. nitrogen deficiency. This has been proposed to promote N_2 fixation in adjacent surface waters (Deutsch et al., 2007). As hotspots for N turnover processes, OMZs are also major areas of greenhouse gas production, such as nitrous oxide (N_2O) (Arévalo-Martínez et al., 2015;Codispoti, 2010). Modeling results (Bopp et al., 2013;Cocco et al., 2013), predict that O_2 levels will decrease significantly over the next decades in response to climate change and eutrophication. Hence, the future ocean may experience major shifts in nutrient cycling triggered by the possible expansion and intensification of tropical OMZs (Codispoti, 2010).

The following review of the major biogeochemical processes in OMZ waters is based on studies of the Collaborative Research Centre 754 (SFB754) “Climate-Biogeochemistry Interactions in the Tropical Ocean” (www.sfb754.de). The focus here is on the eastern tropical North Atlantic (ETNA) and the eastern tropical South Pacific (ETSP) OMZs, because of their contrasting O_2 concentrations. The ETNA has O_2 concentrations typically above 40 µmol kg^{-1}, while the large and persistent OMZ in the ETSP located off Peru and Chile has O_2 concentrations below the detection limit based on conventional methods (~2 µmol kg^{-1}) (Figure 1). The two contrasting OMZs were chosen to improve our understanding of the role of biogeochemical processes for the development and maintenance of OMZs.

2 Marine biota and viruses in OMZs

2.1 Background

Viruses, microbes, protozoa and metazoa are responsible for remineralization processes under oxic conditions; however, their contributions can change when O_2 concentrations decrease.

Metazoan activity and abundance is most sensitive to lower O_2 concentrations, whereas microbes can thrive under diverse redox conditions using e.g. nitrate as electron acceptor. Microbial, protozoan and metazoan energetics are governed by redox reactions and O_2 is the most thermodynamically favorable electron acceptor (Danovaro et al., 2010;Fenchel and Finlay, 1990). O_2 concentrations, which are saturated in surface waters, are depleted by respiration at depth. The sensitivity and kinetics of metabolic reactions to gradual changes in O_2 concentrations are not well understood under *in situ* conditions. The following section explores recent developments in our understanding of the effect of O_2 on the living organisms and their impact on OMZ biogeochemistry.

2.2 Microbes in OMZ waters

Classically, the most abundant organisms detected in OMZs belong to the Proteobacteria, Bacteroidetes, Thaumarchaeota of the marine group A, Actinobacteria and Planctomycetes (Schunck et al., 2013;Wright et al., 2012). Several candidate clusters have previously been identified among which are the SAR11, SAR324 and SUP05 clusters (Schunck et al., 2013;Wright et al., 2012). Most investigations of the microbial phylogenetic and functional diversity resort to observing and correlating changes in oxygen concentrations to changes in the microbial phylogenetic diversity. Indeed, several studies, including our own datasets corroborate this idea: A combined statistical analysis of our metagenomic data of the ETSP OMZ (Kalvelage et al., 2015) and datasets from the Chilean OMZ (Canfield et al., 2010;Stewart et al., 2011) has resulted in a partitioning of the OMZ in 5 different habitats, namely surface, subsurface (defined as below the mixed layer and above waters with $O_2 > 20 \mu mol\ kg^{-1}$), oxyclines, OMZ core ($O_2 < 5\ \mu mol\ kg^{-1}$) and sulfidic waters (Figure 2). High-resolution sampling in the eastern tropical North Pacific OMZ has shown that the microbial richness is highest at the base of the euphotic zone and the upper oxycline (Beman and Carolan, 2013), often along with high organic flux, low O_2 concentrations and dynamic cycling of carbon (C), nitrogen (N), and sulfur (S). It has been suggested that sinking particles promote a diverse community of heterotrophs, whereas the low abundant microorganisms such as sulfur-oxidizers, purple sulfur bacteria (Chromatiales) and anammox bacteria rather seem to contribute to the OMZs “rare biosphere” (Beman and Carolan, 2013;Pedros-Alio, 2012).

Microorganisms are generally considered responsible for most of the remineralization in the ocean. This view is probably justified with respect to carbon, given the high rates of microbial respiration (del Giorgio and Cole, 1998). Owing to the relatively low N and phosphorous (P) content of dissolved organic matter, however, bacteria may be less important for the remineralization of N and P and in fact often compete with phytoplankton for inorganic nutrients in the surface ocean (Anderson and Williams, 1998;Pahlow and Vézina, 2003). Remineralization of N and P may thus be largely due to zooplankton activity (Caron et al., 1988;Garber, 1984;Pahlow et al., 2008).

2.3 Metazoans in OMZ waters

The adaptive response of marine metazoan animals to O_2 availability has been the focus of several studies (for extensive reviews see Ekau et al., (2010); Seibel, (2011)). Abundance and biomass of metazoans living permanently at extremely low oxygen concentrations is rather low (Auel and Verheye, 2007;Escribano et al., 2009;Fernández-Álamo and Färber-Lorda, 2006;Saltzmann and Wishner, 1997;Wishner et al., 1998). However, many zooplankton and nekton species feed in surface waters during the night and migrate to midwater depth at daybreak to avoid predation (Lampert, 1989), and to conserve energy (McLaren, 1963). This behavior is known as diel vertical migration (DVM) and some, but not all species can conduct DVMs to hypoxic or even anoxic waters. In addition to changes in temperature with depth, DVM organisms experience low O_2 concentrations during daytime as well as elevated pCO_2 (Brewer and Peltzer, 2009;Paulmier et al., 2011). Animals that have evolved physiological (such as metabolic suppression) and/or morphological adaptations (such as increased gill surface area) allowing them to temporarily or permanently cope with O_2 depleted conditions include copepods, e.g. *Eucalanus inermis,* (Flint et al., 1991), euphausiids, e.g. *Euphausia mucronata* (Antezana, 2009), decapods (Pearcy et al., 1977), cephalopods, e.g. *Dosidicus gigas* (Rosa and Seibel, 2010), and teleosts (Friedman et al., 2012;Luo et al., 2000). According to Seibel (2011), adaptations to low oxygen levels are needed below approximately 40 µmol O_2 kg^{-1}. Strong physiological adaptations seem necessary to thrive in the ETSP OMZ, but not in the ETNA OMZ where O_2 concentrations are normally higher than 40 µmol kg^{-1} (Teuber et al., 2013).

The main strategy to survive low oxygen conditions seems to be a down-regulation of aerobic metabolism, which in its extreme form also results in rather sluggish behavior of otherwise highly active animals (e.g., Trübenbach et al. (2013), for *Dosidicus gigas*). The main triggers for down-regulation appear to be temperature and O_2, but also external pCO_2 (Pörtner et al., 2004). Effects of ambient temperature, pO_2 and pCO_2 on metabolic rates of marine species have been studied primarily in single factor experiments (reviewed, e.g., by (Ekau et al., 2010;Seibel, 2011)). In one of the few studies that addressed the effect of all three factors, each of them alone reduced metabolic rates of *Dosidicus gigas* (Rosa and Seibel, 2008). The combined effects on the regulation of aerobic metabolism, however, remain not well understood.

In extreme OMZs, such as in the Eastern Tropical Pacific or the Arabian Sea with anoxic conditions, vertically migrating animals may temporarily switch to an anaerobic metabolism. This is only possible for restricted time periods – ultimately, all metazoans (besides a few exceptions, see Danovaro et al. (2010)) rely on aerobic respiration. In invertebrates, the dominant anaerobic pathway is glycolysis with lactate as an end product. The activity of the enzyme that converts pyruvate to lactate, lactate dehydrogenase (LDH), is used as an indicator of its anaerobic capacity. In the Humboldt Current system, Gonzales & Quiñones (2002) observed that the weight-specific LDH activity was two orders of magnitude higher in *Euphausia mucronata* compared to the copepod *Calanus chilensis*. This inferred that these two key species have very different DVM behaviors (which, in spite of their large phylogenetic difference, proved right). In a scyphomedusa (*Periphylla periphylla*) the LDH activity was significantly higher in those individuals caught in the Californian OMZ than in their open-ocean conspecifics (Thuesen et al., 2005). However, the accumulation of lactate is energetically costly, and the animal must return to oxygenated waters to oxidize lactic acid, and to replenish depleted ATP and phosphocreatine. In teleost fishes, the alcohol dehydrogenase (ADH) catalyzing the reduction of pyruvate to ethanol, was shown to be more active in OMZ species than in ecological analogs of the same family in oxygenated waters (Torres et al., 2012). The end product, ethanol, can be easily excreted via the gills of the fish, thus preventing the accumulation of lactate. Previous studies had concluded that mesopelagic fishes entering OMZs do not switch to anaerobic metabolism to avoid accumulation of lactate (Childress and Seibel, 1998;Friedman et al., 2012).

2.4 Organic matter fluxes mediated by zooplankton and nekton

Zooplankton and nekton organisms are essential components of the biological pump as they are responsible for the agglomeration of organic matter into rapidly sinking fecal pellets. Food is consumed at night in the euphotic zone, whereas during the day pelagic species conducting DVMs respire, excrete and egest in mid-water layers, enhancing export of organic matter from the photic zone (Burd et al., 2010;Hannides et al., 2009;Robinson et al., 2010;Steinberg et al., 2000). Migration depths are species specific and mostly controlled by light intensity (Lampert, 1989).

O_2 concentrations below a certain threshold level hinder DVM of most zooplankton and nekton. On a regional scale (e.g. in the Peruvian upwelling system), studies addressing the vertical distribution of zooplankton demonstrated that the upper boundary of the oxycline is the single most critical factor structuring the habitat of most organisms (Escribano et al., 2009). The expansion and intensification of OMZs may thus reduce zooplankton and nekton mediated fluxes by decreasing DVM. Nevertheless, some specifically adapted species that are able to downregulate their metabolic activity at low oxygen levels actively migrate into severely suboxic to anoxic OMZs (e.g. *Eucalanus inermis* and *Euphausia mucronata*; Escribano et al. (2009)). Estimates of zooplankton and nekton mediated carbon fluxes in OMZ regions are rare. For the northern Chilean upwelling in the ETSP, Escribano (2009) found that migrations of only two key species (*Eucalanus inermis* and *Euphausia mucronata*) contribute approximately 7.2 g C m^{-2} d^{-1} to the OMZ through respiration, mortality, and production of fecal pellets within the OMZ. In comparison, passive sinking of C off northern Chile at 60 m depth is estimated to range from 0.093 to 0.152 g C m^{-2} d^{-1} (Gonzalez et al., 2000). In a much less intense OMZ area (e. g. in the tropical Atlantic at the Bermuda Atlantic Time Series Station), DVM-related transport was found to account for 30% of C and 57% of N export from the euphotic zone, relative to trap particulate C and N (Steinberg et al., 2002), thus demonstrating the significance of DVM as export mechanism.

A specific role of DVMs for the N cycle results from the secretion of ammonium: Ammonium is an important nutrient in the anammox reaction which represents nearly 30-50% of N-loss activity in the OMZ (Codispoti et al., 2001;Emery et al., 1955;Gruber, 2004). Bianchi et al. (2014) suggested that DVMs could supply as much as 30% of the ammonium for the anammox reaction, however assuming no reduction of ammonium excretion at OMZ conditions, which in fact occurs quite drastically (Kiko et al., 2015a;Kiko et al., 2015b). Although the full significance of anammox activity in the ETSP is still not well understood, it may be a major term in the N cycle in that region (see section 4).

2.5 Why viruses are important for (understanding) OMZ biogeochemistry

With an estimated number of 4×10^{30}, viruses outweigh the number of prokaryotes (~1.2×10^{29}) in the ocean by thirty times (Suttle, 2005;Whitman et al., 1998) and parasitize approximate 5-30% of the marine cyanobacteria and heterotrophic bacteria (Ostfeld et al., 2010). Thus, it has been proposed that viruses have potentially profound effects on microbe-driven biogeochemical processes in the oxic waters as well as in OMZ waters (Cassman et al., 2012).

Without viral infection, microbial communities would be dominated by few competitive taxa that most effectively scavenge the available resources (Thingstad and Lignell, 1997). However, viruses can effectively regulate the most active microbes by controlling their numbers. On the other hand, viruses can change nutrient stoichiometry in the water column directly through lytic events. Lysis of bacterial cells leads to a release of organic compounds stored within them (Breitbart, 2012). This transfer of nutrients from living organisms into the dissolved phase is called the 'viral shunt' (Breitbart, 2012). Approximately 5-40% of the organic matter from, e.g., cyanobacteria and other prokaryotes, is recycled to dissolved organic matter (Ostfeld et al., 2010), increasing microbial respiration rates and decreasing the efficiency of carbon transfer to higher trophic levels (Suttle, 2005). Specifically, (cyano)phages in the ETSP have been shown to release micronutrients such as iron into surrounding waters at an estimated flux of 10 pmol L^{-1} d^{-1} (Poorvin et al., 2004). Likewise, virus-induced bacterial lysis is responsible for a global N release of ~1-6 Gt a^{-1}, which significantly supports phytoplankton production (Shelford et al., 2012). Viruses further impact the efficiency of the biological pump (Azam, 1998) by influencing particle formation and disaggregation through discharging adhesive cell components (Peduzzi and Weinbauer, 1993) and cell lysis (Weinbauer et al., 2011), respectively.

Cassman et al. (2012) discovered high abundances of DNA sequences originating from siphoviruses, a family of bacteriophages within the order Caudovirales (see Figure 2 in Clokie et al. (2011)) in the ETSP OMZ core. Siphoviruses are frequently lysogenic (Dwivedi et al., 2013). This supports the hypothesis that viral lysogeny is more active in extreme environments (Maurice et al., 2011;Cassman et al., 2012). If lysogeny is the prevailing mode of existence in OMZ core viruses, one would expect changing environmental conditions such as temperature shifts (Bertani and Nice, 1954;Seeley and Primrose, 1980) to induce lysis of host cells. This would consequently lead to shifts in water column nutrient budgets that cannot be accounted for in biogeochemical models by microbial processes alone.

Bacteriophages often carry auxiliary metabolic genes (AMGs) for critical rate-limiting steps of a host's metabolism (Breitbart, 2012). For example, AMGs have been involved in photosynthesis

(Alperovitch-Lavy et al., 2011), nucleotide metabolism, carbon metabolism, phosphate metabolism, stress response, antioxidation and translational/posttranslational modification (Breitbart, 2012 and references therein). Interestingly, various genes involved in the cycling of nitrogen and sulfur have been also found in viromes of ETSP waters (see Tables S3 and S4 in Cassman et al. (2012)). These studies point towards a role of prokaryotic viruses in driving microbial metabolic diversity and thus biogeochemical processes in OMZ waters.

To approach the role of OMZ microbial viruses in lysis, lysogeny and transfer of AMGs, knowledge of the 'host-virus susceptibility pairs' - which microbes are infected by which viruses – is required. A search of OMZ viral sequences in matching microbial metagenomic libraries failed to identify such pairs (Cassman et al., 2012). The authors conjectured that host microbes of OMZ viruses may be particle-bound and hence have been overlooked due to their removal in pre-filtering steps. As particle-associated microbes are fairly common in OMZs as highly productive environments (Ganesh et al., 2014), the respective viruses would be expected to be associated with particulate matter, too.

3 Fluxes of organic matter in tropical shallow OMZs

Physical diffusive and advective transport processes largely control the supply of O_2 to the OMZ, whereas sinks involve biological processes including respiration of organic matter (OM). In the following section we shortly review key components of organic matter fluxes (passive sinking of particles, physical downward transport of DOM; the role of zooplankton mediated fluxes has already been described in Section 2) in tropical OMZs and synthesize recent ideas on that topic.

3.1 Sinking of particles

Knowledge about particle fluxes in areas of tropical OMZs is scarce and predominantly derived from deep moored traps (Honjo et al., 2008). Only few studies have addressed upper ocean export fluxes and mesopelagic flux attenuation in tropical OMZs, such as Martin et al. (1987), Devol and Hartnett (2001) and VanMooy et al. (2002) for the Eastern Tropical Pacific by means of surface tethered sediment traps, Buesseler et al. (1998) for the Arabian Sea by means of ^{234}Th, and Iversen et al. (2010) at the northern edge of the ETNA OMZ by means of particle camera profiling. In the eastern tropical north Pacific (ETNP; Martin et al. (1987); Van Mooy et al. (2002); Devol and Hartnett (2001)), as well as in the ETSP (Martin et al. 1987; Dale et al. (2015)) mesopelagic POC fluxes were less attenuated with depth (Martin curve exponent ‘b’ of 0.32-

0.81) compared with the widely used “open ocean composite” of b=0.86 (Martin et al. 1987). Those studies indicate that a greater proportion of the sinking OM escapes degradation while sinking through the eastern tropical Pacific OMZ. On the other hand, it has been shown that microbial degradation of organic N and proteins under suboxia is not strongly affected (Pantoja et al., 2009;Pantoja et al., 2004;Van Mooy et al., 2002). Still, little is known about the microbial controls on the decomposition of organic matter under lower O_2 concentrations. An alternative hypothesis could be that the diminished abundance of metazoans in the core of the OMZ results in a lowered flux attenuation. If particles are not repackaged, fed upon, or destroyed, they might sink at greater speeds through the OMZ, which would result in decreased degradation.

3.2 Physical fluxes of DOM

In contrast to particle fluxes, DOM transport is due exclusively to physical transport processes. Here, we discuss horizontal and vertical DOM fluxes induced by mesoscale (horizontal scales of 10 – 100 km) and sub-mesoscale (100 m – 10 km) motion and vertical fluxes due to diapycnal mixing. As an example of lateral eddy transport, elevated DOM concentrations have been detected (+11 µmol C L^{-1}) in the Canada Basin within an eddy originating from the shelf region (Mathis et al., 2007). Lasternas et al. (2013) suggested a mechanism for DOM accumulation within anticyclonic eddies, where nutrient downwelling causes a progressive oligotrophication, enhanced cell mortality and lysis, which results in additional DOM release. Numerical model simulations of the Peruvian upwelling regime show that mesoscale dynamics increase the downward and offshore export of nutrients and biomass out of the coastal surface ocean (Lathuiliere et al., 2010). Gruber et al. (2011) found that mesoscale eddy activity in upwelling regimes results in a net reduction of biological productivity. Additionally, sub-mesoscale upwelling filaments can enhance the off-shelf flux of labile DOM (Alvarez-Salgado et al., 2001). Vertical velocities are higher at sub-mesoscale density fronts (Klein and Lapeyre, 2009;Levy et al., 2012;Thomas et al., 2008), which are prominent features in eastern boundary upwelling systems (Durski and Allen, 2005). These vertical velocities often extend to below the mixed layer (Klein et al., 2008), where they can drive sizeable vertical fluxes of solutes. Mahadevan (2014) proposes the subduction of organic matter-rich surface water into the subsurface layers within submesoscale cold filaments as a new export mechanism, which differs strongly from export via particle sinking. In filaments the organic matter is subducted together with large amounts of O_2, which then can directly be used for decomposition of organic matter. Vertical mixing of DOM from the euphotic into to the upper mesopelagic zone is another important transport mechanism in (sub)tropical waters (Hansell, 2002). The Bermuda Atlantic Time-Series Study provides a well-documented example of this process (Carlson et al., 1994). The efficiency of the downward DOM transport depends on the concentration gradient of DOM between the surface layer and the OMZ, and on the activity of the microbial population along this gradient. Produced by high primary production in upwelling regions, DOM can accumulate in the euphotic zone with maximum concentrations of 100-300 µmol C L^{-1} off Peru (Franz et al., 2012a;Romankevich and Ljutsarev, 1990). Due to the vicinity of the DOM-rich surface layer above and the O_2-depleted waters below the shallow and sharp oxycline of the Peruvian OMZ, physical vertical transport may bring large amounts of labile organic matter to the OMZ, where it may be utilized by heterotrophic communities (Hoppe et al., 2000;Hoppe and Ullrich, 1999;Pantoja et al., 2009). DOM supply via (sub-) mesoscale vertical transport processes and diapycnal mixing may therefore contribute importantly to sustaining microbial activity in the Peruvian OMZ and may thus largely impact biogeochemical cycles. A particular role for N turnover processes is discussed in the following section.

4 The Nitrogen Cycle in OMZ waters

4.1 Background

N is an essential nutrient and a fundamental component of living organisms. OMZ waters play a crucial role in regulating the availability of N containing nutrients and are a main site of nitrous oxide (N_2O) formation in the ocean (see Section 6). OMZs account for around 30–50% of oceanic N loss by heterotrophic denitrification and anammox, the anaerobic ammonium oxidation with nitrite (Codispoti et al., 2001). There is an ongoing debate on whether the marine N budget is balanced (Gruber and Sarmiento, 1997), as several studies have suggested that N loss might exceed N_2 fixation (Gruber and Sarmiento, 1997;2007). Based on the N deficit present in OMZ regions, it has been suggested by model studies, that OMZ waters may provide a niche for N_2 fixation (Deutsch et al., 2007), which had previously not been taken into account. From this background, the following major goals with regard to the N cycle were identified: (i) investigate the O_2 sensitivity of N cycle processes, (ii) unravel the impact of changes in dissolved O_2 on nutrient stochiometry, (iii) better constrain N_2 fixation rates, which may have been underestimated, before, and (iv) identify feedback controls of the N cycle.

In order to approach these goals, a combination of rate measurements of N_2 fixation, nutrient regeneration, N turnover, N loss processes and N_2O production were performed in the ETNA and ETSP OMZ waters. Key players of marine N cycle processes were identified and quantified using meta-omics and mesocosm studies were used to gain insights into controls on nutrient stochiometry in OMZs.

4.2 O_2 - a major control of N cycle processes in two contrasting OMZ regions

Under O_2 depletion, N is continuously removed by anammox, (Francis et al., 2007;Kuypers et al., 2005;Kuypers et al., 2003;Thamdrup and Dalsgaard, 2002), which has been shown to be the dominating N loss process in the OMZ waters off Namibia (Kuypers et al., 2005), Peru (Hamersley et al., 2007) and Chile (Thamdrup et al., 2006). Moreover, N is (i) lost by denitrification (the 4-step reduction of NO_3^- to N_2 (Devol, 2008)), which has been identified as the dominant N loss process in the Arabian Sea OMZ (Ward et al., 2009), or (ii) recycled by both DNRA (the **d**issimilatory **n**itrate **r**eduction to **a**mmonium, as hypothesized by Lam et al. (2009)) and nitrification (the aerobic oxidation of ammonium via NO_2^- to NO_3^- under oxic to suboxic conditions (Ward, 2008)). Although different anaerobic microbial processes may have different O_2 tolerance i.e. as an adaptation to transient O_2 conditions (Jensen et al., 2007;Kuypers et al., 2005) the regulation of these processes in OMZ waters are still poorly understood.

An apparent dominant role of anammox for N loss in the Peruvian and Namibian OMZs challenges our understanding of organic matter remineralization in these regions (see Figure 3 for an overview of N cycle processes in the OMZ off Peru). Previously, organic matter remineralization in OMZ waters with low to non-detectable (<5 µmol kg^{-1}) O_2 concentrations was attributed to heterotrophic denitrification (e.g. Codispoti et al. (2001)). Without remineralization of NH_4^+ from organic matter via denitrification, it is unclear how anammox could be sustained. Combined ^{15}N-incubation experiments and functional gene expression analyses indicate that anammox in the Peruvian OMZ benefits from other N-cycling processes for reactive substrates (Kalvelage et al., 2011). Excretion of ammonium and other reduced N-compounds by diel vertical migrators was also proposed (Bianchi et al., 2014), but recent experiments indicate that ammonium excretion of diel vertical migrators is strongly reduced at anoxia (Kiko et al. 2015 a, Kiko et al. 2015 b). Additionally, anammox activity has been described to depend on export of organic matter (Kalvelage et al., 2013), potentially resulting from the availability of ammonium recycled from particulate organic N (Ganesh et al., 2015). In the absence of significant denitrification, these results indicate that anammox relies on NH_4^+ oxidation and NO_3^- reduction as NO_2^- source. Further, NH_4^+ may be derived from remineralization of organic matter via NO_3^- reduction with a possibly important role of microaerobic respiration (Kalvelage et al., 2015). The overlap between aerobic and anaerobic N-cycling processes in particular in the coastal shelf waters and the upper part of the OMZ is supportive of microaerobic activity in the OMZ. As DNRA was insignificant in the water column during our studies in the ETSP, sedimentary fluxes could be an important ammonium source, particularly for the inner shelf sediments (Bohlen et al., 2011;Kalvelage et al., 2013). However, it has been suggested that sulfate reduction is more widespread in OMZ waters than previously believed and could be responsible for substantial NH_4^+ production (Canfield et al., 2010) and sulfate reducers have been detected in the Peruvian OMZ (Schunck et al., 2013). Direct evidence for the actual link between sulfate reduction and NH_4^+ production is, however, still missing.

In contrast to the ETSP, the open ETNA, with O_2 concentrations usually above 40 µmol kg^{-1}, shows classically no sign of water column N loss (see, e.g., Bange et al. (2010)). It is characterized by nitrification as the only N turnover process in this area (Löscher et al., 2012). However, recent studies on the presence of anoxic mesoscale water masses show a potential for denitrification (Löscher et al., 2015). Still, the impact of those mesoscale eddies for N cycling in that region is to date not clear. The strong difference between the ETNA and ETSP OMZs is mirrored by a diverging δ^{15}N-nitrate signal, which is strongly positive in the ETSP but has negative values in nitrate depleted surface waters of the ETNA (Ryabenko et al., 2012), indicating different N turnover processes characteristic for these two regions.

4.3 The role of nutrient stoichiometry for primary production and N turnover in OMZ waters

Despite the fundamental differences between the OMZs of the ETNA and ETSP with regard to N loss, the results of short-term mesocosm experiments implied N limitation of surface plankton communities in both areas (Franz et al., 2012a;Franz et al., 2012b). The loss of bioavailable N in OMZ waters through denitrification and anammox in combination with the release of reactive phosphorus from sediments exposed to anoxic waters generates extremely low inorganic N:P ratios. This abnormal stoichiometry of nutrients supplied to the euphotic zone can impact primary production. Franz et al. (2012b) investigated the partitioning and elemental composition of dissolved and particulate organic matter during cruises to the tropical South East Pacific and North East Atlantic. Maximum accumulation of POC and PON was observed under high N supply, indicating that primary production was controlled by N availability. Part of the excess P was consumed by non-Redfield production, predominantly by diatoms. While particulate N:P of the accumulated biomass generally exceeded the supply ratio (Franz et al., 2012b), excess P of the dissolved nutrient pool was channeled into release of dissolved organic phosphorus (DOP) by phytoplankton. These results demonstrated that excess P upwelled into the surface ocean overlying O_2-deficient waters represents a net source for DOP and motivated further dedicated mesocosm experiments in the ETNA to elucidate the fate of DOP. Here, a general stimulating effect of DOP on N_2 fixation has been observed (Meyer et al., 2015). Moreover, recent modeling based on large-scale surface data sets of global DON and Atlantic Ocean DOP suggests an important role of DOP for stimulating growth of N_2 fixing organisms (Somes and Oschlies, 2015). This model indicates that the marine N- budget is sensitive to DOP, provided that access to the relatively labile DOP pool expands the ecological niche for N_2 fixing organisms, so called diazotrophs.

Franz et al. (2012a) reported in situ observations along an east-west transect in the ETSP at 10°S stretching from the upwelling region above the narrow continental shelf to the well-stratified oceanic section of the eastern boundary regime. They showed that new production in the coastal upwelling was driven by large-sized phytoplankton (e.g. diatoms) with generally low N:P ratios (<16:1). A deep chlorophyll *a* maximum consisting of nano- (*Synechococcus*, flagellates) and microphytoplankton occurred within a pronounced thermocline in subsurface waters above the shelf break associated with intermediate particulate N:P ratios close to Redfield proportions. High PON:POP (>20:1) ratios were observed in the stratified open ocean section, coinciding with a high abundance of the pico-cyanobacterium *Prochlorococcus.* Excess P was present along the entire transect but did not appear to stimulate growth of N_2 fixing cyanobacteria, as pigment fingerprinting and phylogenetic studies did not indicate the presence of diazotrophic cyanobacteria at most of our sampling stations (Franz et al., 2012a;Löscher et al., 2014), mostly in accordance with other studies from this area (Bonnet et al., 2013;Fernandez et al., 2011;Turk-Kubo et al., 2014). A large fraction of the excess P generated within the OMZ was consumed by non-Redfield processes, likely primary production by large phytoplankton found in shelf surface waters. N_2 fixation in this region responds significantly to Fe and organic carbon additions

(Dekaezemacker et al., 2013). N_2 fixation could be directly limited by inorganic nutrient availability, or indirectly through the stimulation of primary production and the subsequent excretion of dissolved organic matter and/or the formation of micro-environments favorable for heterotrophic N_2 fixation (Dekaezemacker et al., 2013).

It is generally assumed that both zooplankton and heterotrophic bacteria vary much less in their elemental stoichiometry than phytoplankton (e.g., Touratier et al. (2001)). In both cases, the heterotrophs appear to respond to variable nitrogen content in their food by regulating their gross growth efficiency for carbon (Anderson and Williams, 1998;Kiørboe, 1989). In OMZ regions, this implies that strong nutrient limitation in the surface ocean, which is associated with high C:N ratios in primary producers (e.g., data used in Pahlow et al. (2013)), should intensify denitrification in the OMZ relative to the export flux from the surface. Higher surface nutrient concentrations would then be expected to reduce C:N ratios in the export flux and hence have a somewhat mitigating effect. Since denitrification and anammox in the OMZ cause lower nitrate concentrations in upwelled waters, the variable stoichiometry of phytoplankton could add to the positive feedback between denitrification and N_2 fixation by increasing C:N ratios in response to decreasing surface nitrate concentrations. However, one of the predictions of the optimality-based model of N_2 fixation by Pahlow et al. (2013), which is based on the assumption that natural selection should tend to produce organisms optimally adapted to their environment, is that the competitive advantage of diazotrophs is most pronounced under conditions of low dissolved inorganic N and increased dissolved inorganic P (DIN, DIP) availability (Houlton et al., 2008). The ability to compete for DIP should be less important at high DIP. Thus, high phosphate concentrations above the ETSP OMZ might actually reduce the selective advantage of diazotrophs compared to ordinary phytoplankton. This could partially explain why cyanobacterial N_2 fixers were apparently not stimulated by excess phosphate in the abovementioned transect.

4.4 N_2 fixation- an underestimated term of the N budget in OMZs

The atmospheric pool of N_2 is only available to living organisms via biological N_2 fixation, which is restricted to a limited group of prokaryotes (Capone and Carpenter, 1982). Until recently, oceanic N_2 fixation was mainly attributed to phototrophic cyanobacteria, such as *Trichodesmium* or *Crocosphaera*, which due to their light demand are restricted to usually nutrient depleted surface or subsurface waters (Capone et al., 1997;Zehr and Turner, 2001). Thus, estimates of N_2 fixation might be strongly biased as they focused exclusively on N_2 fixation by those cyanobacterial diazotrophs in the euphotic zone (Codispoti, 2007). Model studies (Deutsch et al., 2007), assuming that a N-deficit with respect to Redfield stoichiometry provides a niche for diazotrophs and that a coupling of N loss in OMZs and N_2 fixation in overlying surface waters might restore the N:P ratio towards Redfield proportions.

O_2 concentrations at the sea surface are not favorable for N_2 fixation, as the key enzyme for this process, the nitrogenase, is irreversibly inhibited by O_2 (Dixon and Kahn, 2004). Laboratory culture studies of the unicellular N_2 fixing cyanobacterium *Crocosphaera watsonii* grown under different O_2 levels suggest that respiration at 5% O_2 level could already provide sufficient energy for the energy-consuming N_2 fixation process, hence the low O_2 in OMZ waters would likely favor N_2 fixers (Großkopf and LaRoche, 2012). Moreover, a growing number of different *nifH* sequences (the key functional gene of N_2 fixation, encoding the α subunit of nitrogenase) detected within the Peruvian OMZ (Fernandez et al., 2011;Löscher et al., 2014;Bonnet et al., 2013;Dekaezemacker et al., 2013;Turk-Kubo et al., 2014), as well as in OMZ waters of the ETNA (Joshi, Löscher et al., unpublished), did not belong to common oxygenic phototrophs, but to some unknown diazotrophic microorganisms that might be specifically adapted to O_2 deficient conditions. This broad diversity of diazotrophs, as well as the extension of their habitat to deeper waters might be one reason for the possible underestimation of N gain compared to N loss in the ocean (Codispoti, 2007). While the possibility of N imbalance cannot be fully excluded at this point, estimates for N_2 fixation may have been systematically underestimated when extrapolated from discrete measurements (Codispoti, 2007). A methodological problem associated with the commonly used $^{15}N_2$-tracer technique and subsequent calculation (Montoya et al., 1996) resulted in a significant underestimation of N_2 fixation rates (Mohr et al., 2010). A revised method was subsequently developed (Mohr et al., 2010) and its application in the Atlantic (Großkopf et al., 2012) revealed up to 6-fold higher N_2 fixation rates than those determined with the classical method. Großkopf et al. (2012) extrapolated the revised rates to all ocean basins resulting in a rate of 177 ±8 Tg N yr^{-1}, which still does not compensate for the N loss from the ocean (400 Tg N yr^{-1}, Codispoti, (2007)). If taking into account only the water column N loss of 150 Tg N yr^{-1}, the revised N_2 fixation rate of Großkopf et al. (2012) would balance the water column N budget. However, an imbalance resulting from benthic N loss of ~150 Tg N yr^{-1} (Bohlen et al., 2012) remains to be explained. A recent study demonstrated, that N_2 fixation rates may have largely been misinterpreted as the applied gas stocks were to different degrees contaminated with other

^{15}N compounds, such as nitrate or ammonium (Dabundo et al., 2014). This study raised concern about previously measured N_2 fixation rates. Alternative approaches such as natural N isotope analysis seem to produce substantially higher integrated N_2 fixation rates (Hauss et al., 2013;Sandel et al., 2015).

4.5 Feedback controls of the N cycle in OMZ waters

During aerobic respiration surface derived organic matter is remineralized back to the inorganic forms of carbon and N. These inorganic forms are available again for primary producers after subsequent transport to the surface via mixing or upwelling. N_2 fixing bacteria can counter to some degree the N-loss processes by converting N_2 back to bioavailable ammonium in the OMZ. N_2 fixation and N loss processes predominantly determine the global oceanic N:P ratio since the phosphorus content stays relatively constant.

In OMZs, the N deficit resulting from N loss and the simultaneous release of phosphorus (P) from anoxic shelf sediments (Ingall and Jahnke (1994)), is proposed to provide niches for diazotrophs and thus may promote N_2-fixation. A spatial connection of N loss and N input via N_2 fixation in OMZs has therefore been hypothesized (e.g., Deutsch et al. (2007)). The prevalence of novel *nifH* genes and active N_2 fixation, derived from samples collected directly in the OMZ waters off Peru, where anammox bacteria were abundant and active (Kalvelage et al., 2013;Löscher et al., 2014), supports the view of a positive feedback between N loss and N gain communities (Figure 4). Evidence for co-occurrence of denitrification and N_2 fixation has previously been documented only for an anoxic lake (Halm et al., 2009), and for cyanobacterial aggregates in the Baltic Sea (Klawonn et al., 2015). Recent investigations from Baltic Sea sediments on N_2 fixation and diazotrophic abundance in sediments show, however, that a very close spatial link between N loss and N_2 fixation might exist (Bertics et al., 2013). Still, too little is currently known about the interactions among the stoichiometry of inorganic nutrient supply, primary production, N_2 fixation, and remineralization under anoxic conditions, to allow a definite characterization of the conditions leading to fixed-nitrogen exhaustion in the OMZs.

Model studies, suggest that denitrification of N_2 fixation-derived organic matter may lead to a net N loss that further stimulates N_2 fixation, because 120 moles of nitrate per mole of phosphorus are used to remineralize Redfield organic matter via denitrification (Landolfi et al., 2013). In contrast, N_2 fixation fixes only 16 moles N (per mole P). Because of those stoichiometric constraints, denitrification of newly fixed N would lead to a net loss of N, which would then enhance the N deficit, promoting further N_2 fixation, a cycle that ultimately leads to a runaway N-loss (Landolfi et al., 2013). Only by spatial or temporal decoupling of N_2 fixation and N loss, e.g., by reduced remineralization rates in the OMZ (Su et al., 2015), iron limitation or dissolved organic matter cycling, the N inventory may stabilize, otherwise the OMZ would become completely void of fixed inorganic N. That this does not occur in today's major oceanic OMZs indicates that the positive feedback between N_2 fixation and denitrification does not operate at full strength, if at all.

Because denitrification removes more fixed N than is contained in the remineralized organic matter, any addition of fixed N to the surface ocean only exacerbates the problem (Canfield, 2006) unless the corresponding primary production is prevented from being remineralized in the underlying OMZ (Landolfi et al., 2013). The net rate of N loss in OMZs is determined by the balance of remineralization of sinking particulate organic carbon (POC) and O_2 supply to the OMZ. While the supply of O_2 is mostly determined by physical transport, the rate of N loss depends on the activity of the bacteria responsible for denitrification and anammox as well as the POC export and sinking velocity.

The intensity of this feedback may be overestimated in current biogeochemical models, owing to spurious nutrient trapping (Dietze and Loeptien, 2013). The extent of the coupling between primary production at the surface and denitrification in the OMZ, and hence the strength of the positive feedback, is a strong function of the elemental (C:N:P) stoichiometry of the exported primary production. Phytoplankton C:N:P stoichiometry in turn is influenced by the stoichiometry of inorganic nutrients (Franz et al., 2012a;Franz et al., 2012b). Recently developed process models of primary production and N_2 fixation (Pahlow et al., 2013;Pahlow and Oschlies, 2013) specifically address the response of phytoplankton elemental stoichiometry to ambient nutrient concentrations and light.

Tropical OMZs have been widening and intensifying over recent decades (Stramma et al., 2008), which could also indicate a strengthening of the fixed-N sink. The occurrence of widespread ocean anoxic events in Earth's history (Jenkyns, 2010) is a clear sign that further positive feedbacks in the biogeochemical cycles of O_2 and N may be triggered once a certain tipping point is reached.

5 Oceanic sulfidic events and detoxification by sulfide-oxidizers in the Peruvian upwelling: Open questions

5.1 Background

Burtt (1852) with a study off Peru can be credited with the first observation of the effect of toxic hydrogen sulfide on marine organisms. Burtt states, “The fish, during this evolution, rose in vast numbers from the bottom; and after struggling for some time in convulsions upon the surface, died.” This devastating phenomenon, known as a sulfidic event, is harmful economically to productive coastal fisheries in the Peruvian upwelling but also elsewhere (Hamukuaya et al., 1998;Hart and Currie, 1960;Weeks et al., 2002;Copenhagen, 1953;Naqvi et al., 2000). The next earliest observation off Peru was in the 1970’s which brought further attention to sulfidic events indicating both the occurrence of sulfide by smell, and intriguingly the absence of nitrate and nitrite at the same water depth (Dugdale et al., 1977). The authors correctly incited the microbial removal of sulfide by nitrate reduction to N_2 or N_2O. To date sulfidic events have been reported in three of the five OMZs by only a handful of studies and hence our current understanding of their regulation, initiation and termination is still limited. Possible analogs for oceanic events are permanently sulfidic areas in enclosed basins of the Baltic Sea (Brettar et al., 2006;Brettar and Rheinheimer, 1991;Glaubitz et al., 2009), the Black Sea (Glaubitz et al., 2010;Jørgensen et al., 1991;Sorokin et al., 1995), the Cariaco basin off Venezuela (Hayes et al., 2006;Taylor et al., 2001;Zhang and Millero, 1993) and Saanich Inlet in Canada (Tebo and Emerson, 1986;Walsh et al., 2009). Oceanic sulfidic events are understood to mostly originate from sulfide production in sediments (Figure 5). Here, the sulfide accumulates to milli-molar concentrations under O_2 and nitrate-free conditions and is released by a diffusive flux into the overlying pelagic water column where it reaches low micro-molar concentrations (Lavik et al., 2009;Schunck et al., 2013). These events are then terminated or detoxified in the pelagic water column by a community of sulfide-oxidizing bacteria. This occurs when sulfide and nitrate are both present thus stimulating sulfide-oxidizing nitrate-reducing bacteria (soNRB). soNRB re-oxidize sulfide back to sulfate or elemental sulfur while reducing nitrate to either N_2 via autotrophic denitrification or NH_4^+ via dissimilatory nitrate reduction to ammonium (Lam and Kuypers, 2011). If nitrate is limiting, sulfur is the more likely end product of sulfide oxidation, which occurs in the following reaction stoichiometry for the denitrification pathway, $2NO^-_3 + 5HS^- + 7H^+ \rightarrow N_2 + 5S^0 + 6H_2O$. A steady state is reached when the diffusive fluxes (mmol m^{-2} d^{-1}) of nitrate and sulfide are in a 1:2.5 ratio.

If the sulfide flux exceeds the nitrate flux by more than a factor of 2.5, then sulfide will diffuse into the oxic layer (Lam and Kuypers, 2011). Importantly, the activity of soNRB help to detoxify sulfide to sulfur, preventing it from reaching overlying productive surface waters, hence most sulfidic events likely go unnoticed (Lavik et al., 2009). However, with the increase in eutrophication and the expansion of OMZs in both the Atlantic and Pacific (Stramma et al., 2008), sulfidic events are expected to become more frequent., as already demonstrated for a time series station in the Baltic Sea (Lennartz et al., 2014).

5.2 Sulfidic events off Peru

The first quantitative measurements and detailed profiles of a sulfidic event in the Peruvian upwelling came from Schunck et al. (2013). During RV Meteor cruise M77/3 in January 2009 sulfidic waters covered >5500 km^2 and contained approximately 2.2 x 10^4 tons of sulfide, making it one of the largest plumes recorded. A total of 9 stations were taken along the coastal transect from Lima to Pisco which showed a ~80 m thick sulfide-rich layer extending at times just below the oxycline. At this interface oxygen (< 1 µmol kg^{-1}), nitrate (<1 µmol kg^{-1}) and nitrite (2 µmol kg^{-1}) profiles overlapped with detectable sulfide concentrations. Stable isotope rate measurements and targeted gene assays using quantitative PCR indicated that various oxidants could have been used by the microbial community to oxidize sulfide at the time of sampling. The most abundant sulfide oxidizers identified from the 16S rRNA diversity belonged to the phylum proteobacteria within the subphylum gamma-, including the SUP05/ARCTIC96BD-19–clade, *Candidatus Ruthia magnifica*, and *Candidatus Vesicomyosocius okutanii*, but also epsilon- such as *Sulfurovum* spp. Metagenomics confirmed that all were capable of sulfide or sulfur oxidation, either with nitrate and oxygen (facultative soNRB) or exclusively with oxygen. Indeed, both subphyla appear to be ubiquitous in other seasonally oxic/anoxic waters and OMZs, (Canfield et al., 2010;Lavik et al., 2009;Stevens and Ulloa, 2008;Stewart et al., 2011;Stewart et al., 2012;Walsh et al., 2009;Swan et al., 2011). Both gamma- and epsilon- proteobacteria members are known chemolithoautotrophs, which assimilate carbon dioxide as the carbon source without the use of sunlight. Subsurface C- assimilation rates were between 0.9 to 1.4 µmol C L^{-1} d^{-1} during this sulfidic event. In this study, “dark” primary production had contributed up to 25% of the total CO_2 fixation in the Peruvian upwelling region at the time of sampling, which is comparable to values observed in the Baltic and Black Seas (Schunck et al. (2013) and references therein). Paradoxically, some of these studies showed that measured rates of CO_2 assimilation exceed rates possible by chemolithoautotrophic processes alone. Thus, while chemolithoautotrophic CO_2-fixation is considered a significant process, the specific activity and main contributors of CO_2-fixation during sulfidic events (down to the genus-level) still remain unknown.

Different from our current knowledge of OMZ sulfur cycling is whether the production of sulfide can originate as well from pelagic waters itself. Simultaneous reduction of different electron acceptors (like NO_3^-, SO_4^{2-} and CO_2) can occur in defined niches where particle aggregates have formed and are sinking through the water column (Wright et al., 2012). These aggregates, more commonly known as marine snow, contain micro-scale redoxclines under anoxic conditions (Alldredge and Cohen, 1987;Karl and Tilbrook, 1994;Woebken et al., 2007). Moreover, aggregate communities appear to be distinct from bulk water collected samples (Fuchsman et al., 2011). These communities were suggested to have active manganese reduction, sulfate reduction and sulfide oxidation at the interior of the aggregates. How much sulfide is generated in the water column during a sulfidic event is not well resolved. Nevertheless, *in situ* incubation experiments done in the Chilean upwelling have shown the capacity for sulfate reduction in the offshore OMZ occurring under thermodynamically unfavorable nitrate-rich conditions. In separate incubations measured rates of potential sulfide oxidation were larger than rates of sulfate reduction indicating that any produced sulfide is immediately re-oxidized (Canfield et al., 2010). The authors intriguingly suggested an active but cryptic sulfur cycle linked to nitrogen cycling in the pelagic OMZ. From a biogeochemical perspective large-scale sulfate-reduction coupled to organic matter remineralization releasing inorganic nitrogen could represent a significant supply of ammonium for anammox bacteria.

6 Trace gases

6.1 Background

The upper 1000 m of the ocean (incl. the euphotic zone) are the key regions where the production of climate-relevant trace gases such as carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4) and dimethyl sulfide (DMS) occurs (see, e.g., Liss and Johnson (2014)). While the pathways of CO_2 and DMS are dominated by phytoplankton in the oxic euphotic zone, N_2O and CH_4 pathways are dominated by microbial processes at midwater depth (i.e. in the OMZ). This is especially important since some OMZs are connected to coastal upwelling regions where OMZ waters — enriched in both nutrients and trace gases such as CO_2, N_2O and CH_4 — are brought to the surface fuelling phytoplankton blooms and releasing trace gases to the atmosphere (see, e.g., Capone and Hutchins (2013)). Thus, although they are usually not in direct contact with the atmosphere, OMZs play an important role for oceanic emissions of climate-relevant trace gases (see e.g. Arévalo-Martinez et al. (2015)).

6.2 Nitrous oxide (N_2O) in OMZ

A comprehensive overview of both nitrous oxide (N_2O) distributions and pathways in OMZ has been published in (Naqvi et al., 2010). Therefore, we concentrate here on recent findings from the ETNA and ETSP.

N_2O production in the ocean is dominated by microbial nitrification and denitrification processes. It is formed as a by-product during nitrification and as an intermediate during denitrification. The paradigm that N_2O is exclusively produced by bacteria has been challenged by the discovery of nitrifying (i.e. NH_4^+ oxidising) archaea dominating N_2O production in the ETSP and ETNA (Löscher et al., 2012), which is supported by results of a culture study (Löscher et al., 2012) and a marine microbial enrichment experiment (Santoro et al., 2011). The production of N_2O by archaea (and bacteria) depends on dissolved O_2 and is increasing with decreasing O_2 concentrations (Frame and Casciotti, 2010;Löscher et al., 2012). Denitrifying bacteria do not produce N_2O in the presence of O_2 (> 10 µmol kg^{-1}); however, when O_2 concentrations are approaching 0 µmol kg^{-1}, N_2O is consumed during denitrification. There is no N_2O production under anoxic conditions. The significance of N_2O production during anammox (Kartal et al., 2007) and DNRA (Giblin et al., 2013) in OMZs (see Section 5) remains to be proven.

The detailed investigation of ΔN_2O/AOU (= excess N_2O/apparent oxygen utilization) and $\Delta N_2O/\Delta^{15}NO_3^-$ relationships from the ETNA and ETSP revealed two facts (Ryabenko et al., 2012): (i) The lower O_2 concentrations found in the core of the OMZ of the ETSP (< 5 µmol kg^{-1}) favour N_2O consumption by denitrification which is not observed in the ETNA because of its comparably high O_2 concentrations and (ii) the maximum observed N_2O concentrations were higher in the ETSP than in the ETNA. This is in line with the results of two model studies of N_2O in the ETSP by Zamora et al. (2012) and Cornejo and Farias (2012), which suggested that the switching point between N_2O production and N_2O consumption occurs at higher O_2 concentration (~ 8-10 µmol kg^{-1}) than previously thought.

In contrast to the open ocean, OMZs in coastal (i.e. shelf) regions show a higher spatial and temporal variability: Seasonally occurring suboxic or even anoxic/sulfidic OMZs have been observed in coastal regions worldwide (see e.g. Diaz and Rosenberg (2008)). One of the most prominent areas where widespread sulfidic conditions have been recently observed is the shelf off Peru (Schunck et al., 2013) (Section 5). Figure 6 shows the distribution of N_2O, water temperature, nutrients and H_2S during the sulfidic event described by Schunck et al. (2013) on the shelf off Peru during December 2008/January 2009. Here, extreme N_2O concentrations are found at the boundary to the H_2S containing bottom waters. No N_2O is found in the core sulfidic layer. This suggests again that there is a narrow range of low O_2 concentrations which is associated with exceptionally high N_2O production. As soon as the O_2 concentrations are close to zero (anoxic/sulfidic conditions) N_2O production turns into N_2O consumption. Similar N_2O distributions during anoxic/sulfidic events were found off the west coast of India, in the Gotland Deep (central Baltic Sea) and in Saanich Inlet (Brettar and Rheinheimer, 1991;Naqvi et al., 2000;Cohen, 1978). Brettar and Rheinheimer (1991) suggested a close coupling between H_2S oxidation and NO_3^- reduction in a narrow layer where NO_3^- and H_2S coexist. This is in line with recent findings from the anoxic event off Peru by Schunck et al. (2013) and similar to the suggestion of a cryptic sulfur cycle where sulfate reduction is coupled to rapid H_2S oxidation by NO_3^- proposed for the OMZ off Chile by Canfield et al. (2010).

6.3 The role of OMZs in trace gas emissions

In OMZs with O_2 concentrations below 20 µmol kg^{-1}, N_2O production does not take place in the core of the OMZ. Instead, N_2O production is found at the oxycline. Exceptionally high N_2O concentrations have so far only been found in temporarily occurring anoxic/sulfidic regions off Peru/Chile and West India (Naqvi et al., 2010;Farías et al., 2015). Stagnant sulfidic systems such as in the Baltic and Black Seas as well as the Cariaco Basin, have shown only slightly enhanced N_2O concentrations at the oxic/anoxic interfaces (Bange et al., 2010, and references therein). This implies that significant pulses of N_2O emissions to the atmosphere occur only when a shallow coastal system rapidly shifts from oxic to anoxic/sulfidic conditions and vice versa (Bange et al., 2010). This can be explained by a lag of N_2O reduction by denitrifiers, when they switch from oxygen to nitrogen respiration (Codispoti, 2010) or N_2O production during the reestablishment of nitrification after O_2 ventilation (Schweiger et al., 2007).

CH_4 production is also tightly connected to OMZs (see overview in Naqvi et al., 2010). Similar to N_2O, upwelling areas are considerable hotspots for CH_4 emissions, albeit organic material-enriched shallow coastal zones such as estuaries and mangroves or shallow sediments with geological CH_4 sources show higher emissions (Bakker et al., 2014).

Since DMS is produced by phytoplankton in the euphotic zone, an accumulation of DMS in OMZs appears unlikely. However, measurements at the Candolim Time-Series Station (CaTS) on the shelf off Goa (India) revealed an unprecedented 40-fold increase in DMS concentrations in the sulfidic layers during an anoxic event (Shenoy et al., 2012). These high concentrations could not be explained by any known pathways and may imply an unknown — most likely microbial — DMS production pathway under anoxic conditions either in the water column or in the underlying sediments (Shenoy et al., 2012). Only recently it has been shown that phytoplankton communities exposed to anoxic conditions increase their DMS production significantly (Omori et al., 2015). This implies a potential accumulation of DMS at oxic/anoxic boundaries of coastal OMZs which, in turn, might result in high DMS emissions from shallow coastal zones during anoxic/sulfidic events.

6.4 Trace gas production in OMZ and environmental changes

Trace gas production in OMZs is expected to be influenced primarily by deoxygenation (Naqvi et al., 2010;Stramma et al., 2012). It is also well-known that eutrophication, warming and supply of limiting nutrients (e.g. iron) will increase subsurface respiration of organic material, which leads to deoxygenation in open ocean and coastal OMZs (Bijma et al., 2013;Gruber, 2011). Acidification of the upper ocean may result in a decrease of calcium carbonate (produced by calcifying organisms), which can act as ballast material for sinking organic matter. Less ballast means a reduction in the sinking speed of organic particles, which could increase the residence time of organic material and cause higher respiration rates (Riebesell et al., 2009). Therefore, on-going environmental changes such as deoxygenation, eutrophication, warming and acidification have both direct and indirect effects on trace gas production in OMZs. In general, we might expect enhanced production of N_2O, CH_4 and DMS in OMZs because of the on-going loss of O_2.

Deoxygenation in open ocean and coastal environments may lead, on the one hand, to enhanced N_2O production when approaching the N_2O production/consumption switching point (see above), but on the other hand, when O_2 concentrations fall below the switching point this may lead to a consumption of N_2O (Zamora et al., 2012). Moreover, we do not know whether the frequency of coastal anoxic events will continue to increase and how this may affect the coastal net N_2O production/consumption. A recent modelling study on the influence of anthropogenic nitrogen aerosol deposition and its effect on N_2O production has revealed that the effect is small on a global scale but that the OMZ of the Arabian Sea is especially sensitive to atmospheric nitrogen deposition resulting in an enhanced N_2O production (Suntharalingam et al., 2012).

7 Summary & Outlook

In the following, the predominant processes and biogeochemical interplays are summarized for the ETNA and ETSP, respectively (Figure 7). Our major findings on microbial species distribution and functionality are derived from the ETSP study site: In accordance with several previous studies (Stevens and Ulloa, 2008;Stewart et al., 2012) a large part of the microbial community has been identified to be phylogenetically similar throughout the OMZ. This microbial community does not show pronounced variations on a horizontal perspective, neither with regard to phylogeny nor to functionality, but expresses pronounced vertical patterns (Neulinger and Löscher, unpublished). This overlap in the distributions of microorganisms is also reflected in one of our major findings on N cycle processes, which shows that anaerobic processes such as anammox and denitrification occur along with classical aerobic processes such as nitrification (Kalvelage et al., 2011;Löscher et al., 2012). This combined with the strong correlation between N cycling processes in the OMZ and the organic matter export point towards an important role of microniches, i.e. in aggregated particles containing strong redox gradients that possibly allow the co-occurrence of anaerobic and aerobic processes.

We hypothesize that DOM supply via (sub-) mesoscale vertical transport processes and diapycnal mixing is generally highly important to sustain microbial activity in the Peruvian OMZ. While DOM is transported via horizontal or vertical mixing, large fractions of the POM can be exported to the OMZ via DVM, thus fueling N loss in OMZ waters. Although some organisms performing DVM have certain strategies to cope with anoxic conditions, mostly by down-regulating the aerobic metabolism, there are limits for zooplankton and nekton. Thus, we expect a reduction of OM export by DVM with a further expansion and deoxygenation of OMZs, which might then alter degradation mechanisms due to changes in particle characteristics. A quantification of DOM and POM import and export rates to and from the ETNA is currently not available, an extensive discussion of POC dynamics from the ETSP OMZs is provided in this issue (Dale et al., 2015). Information on the character of microbial processes responsible for POM degradation within the OMZ is however missing.

We suggest that OMZs can reverse the role of remineralization for N cycling, as anoxic remineralization causes net removal of fixed nitrogen, e.g., through denitrification or anammox. Enhanced primary production due to N_2 fixation strengthens the net fixed-nitrogen removal and could trigger a positive feedback leading to the total removal of all fixed nitrogen from an OMZ. An explanation for why this does not happen in the present ocean could be the variable stoichiometry in primary production and the decreased remineralization rates under anoxic conditions. In both systems, the ETNA and ETSP primary production could be stimulated by the exclusive addition of N, but not by a combined addition of N and P sources or solely P (Franz et al., 2012b). This indicates N limitation in both areas, which might either result from multiple factors; lower biomass production and consecutively lower organic matter export, a decrease in the N:P composition in primary producers, or in enhanced diazotrophy. We could confirm that non-Redfieldian primary production occurs and that diazotrophy is indeed enhanced in OMZ waters (Löscher et al., 2014), and is directly coupled to N loss.

We further found an enormous stimulation of all N turnover processes connected to a sulfidic event in shallow coastal waters, which was linked to benthic processes. Here, a specific microbial community is present, which seems to couple the N and S cycles (Canfield et al., 2010). Within this sulfidic zone, we found high rates of dark carbon fixation which account for ~25% of total CO_2 fixation in the water column. The regulation of sulfidic events in the Peruvian upwelling still remains a major open question, as so far most reports have been largely based on qualitative observations (Burtt, 1852;Cabello et al., 2002;de Lavalle y Garcia, 1917;Dugdale et al., 1977;Libes and Deuser, 1988;Sorokin, 1978). Steps are now being taken to set up a continuous monitoring program via regional collaborations to better establish a baseline for sulfide seasonality, intensity and frequency in the Peruvian upwelling region. This will certainly be critical if we want to assess the significance of sulfidic events to biogeochemical cycling of carbon and the impact they may have on regional productivity as a result of global change.

Massive supersaturation of N_2O, connected to sulfidic plumes, has been detected repeatedly. OMZs are important sites of enhanced production of climate relevant trace gases such as N_2O, CH_4, and DMS. N_2O production is significantly enhanced at oxic/anoxic boundaries of OMZs and we suggest that it mainly results from habitat compression, where in extreme cases (such as sulfidic events, sharpening gradients) nitrification and denitrification can occur simultaneously. Maximum N_2O concentrations and subsequent emissions to the atmosphere have been observed in dynamic coastal systems that rapidly shift from oxic to anoxic conditions and vice versa. Although OMZs are usually not in direct contact with the atmosphere, their vicinity to coastal upwelling systems plays an important role for oceanic emissions of climate-relevant trace gases such as N_2O, CH_4, and DMS.

While there is a growing amount of data on the pelagic N cycle in OMZ waters, quantitative estimates of microbial production and respiration, particularly at ultra-low O_2 levels, are rather scarce. Further unresolved is the role of particulate organic matter that could act as microniches for microbes and thus host certain processes such as microaerobic respiration in OMZ waters. By containing strong redox gradients in relatively narrow vicinity, and by providing nutrients and trace metals, particles might strongly influence biogeochemical cycles. It is well-known that in the core of OMZs adjacent to coastal upwelling regions, such as those found off Peru, Mauritania and the Arabian Sea, a pronounced POM/particle-enriched turbid layer (a so-called intermediate nepheloid layer) exists (see, e.g., Stramma et al. (2013); Naqvi et al. (1993); Fischer et al. (2009)). The microbial activity of the nepheloid layer is supposed to be high and thus it seems to play a role for the biogeochemistry and the maintenance of the OMZ, but it is hitherto not very well defined, neither qualitatively nor quantitatively, which may be an important missing factor for biogeochemical estimates.

Marine ecosystems and biogeochemical cycles are increasingly impacted by a growing number of stress factors, some of which act locally, such as eutrophication and pollution, others globally. Global stressors are associated with anthropogenic carbon dioxide (CO_2) emissions and affect the ocean either directly through CO_2-induced acidification or indirectly through climate change-induced ocean warming and deoxygenation (Ciais et al., 2013). How these stressors will impact marine ecosystems and biogeochemistry, individually or in combination, is still largely unknown.

Ocean warming, acidification and deoxygenation occur globally and simultaneously, although with distinct regional differences. Through increased stratification and decreased nutrient supply to the surface layer, ocean warming is expected to decrease the biological production in the already stratified low to mid latitudes.

While research on ocean warming is relatively advanced, far less is known about the impacts of ocean acidification and deoxygenation on marine organisms and ecosystems. Because the three stressors have mostly been studied in isolation, knowledge on the combined effects of two or more of them is scarce. In principle, additive, synergistic (more than additive) and antagonistic (less than additive, i.e. compensatory) interactions of effects are possible, but *a priori* it is impossible to judge what the combined effects will be. One example for a synergistic effect is that of ocean acidification narrowing the thermal tolerance window of some organisms, amplifying the impact of warming (Pörtner and Farrell, 2008). However, we consider interactions among stressors in marine communities largely understudied.

8 Open questions

Major issues remaining unresolved, in addition to those highlighted above, concern (1) a mechanistic understanding of organic matter degradation and nutrient cycling at low or variable oxygen concentrations in the water column and the role of DVM for organic matter supply to the OMZ, (2) the sensitivities of heterotrophic microbes and their sensitivity to low oxygen conditions, and (3) biogeochemical feedback processes in oxygen minimum zones and their impacts on local to global scales.

Future studies should combine measurements of particle flux, zooplankton abundance, microbial activities and O_2 concentrations in order to answer the following key questions:

I. What is the effect of low oxygen conditions (below 20 µmol kg^{-1}) on organic matter degradation? And what is the partitioning between DOM and POM in OMZ waters?

II. How do the rates of nutrient cycling and loss in OMZs relate to particles and associated microniches?

III. How does nutrient stoichiometry influence phytoplankton production and succession and what is the ultimate fate of excess phosphate?

IV. What are the rates of oxygen supply and consumption in the upper OMZ? And what is regulating respiration rates?

V. Do small-scale processes affect fluxes on larger scales? And how can models represent these important processes?

Acknowledgements

We thank IMARPE and INDP for close collaboration and support. We further thank the authorities of Peru, Cape Verde and Mauritania for the permission to work in their territorial waters. We acknowledge the support of the captains, crews of R/V Meteor and the chief scientists. We thank A. Dale for discussion of the benthic perspective of the manuscript. Financial support for this study was provided by the DFG Sonderforschungsbereich 754 (www.sfb754.de), and the Max Planck Society (MPG).

References

Alldredge, A. L., and Cohen, Y.: Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets., Science, 235, 689-691, 1987.

Alvarez-Salgado, X. A., Doval, M. D., Borges, A. V., Joint, I., Frankignoulle, M., Woodward, E. M. S., and Figueiras, F. G.: Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System, Progress in Oceanography, 51, 321-337, 10.1016/s0079-6611(01)00073-8, 2001.

Anderson, T. R., and Williams, P. J. r. l. B.: Modelling the seasonal cycle of dissolved organic carbon at Station E$_1$ in the English Channel, Estuarine, Coastal and Shelf Science, 46, 93-109, 1998.

Antezana, T.: Species-specific patterns of diel migration into the Oxygen Minimum Zone by euphausiids in the Humboldt Current Ecosystem, Progress in Oceanography, 83, 228-236, 2009.

Arévalo-Martínez, D. L., Kock, A., Löscher, C. R., Schmitz, R. A., and Bange, H. W.: Evidence of massive nitrous oxide emissions from the tropical South Pacific Ocean, Nature Geosci., 8, 530-533, 2015.

Auel, H., and Verheye, H. M.: Hypoxia tolerance in the copepod Calanoides carinatus and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela, Front. J. Exp. Mar. Biology and Ecology, 352, 234-243 2007.

Azam, F.: Microbial control of oceanic carbon flux: the plot thickens, Science, 280, 694-696, 1998.

Bakker, D. C. E., Bange, H. W., Gruber, N., Johannessen, T., Upstill-Goddard, R. C., Borges, A. V., Delille, B., Löscher, C. R., Naqvi, S. W. A., Omar, A. M., and Santana-Casiano, J. M.: Air-sea interactions of natural long-lived greenhouse gases (CO2, N2O, CH4) in a changing climate, in: Ocean-Atmosphere Interactions of Gases and Particles, edited by: Liss, P. S., and Johnson, M. T., Springer Verlag, Heidelberg, 117-174, 2014.

Bange, H. W., Freing, A., Kock, A., and Löscher, C. R.: Marine Pathways to Nitrous Oxide, in: Nitrous oxide and Climate Change, edited by: Smith, K. A., Earthscan, London, Washington, 27, 2010.

Banse, K., Naqvi, S. W. A., Narvekar, P. V., Postel, J. R., and Jayakumar, D. A.: Oxygen minimum zone of the open Arabian Sea: Variability of oxygen and nitrite from daily to decadal timescales, Biogeosci., 11, 2237-2261, 2014.

Beman, J. M., and Carolan, M. T.: Deoxygenation alters bacterial diversity and community composition in the oceans largest oxygen minimum zone, Nat Commun, 4, 2013.

Bertani, G., and Nice, S. J.: Studies on lysogenesis II. P1: The effect of temperature on the lysogenization of *Shigella dysenteriae* with phage P1, Journal of bacteriology, 67, 202, 1954.

Bertics, V. J., Löscher, C. R., Salonen, I., Dale, A. W., Gier, J., Schmitz, R. A., and Treude, T.: Occurrence of benthic microbial nitrogen fixation coupled to sulfate reduction in the seasonally hypoxic Eckernförde Bay, Baltic Sea, Biogeosciences, 10, 1243-1258, 2013.

Bianchi, D., Babbin, A. R., and Galbraith, E. D.: Enhancement of anammox by the excretion of diel vertical migrators, Proceedings of the National Academy of Sciences of the United States of America, 111, 15653-15658, 10.1073/pnas.1410790111, 2014.

Bijma, J., Portner, H.-O., Yesson, C., and Rogers, A. D.: Climate change and the oceans--what does the future hold?, Marine pollution bulletin, 74, 495-505, 10.1016/j.marpolbul.2013.07.022, 2013.

Bohlen, L., Dale, A. W., Sommer, S., Mosch, T., Hensen, C., Noffke, A., Scholz, F., and Wallmann, K.: Benthic Nitrogen Cycling Traversing the Peruvian Oxygen Minimum Zone, Geochimica et Cosmochimica Acta, 75, 6094-6111, DOI 10.1016/j.gca.2011.08.010, 2011.

Bohlen, L., Dale, A. W., and Wallmann, K.: Simple transfer functions for calculating benthic fixed nitrogen losses and C:N:P regeneration ratios in global biogeochemical models, Glob. Biogeochem. Cycle, 26, doi:10.1029/2011GB004198, 2012.

Bonnet, S., Dekaezemacker, J., Turk-Kubo, K. A., Moutin, T., Hamersley, R. M., Grosso, O., Zehr, J. P., and Capone, D. G.: Aphotic N2 Fixation in the Eastern Tropical South Pacific Ocean, PlosOne, 8, e81265. doi:10.1371/journal.pone.0081265, 2013.

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., and Vichi, M.: Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models, Biogeosciences, 10, 6225-6245, doi:10.5194/bg-10-6225-2013, 2013.

Brettar, I., and Rheinheimer, G.: Denitrification in the Central Baltic - Evidence for H2s-Oxidation as Motor of Denitrification at the Oxic-Anoxic Interface, Mar. Ecol.-Prog. Ser., 77, 157-169, 10.3354/meps077157, 1991.

Brettar, I., Labrenz, M., Flavier, S., Botel, J., Kuosa, H., Christen, R., and Hofle, M. G.: Identification of a *Thiomicrospira denitrificans*-Like Epsilonproteobacterium as a Catalyst for Autotrophic Denitrification in the Central Baltic Sea, Appl Environ Microbiol, 72, 1364-1372, Doi 10.1128/Aem.72.2.1364-1372.2006, 2006.

Brewer, P. G., and Peltzer, E. T.: Limits to Marine Life, Science, 324, 347-348, doi:10.1126/science.1170756., 2009.

Buesseler, K. O., Ball, L., Andrews, J., Benitez-Nelson, C., Belastock, R., Chai, F., and Chao, Y.: Upper Ocean Export of Particulate Organic Carbon in the Arabian Sea derived from Thorium-234., Deep-Sea Research Part II 45, 2461-2487, 1998.

Burd, A. B., Hansell, D. A., Steinberg, D. K., Anderson, T. R., Aristegui, J., Baltar, F., Beaupre, S. R., Buesseler, K. O., DeHairs, F., Jackson, G. A., Kadko, D. C., Koppelmann, 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 Research Part Ii-Topical Studies in Oceanography, 57, 1557-1571, 10.1016/j.dsr2.2010.02.022, 2010.

Burtt, J.: On fish destroyed by sulphuretted hydrogen in the Bay of Callao, Am J Sci, 2, 433-434, 1852.

Cabello, R., Tam, J., and Jacinto, M. E.: Procesos naturales y antropogénicos asociados al evento de mortalidad de conchas de abanico ocurrido en la bahía de Paracas (Pisco, Perú) en junio del 2000, Rev.Peru. Biol., 9, 49-65, 2002.

Canfield, D. E.: Models of oxic respiration, denitrification and sulfate reduction in zones of coastal upwelling, Geochimica et Cosmochimica Acta, 70, 5753-5765, 2006.

Canfield, D. E., and Thamdrup, B.: Towards a consistent classification scheme for geochemical environments, or, why we wish the term 'suboxic' would go away, Geobiol., 7, 385-392, 2009.

Canfield, D. E., Stewart, F. J., Thamdrup, B., De Brabandere, L., Dalsgaard, T., Delong, E. F., Revsbech, N. P., and Ulloa, O.: A Cryptic Sulfur Cycle in Oxygen-Minimum-Zone Waters off the Chilean Coast, Science, 330, 1375-1378, 10.1126/science.1196889, 2010.

Capone, D. G., and Carpenter, E. J.: Nitrogen-Fixation in the Marine-Environment, Science, 217, 1140-1142, 1982.

Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B., and Carpenter, E. J.: Trichodesmium, a globally significant marine cyanobacterium, Science, 276, 1221-1229, 1997.

Capone, D. G., and Hutchins, D. A.: Microbial biogeochemistry of coastal upwelling regimes in a changing ocean, Nature Geoscience, 6, 711-717, 10.1038/ngeo1916, 2013.

Carlson, C. A., Ducklow, H. W., and Michaels, A. F.: ANNUAL FLUX OF DISSOLVED ORGANIC-CARBON FROM THE EUPHOTIC ZONE IN THE NORTHWESTERN SARGASSO SEA, Nature, 371, 405-408, 10.1038/371405a0, 1994.

Caron, D. A., Goldman, J. C., and Dennett, M. R.: Experimental demonstration of the roles of bacteria and bacterivorous protozoa in plankton nutrient cycles, Hydrobiologia, 159, 27-40, 1988.

Cassman, N., Prieto-Davó, A., Walsh, K., Silva, G. G. Z., Angly, F. E., Akhter, S., Barott, K., Busch, J., McDole, T., Haggerty, J. M., Willner, D., Alarcón, G., Ulloa, O., DeLong, E. F., Dutilh, B. E., Rohwer, F. L., and Dinsdale, E. A.: Oxygen minimum zones harbour novel viral communities with low diversity, Environ. Microbiol., 14, 3043-3065, 10.1111/j.1462-2920.2012.02891.x, 2012.

Childress, J. J., and Seibel, B. A.: Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers, Journal of Experimental Biology, 201, 1223-1232, 1998.

Ciais, P., C. Sabine, G. Bala, L. Bopp, V. Brovkin, J. Canadell, A. Chhabra, R. DeFries, J. Galloway, M. Heimann, C. Jones, C. Le Quéré, R.B. Myneni, S. Piao, and Thornton, P.: Carbon and Other Biogeochemical Cycles, in: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Stocker, T. F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and Midgley, P. M., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.

Cocco, V., Joos, F., Steinacher, M., Frölicher, T. L., Bopp, L., Dunne, J., Gehlen, M., Heinze, C., Orr, J., Oschlies, A., Schneider, B., Segschneider, J., and Tjiputra, J.: Oxygen and indicators of stress for marine life in multi-model global warming projections, Biogeosciences, 10, 1849-1868, doi:10.5194/bg-10-1849-2013, 2013.

Codispoti, L. A., Brandes, J. A., Christensen, J. P., Devol, A. H., Naqvi, S. W. A., Paerl, H. W., and Yoshinari, T.: The oceanic fixed nitrogen and nitrous oxide budgets: Moving targets as we enter the anthropocene?, Scientia Marina, 65, 85-105, 2001.

Codispoti, L. A.: An oceanic fixed nitrogen sink exceeding 400 Tg Na(-1) vs the concept of homeostasis in the fixed-nitrogen inventory, Biogeosciences, 4, 233-253, 2007.

Codispoti, L. A.: Interesting Times for Marine N_2O, Science, 327, 1339-1340, 10.1126/science.1184945, 2010.

Cohen, Y.: Consumption of dissolved nitrous oxide in an anoxic basin, Saanich Inlet, British Columbia, Nature, 272, 235-237, 1978.

Copenhagen, W. J.: The periodic mortality of fish in the Walvis region - A phenomenon within the Benguela Current, S Afr Div Sea Fish Invest Rep 14, 1-35, 1953.

Cornejo, M., and Farias, L.: Following the N2O consumption in the oxygen minimum zone of the eastern South Pacific, Biogeosciences, 9, 3205-3212, 10.5194/bg-9-3205-2012, 2012.

Dabundo, R., Lehmann, M. F., Treibergs, L., Tobias, C. R., Altabet, M. A., Moisander, P. H., and Granger, J.: The Contamination of Commercial 15N2 Gas Stocks with 15N–Labeled Nitrate and Ammonium and Consequences for Nitrogen Fixation Measurements, PLoS One, 9, doi:10.1371/journal.pone.0110335, 2014.

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.

Danovaro, R., Dell'Anno, A., Pusceddu, A., Gambi, C., Heiner, I., and Kristensen, R. M.: The first metazoa living in permanently anoxic conditions, Bmc Biology, 8, 3010.1186/1741-7007-8-30, 2010.

de Lavalle y Garcia, J. A.: Informe preliminar sobre la causa de la mortalidad anormal de las aves ocurrida en el mes de marzo del presente año., Memoria Companla Administradova del Guano,, Lima, 8a, 61-88, 1917.

Dekaezemacker, J., Bonnet, S., Grosso, O., Moutin, T., Bressac, M., and Capone, D. G.: Evidence of active dinitrogen fixation in surface waters of the eastern tropical South Pacific during El Nino and La Nina events and evaluation of its potential nutrient controls, Glob. Biogeochem. Cycle, 27, 768-779, 10.1002/gbc.20063, 2013.

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

Deutsch, C., Sarmiento, J. L., Sigman, D. M., Gruber, N., and Dunne, J. P.: Spatial coupling of nitrogen inputs and losses in the ocean, Nature, 445, 163-167, 10.1038/nature05392, 2007.

Devol, A. H., and Hartnett, H. E.: Role of the oxygen minimum zone in transfer of organic carbon to the deep ocean., Limnology and Oceanography., 46, 1684-1690, 2001.

Devol, A. H.: Denitrification including anammox, in: Nitrogen in the Marine Environment, 2nd Edition, edited by: Capone, D. G., Bronk, D. A., Mulholland, M. R., and Carpenter, E. J., Elsevier, Amsterdam, 263-301, 2008.

Diaz, R. J., and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science, 321, 926-929, 10.1126/science.1156401, 2008.

Dietze, H., and Loeptien, U.: Revisiting ``nutrient trapping'' in global coupled biogeochemical ocean circulation models, Glob. Biogeochem. Cycle, 27, 265-284, 2013.

Dixon, R., and Kahn, D.: Genetic Regulation of biological Nitrogen Fixation, Nature Reviews, 2, 621-631, 2004.

Dugdale, R. C., Goering, J. J., Barber, R. T., Smith, R. L., and Packard, T. T.: Denitrification and Hydrogen Sulfide in the Peru Upwelling Region during 1976, Deep-Sea Research, 24, 1977.

Durski, S. M., and Allen, J. S.: Finite-amplitude evolution of instabilities associated with the coastal upwelling front, Journal of Physical Oceanography, 35, 1606-1628, 10.1175/jpo2762.1, 2005.

Ekau, W., Auel, H., Pörtner, H.-O., and Gilbert, D.: Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish), Biogeosciences, 7, 1669-1699, 2010.

Emery, K. O., Orr, W. L., and Rittenberg, S. C.: Nutrient budget in the ocean, in: Essays in the Natural Sciences in Honor of Captain Alan Hanock, Univ. of S. Calif. Press,, Los Angeles, 299-309, 1955.

Escribano, R., Hidalgo, P., and Krautz, C.: Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000, Deep-Sea Research Part Ii-Topical Studies in Oceanography, 56, 1049-1060, 10.1016/j.dsr2.2008.09.009, 2009.

Farías, L., Besoain, V., and García-Loyola, S.: Presence of nitrous oxide hotspots in the coastal upwelling area off central Chile: an anlysis of temproral variability based on ten years of a biogeochemiocal time series, Environ. Res. Lett., 10, 044017, 2015.

Fenchel, T., and Finlay, B.: Anaerobic free living protozoa: growth efficiencies and the structure of anaerobic communities., FEMS Microbiof Ecol, 74, 269-276, 1990.

Fernández-Álamo, M. A., and Färber-Lorda, J.: Zooplankton and the oceanography of the eastern tropical Pacific: a review, Prog. Oceanogr., 69, 2006.

Fernandez, C., Farias, L., and Ulloa, O.: Nitrogen Fixation in Denitrified Marine Waters, Plos One, 6, 9, e20539 10.1371/journal.pone.0020539, 2011.

Fischer, G., Karakas, G., Blaas, M., Ratmeyer, V., Nowald, N., Schlitzer, R., Helmke, P., Davenport, R., Donner, B., Neuer, S., and Wefer, G.: Mineral ballast and particle settling rates in the coastal upwelling system off NW Africa and the South Atlantic, International Journal of Earth Sciences, 98, 281-298, 10.1007/s00531-007-0234-7, 2009.

Flint, M., Drits, A., and Pasternak, A.: Characteristic features of body composition and metabolism in some interzonal copepods, Marine Biology, 111, 199-205, 1991.

Frame, C. H., and Casciotti, K. L.: Biogeochemical controls and isotopic signatures of nitrous oxide production by a marine ammonia-oxidizing bacterium, Biogeosciences, 7, 2695-2709, 10.5194/bg-7-2695-2010, 2010.

Francis, C. A., Beman, J. M., and Kuypers, M. M. M.: New processes and players in the nitrogen cycle: the microbial ecology of anaerobic and archaeal ammonia oxidation, Isme Journal, 1, 19-27, 10.1038/ismej.2007.8, 2007.

Franz, J., Krahmann, G., Lavik, G., Grasse, P., Dittmar, T., and Riebesell, U.: Dynamics and stoichiometry of nutrients and phytoplankton in waters influenced by the oxygen minimum zone in the eastern tropical Pacific, Deep-Sea Research Part I: Oceanographic Research Papers, 62, 20-31, 2012a.

Franz, J. M. S., Hauss, H., Sommer, U., Dittmar, T., and Riebesell, U.: Production, partitioning and stoichiometry of organic matter under variable nutrient supply during mesocosm experiments in the tropical Pacific and Atlantic Ocean, Biogeosciences, 9, 4629-4643, 2012b.

Friedman, J. R., Condon, N. E., and Drazen, J. C.: Gill surface area and metabolic enzyme activities of demersal fishes associated with the oxygen minimum zone off California, Limnol. Oceanogr., 57, 1701, 2012.

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, 10.1111/j.1574-6941.2011.01189.x, 2011.

Ganesh, S., Parris, D. J., DeLong, E. F., and Stewart, F. J.: Metagenomic analysis of size-fractionated picoplankton in a marine oxygen minimum zone, ISME J, 8, 187-211, 2014.

Ganesh, S., Bristow, L. A., Larsen, M., Sarode, N., Thamdrup, B., and Stewart, F. J.: Size-fraction partitioning of community gene transcription and nitrogen metabolism in a marine oxygen minimum zone, ISME J, 1-15, doi:10.1038/ismej.2015.44, 2015.

Garber, J. H.: Laboratory Study of Nitrogen and Phosphorus Remineralization during the Decomposition of Coastal Plankton and Seston, Estuarine, Coastal and Shelf Science, 18, 685-702, 1984.

Giblin, A. E., Tobias, C. R., Song, B., Weston, N., Banta, G. T., and Rivera-Monroy, V. H.: Dissimilatory nitrate reduction to ammonium (DNRA), Oceanography, 26, 124-131, doi.org/10.5670/oceanog.2013.54., 2013.

Glaubitz, S., Lueders, T., Abraham, W. R., Jost, G., Jürgens, K., and Labrenz, M.: ^{13}C-isotope analyses reveal that chemolithoautotrophic *Gamma-* and *Epsilonproteobacteria* feed a microbial food web in a pelagic redoxcline of the central Baltic Sea, Environ Microbiol, 11, 326-337, DOI 10.1111/j.1462-2920.2008.01770.x, 2009.

Glaubitz, S., Labrenz, M., Jost, G., and Jürgens, K.: Diversity of active chemolithoautotrophic prokaryotes in the sulfidic zone of a Black Sea pelagic redoxcline as determined by rRNA-based stable isotope probing, FEMS Microbiol Ecol, 74, 32-41, DOI 10.1111/j.1574-6941.2010.00944.x, 2010.

Gonzalez, H. E., Ortiz, V. C., and Sobarzo, M.: The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23 degrees S), before and during the 1997-1998 El Nino, Journal of Plankton Research, 22, 499-529, 10.1093/plankt/22.3.499, 2000.

González, R. R., and Quiñones, R. A.: LDH activity in Euphausia mucronata and Calanus chilensis: implications for vertical migration behaviour, Journal of Plankton Research, 24, 1349-1356, 2002.

Großkopf, T., and LaRoche, J.: Direct and Indirect Costs of Dinitrogen Fixation in *Crocosphaera watsonii* WH8501 and Possible Implications for the Nitrogen Cycle, Frontiers in microbiology, 3, 236-236, 10.3389/fmicb.2012.00236, 2012.

Großkopf, T., Mohr, W., Baustian, T., Schunck, H., Gill, D., Kuypers, M. M. M., Lavik, G., Schmitz, R. A., Wallace, D. W. R., and LaRoche, J.: Doubling of marine dinitrogen-fixation rates based on direct measurements, Nature, 488, 361-364, 10.1038/nature11338, 2012.

Gruber, N., and Sarmiento, J. L.: Global patterns of marine nitrogen fixation and denitrification, Glob. Biogeochem. Cycle, 11, 235-266, 1997.

Gruber, N.: The dynamics of the marine nitrogen cycle and its influence on atmospheric CO2 variations, in: The ocean carbon cycle and climate, NATO ASI Series, edited by: Follows, M., and Oguz, T., Kluwer Academic, Dordrecht, 97-148, 2004.

Gruber, N.: Warming up, turning sour, losing breath: ocean biogeochemistry under global change, Philos. Trans. R. Soc. A-Math. Phys. Eng. Sci., 369, 1980-1996, 10.1098/rsta.2011.0003, 2011.

Gruber, N., Lachkar, Z., Frenzel, H., Marchesiello, P., Münnich, M., McWillisams, J., C., , Nagai, T., and Plattner, G.: Eddy-induced reduction of biological production in eastern boundary upwelling systems, Nature Geoscience 4, 787–792, doi:10.1038/ngeo1273, 2011.

Halm, H., Musat, N., Lam, P., Langlois, R., Musat, F., Peduzzi, S., Lavik, G., Schubert, C. J., Sinha, B., LaRoche, J., and Kuypers, M. M. M.: Co-occurrence of denitrification and nitrogen fixation in a meromictic lake, Lake Cadagno (Switzerland), Environ. Microbiol., 11, 1945-1958, 10.1111/j.1462-2920.2009.01917.x, 2009.

Hamersley, M. R., Lavik, G., Woebken, D., Rattray, J. E., Lam, P., Hopmans, E. C., Damste, J. S. S., Kruger, S., Graco, M., Gutierrez, D., and Kuypers, M. M. M.: Anaerobic ammonium oxidation in the Peruvian oxygen minimum zone, Limnology and Oceanography, 52, 923-933, 2007.

Hamukuaya, H., O'Toole, M. J., and Woodhead, P. M. J.: Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994, S Afr J Mar Sci, 19, 57-59, 1998.

Hannides, C. C. S., Landry, M. R., Benitez-Nelson, C. R., Styles, R. M., Montoya, J. P., and Karl, D. M.: Export stoichiometry and migrant-mediated flux of phosphorus in the North Pacific Subtropical Gyre, Deep-Sea Research Part I-Oceanographic Research Papers, 56, 73-88, 10.1016/j.dsr.2008.08.003, 2009.

Hansell, D. A.: DOC in the global ocean cycle, In: D. A. Hansell and C. A. Carlson [eds.], Biogeochemistry of marine dissolved organic matter. Elsevier., 2002.

Hart, T. J., and Currie, R. I.: The Benguela Current. In: Discovery Report 31., in, Cambridge University Press, Cambridge, 123-298, 1960.

Hauss, H., Franz, J. M. S., Hansen, T., Struck, U., and Sommer, U.: Relative inputs of upwelled and atmospheric nitrogen to the eastern tropical North Atlantic food web: Spatial distribution of δ\ce^15N in mesozooplankton and relation to dissolved nutrient dynamics, Deep-Sea Research Part I: Oceanographic Research Papers, 75, 135-145, 2013.

Hayes, M. K., Taylor, G. T., Astor, Y., and Scranton, M. I.: Vertical distributions of thiosulfate and sulfite in the Cariaco Basin, Limnol Oceanogr, 51, 280-287, 2006.

Honjo, S., Manganini, S. J., Krishfield, R. A., and Francois, R.: Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: A synthesis of global sediment trap programs since 1983, Progress in Oceanography, 76, 217-285, 10.1016/j.pocean.2007.11.003, 2008.

Hoppe, H.-G., Ullrich, S., von Bröckel, K., and Sellmer, C.: Bacterial C-demand (mineralization) in the aphotic depths of the Arabian Sea exceeds measured C-fluxes from the euphotic zone. , In: B. Donner, G. Wefer: Berichte aus dem Fachbereich Geowissenschaften, Universität Bremen, No 162:51., 2000.

Hoppe, H. G., and Ullrich, S.: Profiles of ectoenzymes in the Indian Ocean: phenomena of phosphatase activity in the mesopelagic zone, Aquatic Microbial Ecology, 19, 139-148, 10.3354/ame019139, 1999.

Houlton, B. Z., Wang, Y.-P., Vitousek, P. M., and Field, C. B.: A unifying framework for dinitrogen fixation in the terrestrial biosphere, 454, 327-330, doi:10.1038/nature07028, 2008.

Ingall, E., and Jahnke, R.: Evidence for enhanced phosphorus regeneration from marine sediments overlain by oxygen depleted waters., Geochimica et Cosmochimica Acta 58, 2571-2575, 1994.

Iversen, M. H., Nowald, N., Ploug, H., Jackson, G. A., and Fischer, G.: High resolution profiles of vertical particulate organic matter export off Cape Blanc, Mauritania: Degradation processes and ballasting effects, Deep-Sea Research Part I-Oceanographic Research Papers, 57, 771-784, 10.1016/j.dsr.2010.03.007, 2010.

Jenkyns, H. C.: Geochemistry of oceanic anoxic events, Geochemistry Geophysics Geosystems, 11, 2010.

Jensen, M. M., Thamdrup, B., and Dalsgaard, T.: Effects of specific inhibitors on anammox and denitrification in marine sediments, Applied and Environmental Microbiology, 73, 3151-3158, 10.1128/aem.01898-06, 2007.

Jørgensen, B. B., Fossing, H., Wirsen, C. O., and Jannasch, H. W.: Sulfide oxidation in the anoxic Black Sea chemocline, Deep-Sea Res, 38, S1083-S1103, 1991.

Kalvelage, T., Jensen, M. M., Contreras, S., Revsbech, N. P., Lam, P., Gunter, M., LaRoche, J., Lavik, G., and Kuypers, M. M. M.: Oxygen Sensitivity of Anammox and Coupled N-Cycle Processes in Oxygen Minimum Zones, PLoS ONE, 6, 12, 10.1371/journal.pone.0029299, 2011.

Kalvelage, T., Lavik, G., Lam, P., Contreras, S., Arteaga, L., Loscher, C. R., Oschlies, A., Paulmier, A., Stramma, L., and Kuypers, M. M. M.: Nitrogen cycling driven by organic matter export in the South Pacific oxygen minimum zone, Nature Geoscience, 6, 228-234, 2013.

Kalvelage, T., Lavik, G., Jensen, M. M., Revsbech, N. P., Löscher, C. R., Schunck, H., Desai, D. K., Hauss, H., Kiko, R., Holtappels, M., LaRoche, J., Schmitz, R. A., Graco, M. I., and Kuypers, M. M. M.: Aerobic microbial respiration in oceanic oxygen minimum zone, PlosOne, 10, doi:10.1371/journal.pone.0133526, 2015.

Karl, D. M., and Tilbrook, B. D.: Production and transport of methane in oceanic particulate organic matter, Nature, 368, 732 - 734, doi:10.1038/368732a0, 1994.

Kartal, B., Kuypers, M. M. M., Lavik, G., Schalk, J., den Camp, H., Jetten, M. S. M., and Strous, M.: Anammox bacteria disguised as denitrifiers: nitrate reduction to dinitrogen gas via nitrite and ammonium, Environ. Microbiol., 9, 635-642, 10.1111/j.1462-2920.2006.01183.x, 2007.

Kiko, R., Hauss, H., Dengler, M., Sommer, S., and Melzner, F.: The squat lobster Pleuroncodes monodon tolerates anoxic “dead zone” conditions off Peru, Marine Biology, 162, 1-9, doi: 10.1007/s00227-015-2709-6, 2015a.

Kiko, R., Hauss., H., Buchholz, F., and Melzner, F.: Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions, Biogeosciences Discussions, accepted, 2015b.

Kiørboe, T.: Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod, Marine Ecology Progress Series, 55, 229-234, 1989.

Klawonn, I., Bonaglia, S., Bruchert, V., and Ploug, H.: Aerobic and anaerobic nitrogen transformation processes in N2-fixing cyanobacterial aggregates, ISME J, 9, 1456-1466, 2015.

Klein, P., Hua, B. L., Lapeyre, G., Capet, X., Le Gentil, S., and Sasaki, H.: Upper ocean turbulence from high-resolution 3D simulations, Journal of Physical Oceanography, 38, 1748-1763, 10.1175/2007jpo3773.1, 2008.

Klein, P., and Lapeyre, G.: The Oceanic Vertical Pump Induced by Mesoscale and Submesoscale Turbulence, in: Annual Review of Marine Science, Annual Review of Marine Science, 351-375, 2009.

Kuypers, M. M. M., Sliekers, 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, 10.1038/nature01472, 2003.

Kuypers, M. M. M., van Breugel, Y., Schouten, S., Erba, E., and Sinninghe, D. J. S.: N2-fixing cyanobacteria supplied nutrient N for Cretaceous oceanic anoxic events, Geology, 32, 853-856, 2004.

Kuypers, M. M. M., Lavik, G., Woebken, D., Schmid, M., Fuchs, B. M., Amann, R., Jorgensen, B. B., and Jetten, M. S. M.: Massive nitrogen loss from the Benguela upwelling system through anaerobic ammonium oxidation, Proceedings of the National Academy of Sciences of the United States of America, 102, 6478-6483, 10.1073/pnas.0502088102, 2005.

Lam, P., Lavik, G., Jensen, M. M., van de Vossenberg, J., Schmid, M., Woebken, D., Dimitri, G., Amann, R., Jetten, M. S. M., and Kuypers, M. M. M.: Revising the nitrogen cycle in the Peruvian oxygen minimum zone, Proc. Natl. Acad. Sci. U. S. A., 106, 4752-4757, 10.1073/pnas.0812444106, 2009.

Lam, P., and Kuypers, M. M. M.: Microbial nitrogen cycling processes in oxygen minimum zones., Ann Rev Mar Sci., 3, 317-345, 2011.

Lampert, W.: The adaptive significance of diel vertical migration of zooplankton, Functional Ecology, 3, 21-27, 1989.

Landolfi, A., Dietze, H., Koeve, W., and Oschlies, A.: Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle, Biogeosciences, 10, 1351-1363, 2013.

Lasternas, S., Piedeleu, M., Sangrà, P., Duarte, C. M., and Agustí, S.: Forcing of dissolved organic carbon release by phytoplankton by anticyclonic mesoscale eddies in the subtropical NE Atlantic Ocean, Biogeosciences, 10, 2129-2143, doi:10.5194/bg-10-2129-2013, 2013.

Lathuiliere, C., Echevin, V., Levy, M., and Madec, G.: On the role of the mesoscale circulation on an idealized coastal upwelling ecosystem, Journal of Geophysical Research-Oceans, 115, 10.1029/2009jc005827, 2010.

Lavik, G., Stuhrmann, T., Bruchert, V., Van der Plas, A., Mohrholz, V., Lam, P., Mussmann, M., Fuchs, B. M., Amann, R., Lass, U., and Kuypers, M. M. M.: Detoxification of sulphidic African shelf waters by blooming chemolithotrophs, Nature, 457, 581-584, Doi 10.1038/Nature07588, 2009.

Lennartz, S. T., Lehmann, A., Herrford, J., Malien, F., Hansen, H.-P., Biester, H., and Bange, H. W.: Long-term trends at the Boknis Eck time series station (Baltic Sea), 1957–2013: does climate change counteract the decline in eutrophication?, Biogeosciences, 11, 6323-6339, doi:10.5194/bg-11-6323-2014, 2014.

Levy, M., Ferrari, R., Franks, P. J. S., Martin, A. P., and Riviere, P.: Bringing physics to life at the submesoscale, Geophysical Research Letters, 39, 10.1029/2012gl052756, 2012.

Libes, S. M., and Deuser, W. G.: The Isotope Geochemistry of Particulate Nitrogen in the Peru Upwelling Area and the Gulf of Maine, Deep-Sea Research I, 35, 517-533, Doi 10.1016/0198-0149(88)90129-X, 1988.

Liss, P. S., and Johnson, M. T.: Ocean-Atmosphere Interactions of Gases and Particles, Springer, Heidelberg, 315 pp., 2014.

Löscher, C. R., Kock, A., Könneke, M., LaRoche, J., Bange, H. W., and Schmitz, R. A.: Production of oceanic nitrous oxide by ammonia-oxidizing archaea, Biogeosciences 9, 2419-2429, 2012.

Löscher, C. R., Großkopf, T., Desai, F., Gill, D., Schunck, H., Croot, P., Schlosser, C., Neulinger, S. C., Lavik, G., Kuypers, M. M. M., LaRoche, J., and Schmitz, R. A.: Facets of diazotrophy in the oxygen minimum zone off Peru, ISME J, 8, 2180-2192, doi: 10.1038/ismej.2014.71, 2014.

Löscher, C. R., Fischer, M. A., Neulinger, S. C., Philippi, M., Fiedler, B., Hauss, H., Körtzinger, A., Karstensen, J., Künzel, S., Schütte, F., and Singh, A.: Hidden biosphere in an Atlantic open ocean dead zone eddy reveals future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic, Biogeosciences Discuss., 12, 14175-14213, doi:10.5194/bgd-12-14175-2015, 2015.

Luo, J., Ortner, P. B., Forcucci, D., and Cummings, S. R.: Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 47, 1451-1473, 2000.

Mahadevan: Ocean science: Eddy effects on biogeochemistry, Nature Geoscience, 506, 168-169, doi:10.1038/nature13048, 2014.

Martin, J. H., Knauer, G. A., Karl, D. M., and Broenkow, W. W.: VERTEX - CARBON CYCLING IN THE NORTHEAST PACIFIC, Deep-Sea Research Part a-Oceanographic Research Papers, 34, 267-285, 10.1016/0198-0149(87)90086-0, 1987.

Mathis, J. T., Pickart, R. S., Hansell, D. A., Kadko, D., and Bates, N. R.: Eddy transport of organic carbon and nutrients from the Chukchi Shelf: Impact on the upper halocline of the western Arctic Ocean, Journal of Geophysical Research-Oceans, 112, 10.1029/2006jc003899, 2007.

McLaren, I. A.: Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration, Journal of the Fisheries Board of Canada, 20, 685-727, 1963.

Meyer, J., Löscher, C. R., Neulinger, S. C., Reichel, A. F., Loginova, A., Borchard, C., Schmitz, R. A., Hauss, H., Kiko, R., and Riebesell, U.: Changing nutrient stoichiometry affects phytoplankton production, DOP build up and dinitrogen fixation – a mesocosm experiment in the eastern tropical North Atlantic, Biogeosciences Discuss., 12, 9991-10029, doi:10.5194/bgd-12-9991-2015, 2015.

Mohr, W., Grosskopf, T., Wallace, D. W. R., and LaRoche, J.: Methodological underestimation of oceanic nitrogen fixation rates, PLoS One, 5, e12583, 2010.

Montoya, J. P., Voss, M., Kahler, P., and Capone, D. G.: A simple, high-precision, high-sensitivity tracer assay for N_2 fixation, Appl. Environ. Microbiol., 62, 986-993, 1996.

Naqvi, S. W. A., Kumar, M. D., Narvekar, P. V., Desousa, S. N., George, M. D., and Dsilva, C.: An Intermediate Nepheloid Layer Associated with High Microbial Metabolic Rates and Denitrification in the Northwest Indian-Ocean, Journal of Geophysical Research-Oceans, 98, 16469-16479, 10.1029/93jc00973, 1993.

Naqvi, S. W. A., Jayakumar, D. A., Narveka, P. V., Naik, H., Sarma, V. V. S. S., D'Souza, W., Joseph, S., and George, M. D.: Increased marine production of N_2O due to intensifying anoxia on the Indian continental shelf, Nature, 408, 346-349, 2000.

Naqvi, S. W. A., Bange, H. W., Farías, L., Monteiro, P. M. S., Scranton, M. I., and Zhang, J.: Marine hypoxia/anoxia as a source of CH_4 and N_2O, Biogeosciences, 7, 2159-2190, 2010.

Omori, Y., Tanimoto, H., Inomata, S., Wada, S., Thume, K., and Pohnert, G.: Enhancement of dimethylsulfuide production by anoxic stress in natural seawater, Geophys. Res. Lett., 42, 4047-4053, doi:10.1002/2015GL063546, 2015.

Pahlow, M., and Vézina, A. F.: Adaptive model of DOM dynamics in the surface ocean, Journal of Marine Research, 61, 127-146, 2003.

Pahlow, M., Vézina, A. F., Casault, B., Maass, H., Malloch, L., Wright, D. G., and Lu, Y.: Adaptive model of plankton dynamics for the North Atlantic, Progress in Oceanography, 76, 151-191, 2008.

Pahlow, M., Dietze, H., and Oschlies, A.: Optimality-based model of phytoplankton growth and diazotrophy, Marine Ecology Progress Series, 489, 1-16, 2013.

Pahlow, M., and Oschlies, A.: Optimal allocation backs Droop's cell-quota model, Marine Ecology Progress Series, 473, 1-5, 2013.

Pantoja, S., Sepulveda, J. S., and Gonzalez, H. E.: Decomposition of sinking proteinaceous material during fall in the oxygen minimum zone off northern Chile, Deep-Sea Research Part I-Oceanographic Research Papers, 51, 55-70, 10.1016/j.dsr.2003.09.005, 2004.

Pantoja, S., Rossel, P., Castro, R., Cuevas, L. A., Daneri, G., and Cordova, C.: Microbial degradation rates of small peptides and amino acids in the oxygen minimum zone of Chilean coastal waters, Deep-Sea Research Part Ii-Topical Studies in Oceanography, 56, 1019-1026, 10.1016/j.dsr2.2008.09.007, 2009.

Paulmier, A., and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, Progress in Oceanography 80, 113-128 2009.

Paulmier, A., Ruiz-Pino, D., and Garcon, V.: CO2 maximum in the oxygen minimum zone (OMZ), Biogeosciences, 8, 239-252, 10.5194/bg-8-239-2011, 2011.

Pearcy, W., Krygier, E., Mesecar, R., and Ramsey, F.: Vertical distribution and migration of oceanic micronekton off Oregon, Deep Sea Research, 24, 223-245, 1977.

Pedros-Alio, C.: The rare bacterial biosphere, Annu. Rev. Marine Sci., 4, 449-466, 2012.

Pörtner, H. O., Langenbuch, M., and Reipschläger, A.: Biological impact of elevated ocean CO2 concentrations: lessons from animal physiology and earth history, Journal of Oceanography, 60, 705-718, 2004.

Pörtner, H. O., and Farrell, A. P.: Physiology, climate change, Science, 322, 690-692, 2008.

Revsbech, N. P., Larsen, L. H., Gundersen, J., Dalsgaard, T., Ulloa, O., and Thamdrup, B.: Determination of ultra-low oxygen concentrations in oxygen minimum zones by the STOX sensor, Limnol Oceanogr Meth, 7, 371-381, 2009.

Riebesell, U., Körtzinger, A., and Oschlies, A.: Sensitivities of marine carbon fluxes to ocean change., Proceedings of the National Academy of Sciences, 106, 20602-20609, 2009.

Robinson, C., Steinberg, D. K., Anderson, T. R., Aristegui, J., Carlson, C. A., Frost, J. R., Ghiglione, J. F., Hernandez-Leon, S., Jackson, G. A., Koppelmann, R., Queguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B. H., Tamburini, C., Tanaka, T., Wishner, K. F., and Zhang, J.: Mesopelagic zone ecology and biogeochemistry - a synthesis, Deep-Sea Research Part Ii-Topical Studies in Oceanography, 57, 1504-1518, 10.1016/j.dsr2.2010.02.018, 2010.

Romankevich, E. A., and Ljutsarev, S. V.: Dissolved organic carbon in the Ocean, Marine Chemistry, 30, 161-178, 10.1016/0304-4203(90)90068-n, 1990.

Rosa, R., and Seibel, B. A.: Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: Implications for vertical migration in a pronounced oxygen minimum zone, Progress in Oceanography, 86, 72-80, 2010.

Ryabenko, E., Kock, A., Bange, H. W., Altabet, M. A., and Wallace, D. W. R.: Contrasting biogeochemistry of nitrogen in the Atlantic and Pacific oxygen minimum zones, Biogeosciences, 9, 203-215, 2012.

Saltzmann, J., and Wishner, K. F.: Zooplankton ecology in the eastern tropical Pacific ozygen minimum zone above a seamout: 2. Vertical distribution of copepods, Deep Sea Research I, 44, 931-954, 1997.

Sandel, V., Kiko, R., Brandt, P., Dengler, M., Stemmann, L., Vandromme, P., Sommer, U., and Hauss, H.: Nitrogen Fuelling of the Pelagic Food Web of the Tropical Atlantic, PLoS One, 10, e0131258, 2015.

Santoro, A. E., Buchwald, C., McIlvin, M. R., and Casciotti, K. L.: Isotopic Signature of N_2O Produced by Marine Ammonia-Oxidizing Archaea, Science, 333, 1282-1285, 2011.

Schunck, H., Lavik, G., Desai, D. K., Großkopf, T., Kalvelage, T., Löscher, C. R., Paulmier, A., Contreras, S., Siegel, H., Holtappels, M., Rosenstiel, P., Schilhabel, M. B., Graco, M., Schmitz, R. A., Kuypers, M. M. M., and LaRoche, J.: Giant Hydrogen Sulfide Plume in the Oxygen Minimum Zone off Peru Supports Chemolithoautotrophy, PLoS ONE, 2013.

Schweiger, B., Hansen, H. P., and Bange, H. W.: A time series of hydroxylamine (NH_2OH) in the southwestern Baltic Sea, Geophys. Res. Lett., 34, 5, L24608, 10.1029/2007gl031086, 2007.

Seeley, N. D., and Primrose, S. B.: The effect of temperature on the ecology of aquatic bacteriophages, Journal of General Virology, 46, 87-95, 1980.

Seibel, B. A.: Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones, Journal of Experimental Biology, 214, 326-336, 2011.

Shenoy, D. M., Sujith, K. B., Gauns, M. U., Patil, S., Sarkar, A., Naik, H., Narvekar, P. V., and Naqvi, S. W. A.: Production of dimethylsulphide during the seasonal anoxia off Goa, Biogeochemistry, 110, 47-55, 10.1007/s10533-012-9720-5, 2012.

Somes, C. J., and Oschlies, A. C. G. B.: On the influence of “non-Redfield” dissolved organic nutrient dynamics on the spatial distribution of N2 fixation and the size of the marine fixed nitrogen inventory, Glob. Biogeochem. Cycle, n/a-n/a, doi:10.1002/2014GB005050. , 2015.

Sorokin, Y. I.: Description of primary production and of the heterotrophic microplankton in the peruvian upwelling region, Oceanology, 18, 62-71, 1978.

Sorokin, Y. I., Sorokin, P. Y., Avdeev, V. A., Sorokin, D. Y., and Ilchenko, S. V.: Biomass, Production and Activity of Bacteria in the Black-Sea, with Special Reference to Chemosynthesis and the Sulfur Cycle, Hydrobiologia, 308, 61-76, 1995.

Steinberg, D. K., Carlson, C. A., Bates, N. R., Goldthwait, S. A., Madin, L. P., and Michaels, A. F.: Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea, Deep-Sea Research Part I-Oceanographic Research Papers, 47, 137-158, 10.1016/s0967-0637(99)00052-7, 2000.

Steinberg, D. K., Goldthwait, S. A., and Hansell, D. A.: Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea, Deep Sea Research II, 49, 1445–1461, doi:10.1016/S0967-0637(02)00037-7, 2002.

Stevens, H., and Ulloa, O.: Bacterial diversity in the oxygen minimum zone of the eastern tropical South Pacific, Environ Microbiol, 10, 1244-1259, DOI 10.1111/j.1462-2920.2007.01539.x, 2008.

Stewart, F. J., Ulloa, O., and DeLong, E. F.: Microbial metatranscriptomics in a permanent marine oxygen minimum zone, Environ Microbiol, 14, 23-40, 10.1111/j.1462-2920.2010.02400.x, 2011.

Stewart, F. J., Ulloa, O., and DeLong, E. F.: Microbial metatranscriptomics in a permanent marine oxygen minimum zone, Environ. Microbiol., 14, 23-40, DOI 10.1111/j.1462-2920.2010.02400.x, 2012.

Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding Oxygen-Minimum Zones in the Tropical Oceans, Science, 320, 655-658, 2008.

Stramma, L., Oschlies, A., and Schmidtko, S.: Mismatch between observed and modeled trends in dissolved upper-ocean oxygen over the last 50 yr, Biogeosciences, 9, 4045-4057, 10.5194/bg-9-4045-2012, 2012.

Stramma, L., Bange, H. W., Czeschel, R., Lorenzo, A., and Frank, M.: On the role of mesoscale eddies for the biological productivity and biogeochemistry in the eastern tropical Pacific Ocean off Peru. , Biogeosciences 10, 7293-7306, doi:10.5194/bg-10-7293-2013, 2013.

Su, B., Pahlow, M., Wagner, H., and Oschlies, A.: What prevents nitrogen depletion in the OMZ of the Eastern Tropical South Pacific?, Biogeosciences, 12, 1113–1130, doi: 10.5194/bg-12-1113-2015, 2015.

Suntharalingam, P., Buitenhuis, E., Le Quere, C., Dentener, F., Nevison, C., Butler, J. H., Bange, H. W., and Forster, G.: Quantifying the impact of anthropogenic nitrogen deposition on oceanic nitrous oxide, Geophys. Res. Lett., 39, L07605

10.1029/2011gl050778, 2012.

Swan, B. K., Martinez-Garcia, M., Preston, C. M., Sczyrba, A., Woyke, T., Lamy, D., Reinthaler, T., Poulton, N. J., Masland, E. D. P., Gomez, M. L., Sieracki, M. E., DeLong, E. F., Herndl, G. J., and Stepanauskas, R.: Potential for Chemolithoautotrophy Among Ubiquitous Bacteria Lineages in the Dark Ocean, Science, 333, 1296–1300, doi:10.1126/science.1203690, 2011.

Taylor, G. T., Iabichella, M., Ho, T. Y., Scranton, M. I., Thunell, R. C., Muller-Karger, F., and Varela, R.: Chemoautotrophy in the redox transition zone of the Cariaco Basin: A significant midwater source of organic carbon production, Limnol Oceanogr, 46, 148-163, 2001.

Tebo, B. M., and Emerson, S.: Microbial manganese(II) oxidation in the marine environment: a quantitative study, Biogeochemistry, 2, 149-161, 1986.

Teuber, L., Kiko, R., Seguin, F., and Auel, H. J.: Respiration rates of tropical Atlantic copepods in relation to the oxygen minimum zone, Exp. Mar. Biology and Ecology, 448, 28-36, 2013.

Thamdrup, B., and Dalsgaard, T.: Production of N_2 through anaerobic ammonium oxidation coupled to nitrate reduction in marine sediments, Applied and Environmental Microbiology, 68, 1312-1318, 10.1128/aem.68.3.1312-1318.2002, 2002.

Thamdrup, B., Dalsgaard, T., Jensen, M. M., Ulloa, O., Farias, L., and Escribano, R.: Anaerobic ammonium oxidation in the oxygen-deficient waters off northern Chile, Limnology and Oceanography, 51, 2145-2156, 2006.

Thamdrup, B., Dalsgaard, T., and Revsbech, N. P.: Widespread functional anoxia in the oxygen minimum zone of the eastern South Pacific, Deep-Sea Res. I, 65, 36-45, 2012.

Thomas, L. N., Tandon, A., and Mahadevan, A.: Submesoscale processes and dynamics., In: M. Hecht, H. Hasumi (Eds.), Ocean Modeling in an Eddying Regime. Geophysical Monograph Series, vol. 177, American Geophysical Union, Washington, DC, 17-38., 2008.

Thuesen, E. V., McCullough, K. D., and Childress, J. J.: Metabolic enzyme activities in swimming muscle of medusae: is the scaling of glycolytic activity related to oxygen availability?, JMBA-Journal of the Marine Biological Association of the United Kingdom, 85, 603-612, 2005.

Torres, J. J., Grigsby, M. D., and Clarke, M. E.: Aerobic and anaerobic metabolism in oxygen minimum layer fishes: the role of alcohol dehydrogenase, The Journal of Experimental Biology, 215, 1905-1914, 2012.

Touratier, F., Field, J. G., and Moloney, C. L.: A stoichiometric model relating growth substrate quality (C:N:P ratios) to N:P ratios in the products of heterotrophic release and excretion, Ecological Modelling, 139, 265-291, 2001.

Trübenbach, K., Pegado, M. R., Seibel, B. A., and Rosa, R.: Ventilation rates and activity levels of juvenile jumbo squid under metabolic suppression in the oxygen minimum zone, The Journal of Experimental Biology, 216, 359-368, 2013.

Turk-Kubo, K. A., Karamchandani, M., Capone, D. G., and Zehr, J. P.: The paradox of marine heterotrophic nitrogen fixation: abundances of heterotrophic diazotrophs do not account for nitrogen fixation rates in the Eastern Tropical South Pacific, Environ Microbiol, 16, 3095–3114, doi: 10.1111/1462-2920.12346, 2014.

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, Geochimica Et Cosmochimica Acta, 66, 457-465, 10.1016/s0016-7037(01)00787-6, 2002.

Walsh, D. A., Zaikova, E., Howes, C. G., Song, Y. C., Wright, J. J., Tringe, S. G., Tortell, P. D., and Hallam, S. J.: Metagenome of a Versatile Chemolithoautotroph from Expanding Oceanic Dead Zones, Science, 326, 578-582, DOI 10.1126/science.1175309, 2009.

Ward, B. B.: Nitrification in marine systems, in: Nitrogen in the Marine Environment, 2nd Edition, edited by: Capone, D. G., Bronk, D. A., Mulholland, M. R., and Carpenter, E. J., Elsevier, Amsterdam, 199-261, 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-U77, 10.1038/nature08276, 2009.

Weeks, S. J., Currie, B., and Bakun, A.: Massive emissions of toxic gas in the Atlantic, Nature, 415, 493-494, 10.1038/415493b, 415493b [pii], 2002.

Wishner, K. F., Gowing, M. M., and Gelfman, C.: Mesozooplankton biomass in the upper 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and relationship to oxygen gradients, Deep Sea Research II, 45, 2405 – 2432, 1998.

Woebken, D., Teeling, H., Wecker, P., Dumitriu, A., Kostadinov, I., DeLong, E. F., Amann, R., and Glöckner, F. O.: Fosmids of novel marine planctomycetes from the Namibian and Oregon coast upwelling systems and their cross-comparison with planctomycete genomes., ISME J, 1, 419-435, 2007.

Wright, J. J., Konwar, K. M., and Hallam, S. J.: Microbial ecology of expanding oxygen minimum zones, Nature Reviews Microbiology, 10, 381-394, 10.1038/nrmicro2778, 2012.

Zamora, L. M., Oschlies, A., Bange, H. W., Huebert, K. B., Craig, J. D., Kock, A., and Loescher, C. R.: Nitrous oxide dynamics in low oxygen regions of the Pacific: insights from the MEMENTO database, Biogeosciences, 9, 5007-5022, 10.5194/bg-9-5007-2012, 2012.

Zehr, J. P., and Turner, P. J.: Nitrogen fixation: Nitrogenase genes and gene expression, in: Methods in Microbiology, Vol 30, Methods in Microbiology, Academic Press Inc, San Diego, 271-286, 2001.

Zhang, J. Z., and Millero, F. J.: The Chemistry of the Anoxic Waters in the Cariaco Trench, Deep-Sea Res Pt I, 40, 1023-1041, 1993.

Figures

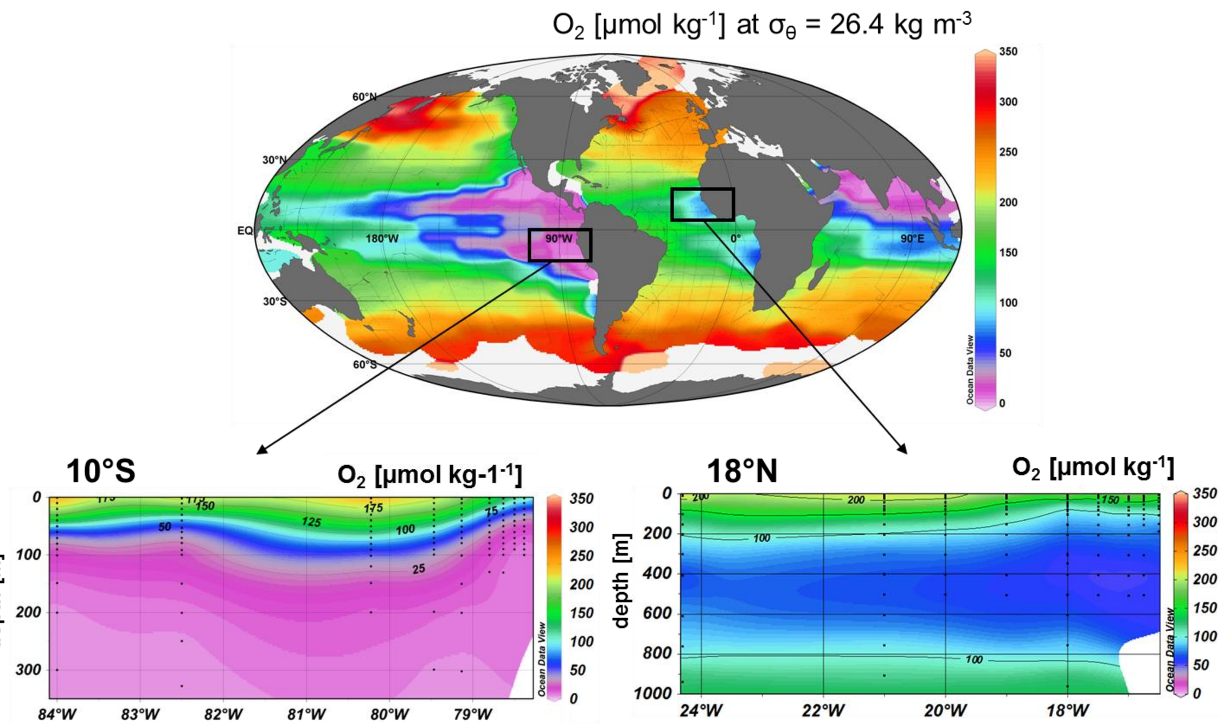

Figure 1. Global distribution of O_2 at σ_Θ= 26.4 kg m^{-3} (~ 400 m depth): The major regions of low oxygen in the world ocean are all located in the tropical oceans, at shallow to intermediate depths. The area off Peru represents one of the most pronounced OMZs. The investigated areas in the eastern tropical South Pacific and the eastern tropical North Atlantic Oceans are marked with black boxes; examples of the O_2 distribution are given along two sections from the coast to the open ocean at 10°S in the OMZ off Peru and at 18°N in the eastern tropical North Atlantic; O_2 concentrations are indicated by the color code.

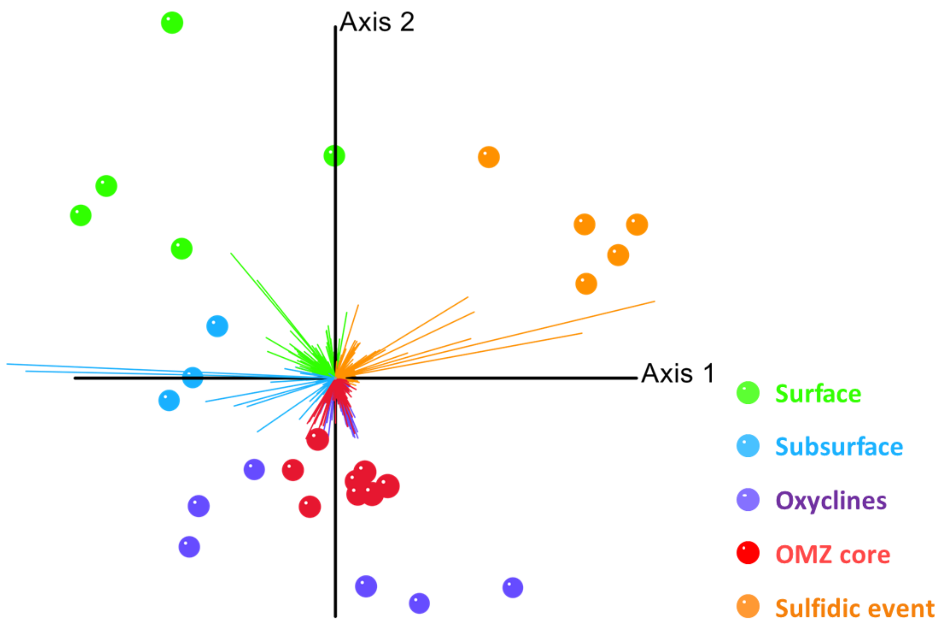

Figure 2. Redundancy analysis ordination model of microbial taxa (vectors) identified from pyrosequencing reads of multiple samples (points) in the ETSP. Spherical k-means clustering revealed a fivefold partitioning that reflects distinct OMZ habitats (see legend). Each point is colored according to the cluster that dominated the microbial population in the respective sample.

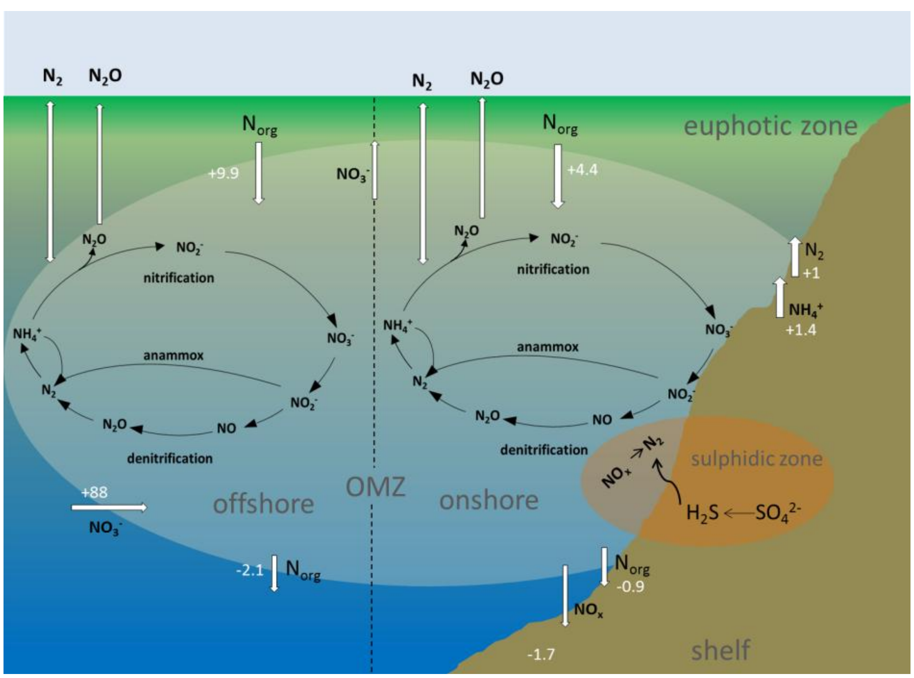

Figure 3. The marine nitrogen (N) cycle with the major onshore and offshore processes in the ETSP OMZ, modified from Kalvelage et al. (2013). Numbers indicate fluxes of N [Tg y^{-1}].

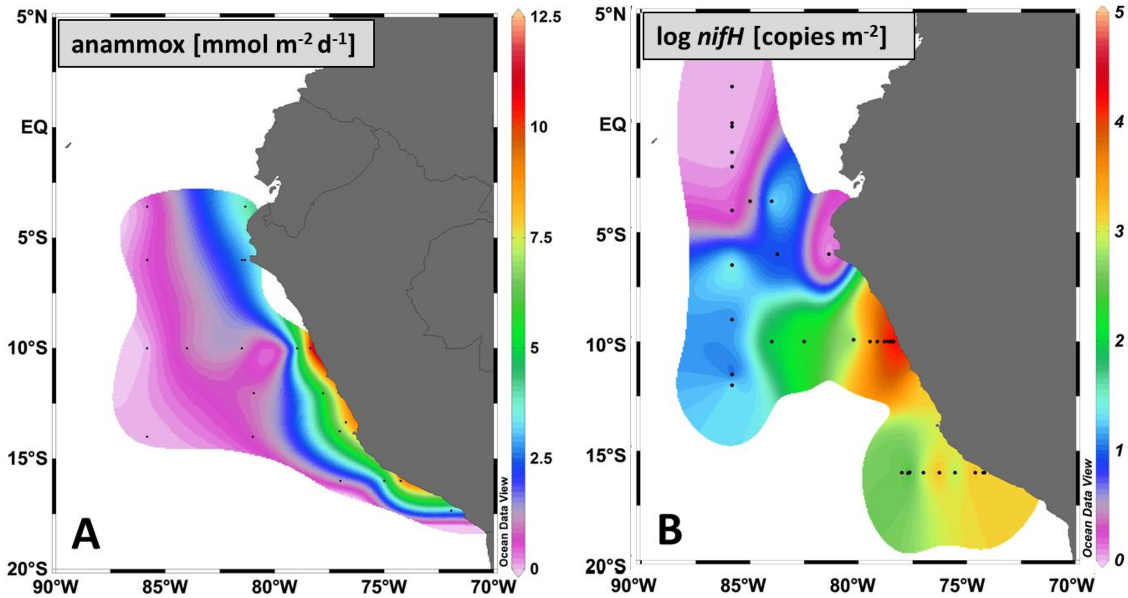

Figure 4. Co-occurrence of anammox as determined by rate measurements and the key functional marker gene for N_2 fixation, *nifH*, in the ETSP OMZ (modified from Kalvelage et al., 2013 and Löscher et al., 2014).

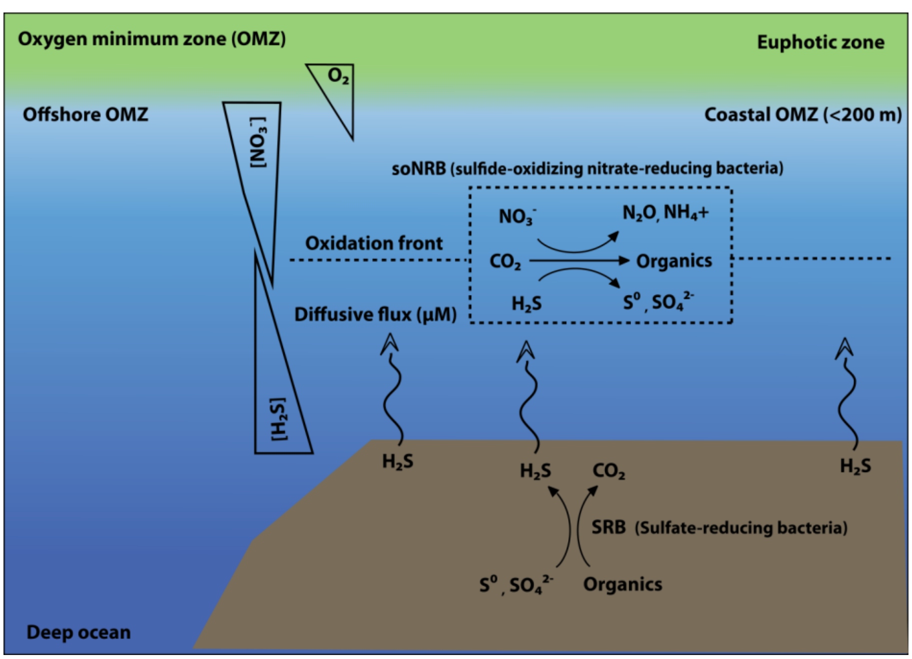

Figure 5. Schematic representation of the dynamics of a sulfidic event occurring in an oxygen minimum zone. The sulfide and nitrate fluxes are shown in steady state. Sulfate-reducing bacteria produce sulfide from the sediment while the complementary detoxification process occurs in the water column at overlapping profiles.

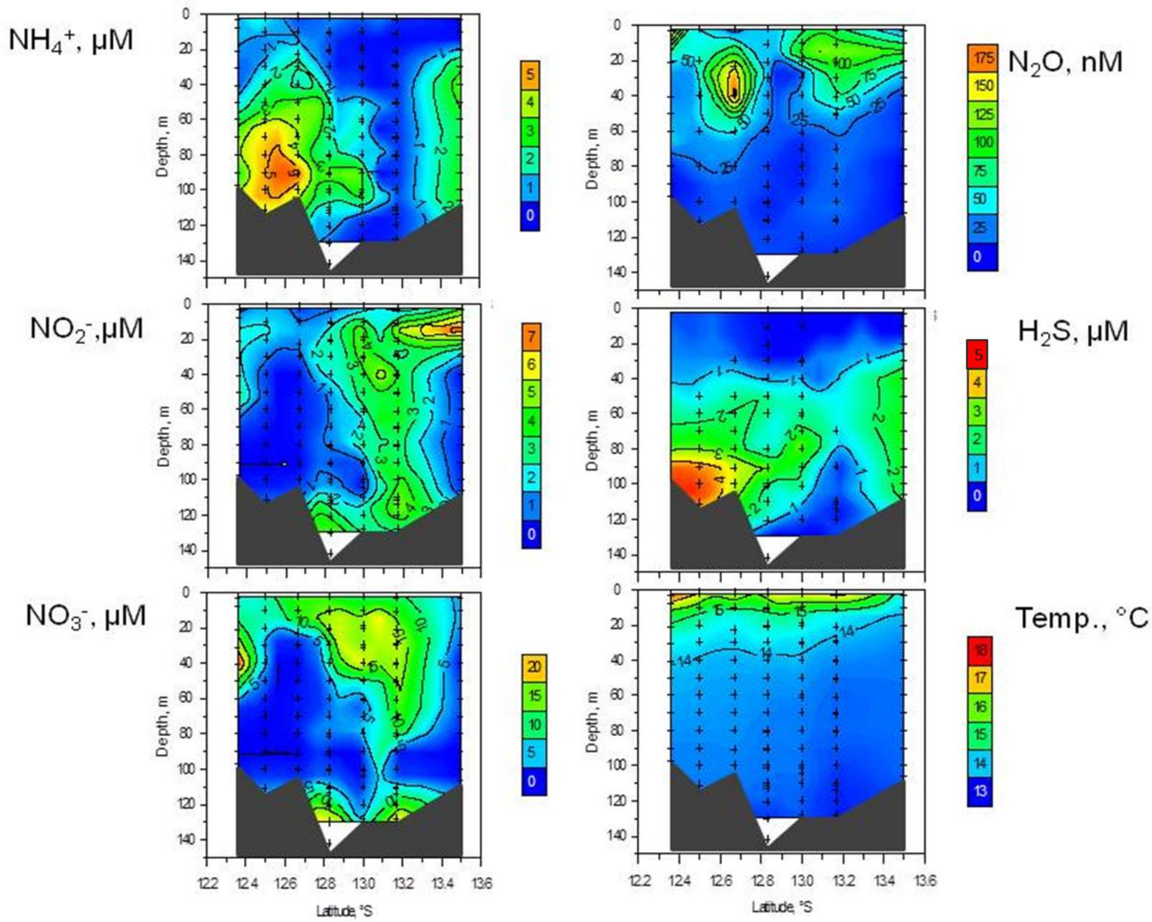

Figure 6. Distributions of N_2O, NH_4^-, NO_2^-, NO_3^-, H_2S, and water temperature during December 2008/January 2009 (R/V Meteor cruise M77/3) on the shelf along the coast of Peru. Max. N_2O concentrations have been detected right above the sulfidic zone, where a sharp oxycline is present and ammonium and nitrate are available.

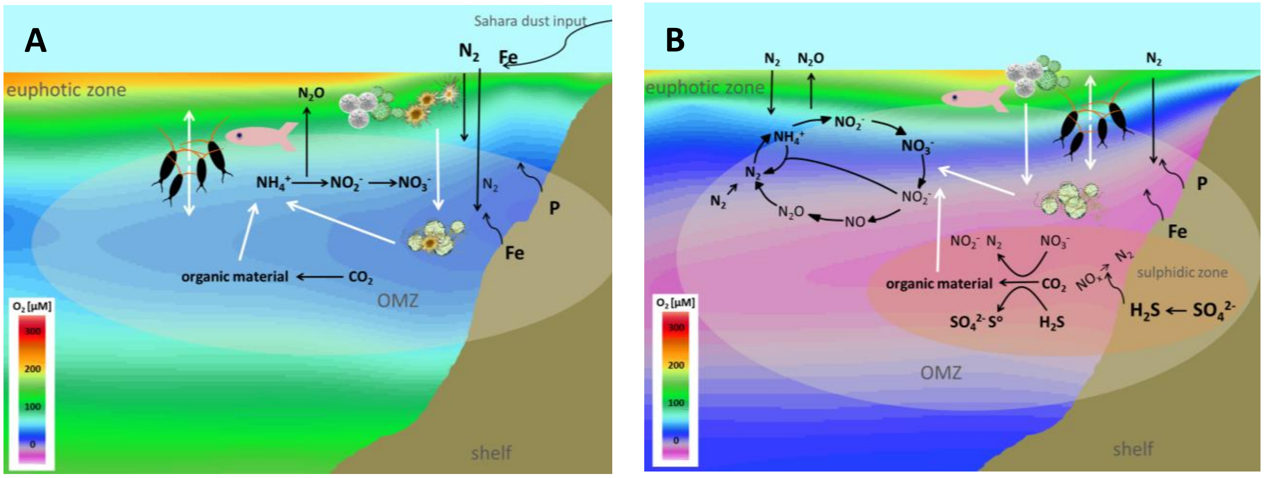

Figure 7. Scheme of the (A) ETNA and (B) ETSP OMZs with major processes identified. The O_2 background is taken from the SOPRAN cruise P399, along 18°N in the ETNA and from the SFB754 cruise M77/3, along 10°S in the ETSP.

Table 1: Definitions of different oxygen conditions used in this article.

	O_2 range	**remarks**
oxic	atmospheric saturation - 20 µmol kg^{-1}	The lower limit is defined from a metabolic view as the concentration where denitrification and anaerobic ammonium oxidation start to occur (Kalvelage et al., 2011)
suboxic	20 µmol kg^{-1} - 2 µmol kg^{-1}	The lower limit is defined by the detection limit conventionally defined for the Winkler titration method
anoxic	2 µmol kg^{-1} - 0 µmol kg^{-1}	0 is defined by the lower detection limit of the STOX sensor (~50 nmol L^{-1}) as the most sensitive detection method applied in our studies (Revsbech et al., 2009)
sulfidic	0 µmol kg^{-1} in the presence of H_2S	Full anoxia with sulfate reduction being present (Naqvi et al., 2010)