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

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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 between 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.

We investigated the pelagic biogeochemistry of OMZs in the eastern tropical North Atlantic and eastern tropical South Pacific during a series of cruise expeditions and mesocosm studies. 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. 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 the nutrient stochiometry 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, which in turn 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 $20\,\mu\text{mol}\,\text{L}^{-1}$) 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, Fig. 1). The estimated volume of OMZs with O_2 concentrations $< 20\,\mu\text{mol}\,\text{L}^{-1}$ is 1 % of the global ocean volume (Lam and Kuypers, 2011). Approximately 0.05 % of the global ocean volume has oxygen levels below 4.5 µM. This is generally considered to be the oxygen level where oxic respiration stops and alternative electron acceptors are used (Karstensen et al., 2008; Keeling et al., 2010). Although no consistent definition of suboxia exists (Canfield and Thamdrup, 2009), water masses with O_2 concentrations $< 20\,\mu\text{mol}\,\text{L}^{-1}$ are generally considered suboxic. Anoxia has been defined by the lowest measurable O_2 concentration. Though because of the continued improvements in oxygen sensors this level is changing with time (Banse et al., 2014; Revsbech et al., 2009; Thamdrup et al., 2012). Thus here, we will not use the term suboxic, but rather state the respective oxygen level, that has been detected. We will refer to anoxia as the absence of oxygen in the presence of hydrogen sulfide (see also critical remarks in Canfield and Thamdrup, 2009).

Several OMZ regions are associated with wind-driven eastern boundary upwelling regions (Capone and Hutchins, 2013). This 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 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 (Stramma et al., 2010).

The effects of O_2-dependent nutrient cycling processes occurring in these relatively small regions (Codispoti, 2010), and is then circulated 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, the 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 is 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) (Codispoti, 2010). Time series measurements of dissolved O_2 and modeling results (see e.g. Stramma et al., 2008), predict that O_2 levels will decrease significantly over the next decades in response to climate change and altered ocean circulation. Hence the future ocean may experience major shifts in nutrient cycling triggered by the possible expansion and intensification of tropical OMZs (Codispoti, 2010). There are numerous feedbacks between oxygen, nutrient cycling and biological productivity (see e.g., Deutsch et al., 2011); however existing knowledge is insufficient to understand past interactions or to adequately assess the potential for future change.

The following review of the major biogeochemical processes in OMZ waters is based on the 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 located off Mauritania has O_2 concentrations typically above 40 µmol L^{-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 L^{-1}) (Fig. 1). The two contrasting OMZs were chosen to improve our understanding of the biogeochemical processes for the development and maintenance of OMZs.

2 OMZ impacts on marine biota: O_2-mediated metabolic constraints

2.1 Background

Microbial, protozoan and metazoan energetics are governed by redox reactions, which is the sum of electron accepting and donating half-reactions. Oxygen is the most thermodynamically favorable electron acceptor (Danovaro et al., 2010; Fenchel and Finlay, 1990). Concentrations, which are saturated in surface waters, are eventually respired down to nanomolar concentrations with depth. This gradient referred to as the oxycline, represents an important transition from aerobic to microaerobic, and then to anaerobic respiration using nitrate (NO_3^-) as the next favorable electron acceptor followed by e.g. NO_2^-, manganese, iron, sulfate (SO_4^{2-}) and carbon dioxide (CO_2), where the latter acceptor is used by methanogens (Wright et al., 2012). These reactions are characteristic for specific O_2 levels. The sensitivity and kinetics of these reactions to gradual changes in oxygen concentrations experienced at or below the oxycline are not well understood under in situ conditions. The following section explores recent developments in our understanding of the effect of oxygen on the microbial community as well as to metazoans.

2.2 Microbes and metazoans in OMZ

Most studies resort to observing and correlating changes in oxygen concentrations to changes in the microbial phylogenetic diversity, while the adaptive response of animals to O_2 availability has been extensively studied in several species (for reviews see Ekau et al., 2010; Seibel, 2011). 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).

High-resolution sampling through the ETNP OMZ has shown that the highest microbial richness is at the base of the euphotic zone or the upper oxycline. This is an area experiencing a high organic flux, low O_2 concentrations and dynamic cycling of carbon (C), nitrogen (N), and sulfur (S) cycles (Beman and Carolan, 2013). The sinking particles likely promote a diverse community of heterotrophs. Whereas the low abundant microorganisms such as sulfur-oxidizers, purple sulfur bacteria (Chromatiales) and anammox bacteria seem to contribute to the OMZs “rare biosphere” (Beman and Carolan, 2013; Pedros-Alio, 2012). Anammox bacteria, for example, usually constitute less than 4 % of the microbial community (Kuypers et al., 2005; Hamersley et al., 2007). The anammox bacteria, which are considered to be strictly anaerobic under laboratory conditions, demonstrate a potentially wider tolerance for O_2 concentrations ($\sim$ 10–20 μmol L^{-1}) in the environment (Hamersley et al., 2007; Jensen et al., 2011; Kuypers et al., 2005). Similarly the first step in denitrification, NO_3^- reduction to NO_2^-, also appears to be O_2-tolerant of up to 25 μmol L^{-1} O_2 (Lipschultz et al., 1990). Moreover, many denitrifiers have facultative metabolisms. Together this indicates that the microaerobic processes of NH_3 and NO_2^- oxidation involved in the production/replenishment of nitrite and nitrate reserves, respectively, may be more tightly coupled in space and time to anammox and denitrification activities (Füssel et al., 2011; Lam et al., 2009; Lipschultz et al., 1990; Kalvelage et al., 2011). These findings could be used to improve on current biogeochemical models of OMZ (Paulmier et al., 2009).

Metazoans living permanently at extremely low oxygen concentrations are rare (Auel and Verheye, 2007; Escribano et al., 2009; Fernández-Álamo and Färber-Lorda, 2006; Saltzmann and Wishner, 1997; Wishner et al., 1998). They more typically feed at surface waters during the night and then migrate beneath the photic zone at daytime to avoid visual predation (Lampert, 1989), and to conserve energy (McLaren, 1963). This behavior is known as diel vertical migration. Diel Vertical Migration species (DVMs) such as zooplankton and nekton may tolerate temporarily hypoxic conditions during migrations in the OMZ water column. In addition to changes in temperature with depth, DVMs will experience at daytime low $p\mathrm{O}_2$ (oxygen partial pressure, p) and elevated $p\mathrm{CO}_2$ (Brewer and Peltzer, 2009; Paulmier et al., 2011). DVMs that have evolved physiological adaptations (such as metabolic suppression) and/or morphology (such as increased gill surface area) allowing them to temporarily cope with hypoxic conditions. These DVMs 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). Strong physiological adaptations seem necessary to thrive in the ETSP OMZ but not in the ETNA OMZ where oxygen levels are considerably higher (Teuber et al., 2013).

The main strategy to survive low oxygen conditions seems to be the DVMs down-regulation of its aerobic metabolism. If down-regulation is extreme then the DVM experiences sluggish behavior (e.g., Trübenbach et al., 2013, for *Dosidicus gigas*). The main triggers for down-regulation appear to be temperature and $p\mathrm{O}_2$, but also external $p\mathrm{CO}_2$ (Pörtner et al., 2004). It has been further shown that an increase in external $p\mathrm{CO}_2$ leads to a decrease in extracellular $p\mathrm{H}$ in several marine invertebrates (Melzner et al., 2009). While the effects of ambient temperature, $p\mathrm{O}_2$ and also $p\mathrm{CO}_2$ on metabolic rates of marine species have been studied primarily in single factor experiments (Ekau et al., 2010; Seibel, 2011), Rosa and Seibel (2008) showed in all cases a reduction in metabolic rates of *Dosidicus gigas* when each factor was independently varied. Though the combined effects on the regulation of DVMs aerobic metabolism is still not well understood.

In extreme OMZs, such as in the Eastern Tropical Pacific or the Arabian Sea, where $p\mathrm{O}_2$ drops to zero, vertically migrating animals may temporarily switch to an anaerobic metabolism. This is only possible for restricted time periods – ultimately, all DVMs (besides a few exceptions, see Danovaro et al., 2010) grow via 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 diel vertical migration behaviors (which, in spite of their large phylogenetic difference, proved right). In 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 have 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).

DVMs which are known to secrete ammonium may have previously unconsidered effects on the biogeochemical cycling of nitrogen in ETSP waters. Ammonium is an important nutrient in the anammox reaction which represents nearly 30–50 % of N-loss activity in the OMZ. Bianchi et al., 2014, have shown that DVMs can supply as much as 30 % of the ammonium for the anammox reaction. The full scope of this activity in ETSP is still not well understood. To move forward we (1) need a better understanding of vertical migration behavior of key DVMs in the core OMZ, (2) we need to investigate what adaptive hypoxic stress responses DVMs may use, and (3) we need to determine the effects of hypoxic conditions on the secretion of metabolic end products. Given the

DVMs' potential importance to the nitrogen budget we hope future work will help to expand on current biogeochemical models.

3 Viruses – the discounted factor

3.1 Background

Viral concentrations in the ocean range from $\sim 3\times10^{6}\,\mathrm{mL}^{-1}$ in the deep sea to $\sim 10^{8}\,\mathrm{mL}^{-1}$ in coastal regions, with several thousand of viral genotypes found in seawater (Suttle, 2005 and references therein). With an estimated 4×10^{30}, viruses outweigh the number of prokaryotes in the ocean by thirty times ($\sim 1.2\times10^{29}$) (Suttle, 2005; Whitman et al., 1998). Moreover an approximate 5–30 % of marine cyanobacteria and heterotrophic bacteria are infected by viruses (Ostfeld et al., 2010).

Although not well studied in OMZ waters, the importance of viral lysis for particle (algae) degradation can have well established implications for aggregate C : N and N : P ratios (Suttle, 2005). They are believed to be strong determinants of microbial metabolic diversity by providing their hosts with auxiliary genes for rate-limiting metabolic steps. Also, through host cell lysis viruses can directly change the stoichiometry of dissolved nutrients in the water column. This can increase microbial respiration rates and decrease the efficiency of carbon transfer to higher trophic levels (Suttle, 2005). Thus, a complete picture of OMZ ecology and biogeochemistry requires the identification and quantification of microbe-virus interactions.

3.2 Viral communities in OMZ

A virome, defined as the whole collection of virus genomes from a particular environment has been under recent investigation in OMZ waters. Cassman and colleagues (2012) demonstrated the existence of depth-specific viromes in the ETSP waters off Iquique, Chile. They compared their data to the ETSP microbiome analysed by Steward et al. (2012). Concentrating on the planktonic none-particle bound community they found that the virome recovered from the oxycline was dominated by eukaryotic viruses, while in contrast bacteriophages were mostly represented in the anoxic core. Both viromes featured a novel sequences and unexpectedly low diversity (in the range of 10^1–10^2 genotypes) compared to viromes of other productive oceanic regions (in the range of 10^3–10^4 genotypes). The virus-microbe ratio (VMR) fluctuated in the oxycline then declined in the anoxic core to around one. Indicating that the viral as well as microbial community structure varied with the decline in oxygen, this seemed consistent with host redox-driven niche partitioning. In the anoxic OMZ core, Cassman et al. (2012) discovered high sequence abundances of siphoviruses, a family of bacteriophages within the order Caudovirales (see Fig. 2 in Clokie et al., 2011). Siphoviruses are more frequently lysogenic (Dwivedi et al., 2013). This supports the hypothesis that viral lysogeny is believed to be more active in extreme environments (Maurice et al., 2011; Cassman et al., 2012).

The study by Cassman et al. (2012) is one of few to relate virology to OMZ biogeochemistry. 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 the numbers of the latter. This principle, known as the “Kill the Winner” hypothesis (Thingstad and Lignell, 1997) compares interactions between viruses and microbial hosts to a “classical” predator–prey relationship.

On the other hand, viruses can change nutrient stoichiometry in the water column directly through lytic events. Lytic events cause bacterial cell lysis and the subsequent 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, for example cyanobacteria and other prokaryotes, is recycled back to dissolved organic matter (Ostfeld et al., 2010). Specifically, (cyano)phages in the ETSP have been shown to release micronutrients such as Fe into the dissolved size class at an estimated flux of $10^1\,\mathrm{pmol\,L^{-1}\,d^{-1}}$ (Poorvin et al., 2004). Likewise, virus-induced bacterial lysis is responsible for a global N release of ∼ 1–6 $\mathrm{Gt\,a^{-1}}$, which significantly supports phytoplankton production (Shelford et al., 2012).

If the prevailing mode of existence in OMZ core viruses is lysogeny (Cassman et al., 2012), one would expect changing environmental conditions such as temperature shifts (e.g. by the El Niño–Southern Oscillation in the ETSP OMZ) to induce lysis of host cells on a massive scale. This would consequently lead to abrupt shifts in water column nutrient budgets that cannot be accounted for in biogeochemical models by microbial processes only. Viruses can also impact particle formation and diaggregation by discharging adhesive cell components (Peduzzi and Weinbauer, 1993) and cell lysis (Weinbauer et al., 2011), respectively.

Bacteriophages often carry auxiliary metabolic genes (AMGs) for critical rate-limiting steps of a host's metabolism (Breitbart, 2012). As examples, 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 sulphur have been also found in viromes of ETSP waters (see Tables S3 and S4 in Cassman et al., 2012). These studies underline the importance of prokaryotic viruses in driving microbial metabolic diversity and suggest this process is likely acting in OMZ.

To better assess the role of OMZ microbial viruses in lysis, lysogeny and transfer of AMGs, it is required to know the “host-virus susceptibility pairs” – which microbes are infected by which viruses. 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. By attachment to particles such as marine snow and fecal pellets, microbes get direct access to the nutrients stored therein and can create protective microenvironments via biofilm formation. This microbial mode of living should thus be fairly common in OMZs as highly productive environments. For a complete picture of OMZ ecology and biogeochemistry it will be important moving forward to identify microbe-virus susceptibility pairs. This may led to further insights on our understanding of virus-driven nutrient cycling in OMZ.

4 Fluxes of organic matter in tropical shallow OMZs

In the following section we shortly review key components of the biological pump (passive sinking of particles, zooplankton mediated fluxes, physical downward transport of DOM) in tropical oxygen minimum zones and synthesize recent ideas on that topic.

4.1 Passive 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. At the eastern tropical Pacific VERTEX cruise stations (Peru, Vertex II, Vertex III, Martin et al., 1987), as well as off Mexico (Van Mooy et al., 2002; Devol and Hartnett, 2001) mesopelagic POC fluxes were less attenuated (Martin curve exponent "b" of 0.319–0.805) than in typical oxygenated ocean regions ("open ocean composite"; $b = 0.858$). Those studies indicate that a greater proportion of the sinking OM escapes degradation while sinking through the ETP OMZ. On the other hand, VanMooy et al. (2002), as well as Pantoja et al. (2004, 2009) have shown that microbial degradation of organic nitrogen and protein under hypoxia is not strongly affected. Still little is known of the microbial controls on the decomposition of organic matter are under lower oxygen concentrations. An alternative hypothesis could be that the diminishing 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. Future studies should combine measurements of particle flux, zooplankton abundance, microbial activities and O_2 concentrations, as changes in flux attenuation would be expected to occur at and below O_2 concentrations.

4.2 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. In addition, many pelagic species conduct diel vertical migrations (DVM) and active transport of OM is connected to these migrations. Food is consumed at night in the euphotic zone, whereas during the day they 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.

Oxygen concentrations below a certain threshold level should 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). According to Seibel (2011), the first threshold is found at 5 kPa of oxygen partial pressure (approximately 40 μmol kg^{-1}). Nevertheless, some specifically adapted species actively migrate into severely hypoxic to anoxic OMZs (e.g. *Eucalanus inermis* and *Euphausia mucronata*; Escribano et al., 2009). In a global analysis of shipboard ADCP data, Bianchi et al. (2013) found that the migration depth is greater in oceanic areas where O_2 concentrations are high, coinciding with the upper oxycline in OMZ areas. Their conclusion that animals actively select their daytime depths according to oxygen content may still be disputed, since they show that the oxycline and the light penetration depth are positively correlated in their dataset. Impaired DVM of less tolerant species as a result of expanding and intensifying OMZs may thus reduce zooplankton and nekton mediated fluxes from the photic zone into the mesopelagic. Estimates of zooplankton and nekton mediated carbon fluxes to the OMZ 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 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ 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 at 0.093 to 0.152 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ (Gonzalez et al., 2000). In a much less intense OMZ area (e. g. 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). Most of the zooplankton sampled from the ETNA covered only the upper 200 m of the water column (Moriarty et al., 2013), this hampered estimations on the DVM-mediated transport of organic matter into the ETNA waters.

4.3 Physical fluxes of DOM

In contrast to particle fluxes, DOM transport is linked 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 for lateral eddy transport, Mathis et al. (2007) found elevated DOM concentrations (by +11 $\mathrm{\mu mol\,C\,L^{-1}}$) in the Canada Basin within an eddy originating from the shelf region. Lasternas et al. (2013) suggest 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 pronounced 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 tracer fluxes. 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 oxygen, 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 bio-available 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 oxygen 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). We hypothesize that DOM supply via (sub-) mesoscale vertical transport processes and diapycnal mixing may therefore contribute importantly to sustaining microbial activity in the Peruvian OMZ.

5 The nitrogen cycle in OMZ waters

5.1 Background

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. 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). However, there are still many open questions regarding the effects of O_2 concentrations on nutrient regeneration, N loss, N_2O production and N_2 fixation processes in O_2 deficient waters. Connected to highly productive eastern boundary upwelling systems, where intermediate waters, often depleted in nitrogen, are forced towards the sea surface, N_2 fixation is thought to be promoted in adjacent surface waters.

The findings obtained in the context of the SFB754 comparing the OMZs of the eastern tropical North Atlantic (ETNA) and the eastern tropical South Pacific (ETSP) Oceans, combine rate measurements of N_2 fixation, nutrient regeneration, N turnover, N loss processes and N_2O production throughout the above mentioned OMZs under various O_2 conditions. Key players of marine N cycle processes were identified and quantified using meta-omic approaches and mesocosm studies. Our results provide insights into spatial coupling of N loss, N_2 fixation and nutrient limitation and identify hotspots of N loss and N_2O production in OMZ waters. This improved our understanding of the impact of low-oxygen conditions on the N cycle, contributing potentially important insights for the ocean's biogeochemistry.

5.2 N cycle processes

Nitrogen is an essential nutrient and a fundamental component of living organisms in general. However, the atmospheric pool of N_2 is only available to living organisms via biological N_2 fixation, which is restricted to a group of prokaryotes called diazotrophs (Capone and Carpenter, 1982). Until recently, oceanic N_2 fixation was mainly attributed

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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).

N_2 fixation is highly sensitive to dissolved O_2, as the key enzyme nitrogenase is irreversibly inhibited by O_2 (Dixon and Kahn, 2004). Thus, the low O_2 conditions present in OMZs sustain a potential niche for diazotrophs. However, large amounts of dissolved inorganic N compounds such as nitrate are commonly present in OMZs, which are classically regarded to inhibit N_2 fixation (Dixon and Kahn, 2004; Leigh and Dodsworth, 2007). N is continuously removed by anammox, (Francis et al., 2007; Kuypers et al., 2005, 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), Arabian Sea (Jensen et al., 2011), Peru (Hamersley et al., 2007) and Chile (Thamdrup et al., 2006). Moreover, N is lost or recycled via denitrification (the 4-step reduction of NO_3^- to N_2, Devol, 2008, DNRA (the **d**issimilatory **n**itrate **r**eduction to **a**mmonia), as hypothesized by Lam et al., 2009) and nitrification (the aerobic oxidation of ammonia via NO_2^- to NO_3^-, Ward, 2008). Although different anaerobic microbial processes may have different oxygen tolerance i.e. as an adoption to transient oxygen conditions (Jensen et al., 2007; Kuypers et al., 2005) the regulation of these processes in OMZ waters are still poorly understood. In OMZs enhanced N loss (Deutsch et al., 2007) resulting in a N deficit and the simultaneous release of phosphorus (P) from anoxic shelf sediments (resulting in high P*, i.e. excess P, 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).

5.3 The nitrogen cycle in two contrasting OMZs: coupling of N_2 fixation and N loss

Contrasting O_2 regimes in the OMZs of the ETNA and the ETSP oceans give strongly different biogeochemistry in terms of the N cycle. While the ETSP, with oxygen concentrations below the detection limit of conventional methods in the OMZ core, is characterized by intense N-loss (Kalvelage et al., 2011, 2013), the ETNA, with O_2 concentrations usually above 40 µmol L^{-1}, shows no sign of water column N-loss (see, e.g., Bange et al. (2010), for an overview of N_2O producing processes in different ocean areas). This difference is mirrored by a diverging d^{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 dissimilar N turnover processes characteristic for these two regions, and correspondingly different impacts on nutrient biogeochemistry.

In the ETNA off Mauritania, processes such as denitrification and anammox are absent from the water column (Ryabenko et al., 2012) due to previously mentioned high O_2 concentrations (> 40 µmol L^{-1}) in sharp contrast to the Benguela upwelling system in the South Atlantic where N loss processes occur (Kalvelage et al., 2011; Lavik et al., 2009). The ETNA is characterized by nitrification as the only N turnover process in this area, with ammonia oxidizing archaea contributing mainly to the first step, which is the oxidation of ammonium to nitrite (Löscher et al., 2012).

In contrast to the ETNA, Kalvelage et al. (2013) demonstrated a dominance of N loss processes in the ETSP using ^{15}N-incubation experiments (an overview of the N cycle processes in the OMZ off Peru is given in Fig. 2). These experiments showed that anammox was the major N loss process in the ETSP during our studies. From oxygen manipulation experiments, we found that anammox activity decreased with increasing O_2, but remained detectable at up to > 15 µmol L^{-1} with particularly high O_2 tolerance in near-shelf coastal waters.

An O_2-tolerance for N loss activity being close to 20 µmol L^{-1} instead of 5 µmol L^{-1} would imply that the ocean volume attributed to N loss might be up to 10 times larger than currently believed. An even higher O_2 tolerance was observed for NO_3^- reduction to NO_2^-, a major source of both NO_2^- and NH_4^+ for the anammox reaction, which also remained active at as much as 25 µmol L^{-1} of O_2. At the same time aerobic processes like ammonia and nitrite oxidation did not show significant rate reduction when O_2 concentrations were decreased from 25 to ∼ 1 µmol L^{-1} in incubation experiments (Kalvelage et al., 2011). However, N_2O production attributed to ammonia oxidation was shown to increase significantly under low O_2 conditions (Löscher et al., 2012, see Sect. 8). Thus, these key processes of the N cycle seem to overlap over a wide range of O_2 concentrations (Kalvelage et al., 2011), extending the habitats of the respective organisms over almost the complete OMZ.

Despite the fundamental differences between the OMZs of the ETNA and ETSP with regard to N loss, we could identify N limitation in short-term mesocosm experiments of surface plankton communities in both areas (Franz et al., 2012a, b). For both OMZ systems, Franz et al. (2012b) showed, that low nutrient N : P ratios in upwelled waters adjacent to OMZs are a net source for dissolved organic phosphorus (DOP), which is believed to promote diazotrophy. Based on these findings, enhanced N loss is expected to result in a decline of organic matter production combined with an increase in DOP release. However, model studies (Deutsch et al., 2007) suggest that a N-deficit with respect to Redfield stochiometry 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 in the open ocean.

N_2 fixation in the upper water column represents a major N-input (> 40 %) into the global ocean; it was conventionally considered most active in nutrient-depleted surface waters, e.g., in the subtropical gyre centers (Sohm et al., 2011). Still, O_2 conditions at the sea surface are not favorable for N_2 fixation. Results from 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, and the low O_2 in OMZ waters would likely favor N_2 fixers (Großkopf and LaRoche, 2012). Moreover, a growing number of *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), as well as in OMZ waters of the ETNA (unpublished data), did not belong to the common oxygenic phototrophs, but to some unknown diazotrophic microorganisms that might be specially adapted to O_2 deficient conditions, and should be further investigated. 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), suggests an even tighter spatial coupling between N loss and N gain communities than previously considered. Evidence for co-occurrence of denitrification and N_2 fixation has previously been documented only for an anoxic lake (Halm et al., 2009), but not for any marine system. This broad diversity of diazotrophs, as well as the extension of their habitat to deeper waters might be one reason for the 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 likely have been significantly 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 $177 \pm 8\,\mathrm{Tg\,N\,yr^{-1}}$, which still does not compensate for the N loss from the ocean ($400\,\mathrm{Tg\,N\,yr^{-1}}$, Codispoti, 2007). If taking into account only the water column N loss of $150\,\mathrm{Tg\,N\,yr^{-1}}$, the revised N_2 fixation rate of Großkopf et al. (2012) would balance the water column N budget. Benthic N loss processes do, however, account for $\sim 300\,\mathrm{Tg\,N\,yr^{-1}}$, thus exceeding water column N loss by far. 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). Those findings demonstrate again the deficiencies in our understanding of the marine N cycle and the challenge to come up with realistic budgets with our state of knowledge.

5.4 Nutrient regeneration, primary production and organic matter export

Due to the N deficiency of upwelled waters, primary production in OMZ-influenced waters is strongly dependent on external N sources, such as N_2 fixation or N input via dust deposition (Ryabenko et al., 2012). Particularly in the ETNA, dust deposition from the Sahara might play an important role, as the d^{15}N-NO_3^- signal is lower than can be explained by N_2 fixation alone (Ryanbenko et al., 2012). However, the high nutrient concentrations in coastal upwelling systems of the ETNA and ETSP fuel primary production, thus those systems belong to the most productive areas in the ocean (Carr, 2002). High primary productivity leads to high organic matter export from the surface layer to intermediate water depths, promoting microbial respiration along with O_2 depletion and ultimately N loss in the ETSP (but not in the ETNA due to relatively high O_2 concentrations).

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. Previously, organic matter remineralization in OMZ waters with low to non-detectable ($< 5\,\mu\text{mol}\,L^{-1}$) oxygen 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). Additionally, the strong correlation between nitrification and anammox activity to the modeled export production rates indicates organic matter supply is the driving mechanism also for autotrophic N-cycling processes. In the absence of significant denitrification these results indicate that anammox relies on NH_4^+ oxidation and NO_3^- reduction as NO_2^- source, and NH_4^+ from remineralization of organic matter via NO_3^- reduction with a possibly important role of microaerobic respiration. The overlap in 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 waters. As DNRA was insignificant in the water column during our studies in the ETSP, sedimentary ammonium 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.

6 Remineralization

6.1 Background

During oxygenic respiration surface derived organic matter is remineralized back to the inorganic forms of carbon and nitrogen. These inorganics can be made available again for primary producers after subsequent transport to the surface via mixing or upwelling. Viruses, bacteria, protozoa and metazoa are responsible for the remineralization processes under oxic conditions; however, their contributions can change when oxygen concentrations decrease. Metazoan activity and abundance is most sensitive to lower oxygen concentrations, whereas, bacteria can thrive under diverse redox conditions using e.g. nitrate as the next favorable electron acceptor. Below the oxycline the OMZ harbors a diversity of bacteria involved in the nitrogen cycle, which have important implications for the global N-budget. Of these organisms denitrifiers and anammox bacteria represent the main contributors to the conversion of bioavailable nitrates to dinitrogen gas lost eventually to the atmosphere. While nitrogen fixing bacteria can counter to some degree the N-loss processes by converting dinitrogen gas back to bioavailable nitrates in the OMZ. N_2 fixation and N loss are thus the predominant processes determining the oceanic N : P ratio since the phosphorus content stays relatively constant.

6.2 Coupling of N loss and N_2 fixation

Denitrification partly reverses the role of remineralization in the nitrogen cycle of OMZ and acts to transform them into net sinks of fixed nitrogen (Landolfi et al., 2013). Because denitrification removes more fixed nitrogen than is contained in the remineralized organic matter, any addition of fixed nitrogen 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 fixed-nitrogen loss in an OMZ is determined by the balance of remineralization of sinking particulate organic carbon (POC) and O_2 supply to the OMZ. While the supply of oxygen is fully determined by physical transport, the rate of nitrogen loss depends on the activity of the bacteria responsible for denitrification and anammox as well as the POC sinking velocity.

The result of high fixed N loss, e.g. by anammox (Kalvelage et al., 2013), is a low N : P ratio in the source upwelling waters supplying the overlying surface ocean. The low inorganic N : P ratio supplied to the surface has been thought to favor nitrogen fixation and thereby trigger a positive feedback stripping the OMZ of fixed nitrogen (Canfield, 2006; Landolfi et al., 2013). 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, b). 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.

6.3 The role of bacteria and zooplankton for remineralization

Bacteria 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 bacterial respiration (del Giorgio and Cole, 1998). Owing to the relatively low N and P content of dissolved organic matter, however, bacteria are 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 is thus mostly due to zooplankton activity (Caron et al., 1988; Garber, 1984; Pahlow et al., 2008). As outlined in Sect. 1 (OMZ impacts on marine biota), most zooplankton avoid intense OMZs, and while some species can temporarily tolerate anoxic conditions and migrate into or through an OMZ (Fernández-Álamo and Färber-Lorda, 2006), their metabolic activity would be negatively impacted. Thus, remineralization due to zooplankton should be mostly restricted to the oxic surface waters in OMZ regions.

6.4 The role of stoichiometry

The loss of bioavailable nitrogen in OMZ waters through denitrification and anammox in combination with the release of reactive phosphorus from sediments exposed to anoxic waters generates extremely low nutrient N : P ratios. This abnormal stoichiometry can impact the nutrients supplied to the euphotic zone, and consequently primary production. Franz et al. (2012b) during a cruise to the tropical South East Pacific and North East Atlantic investigated the partitioning and elemental composition of dissolved and particulate organic matter. 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 phosphorus was consumed by non-Redfield production, predominantly by diatoms. Release of dissolved organic phosphorus (DOP) by phytoplankton further diminished excess P. N : P of the accumulated biomass generally exceeded the supply ratio (Franz et al., 2012b). These results demonstrate that low nutrient N : P conditions in upwelling areas overlying O_2-deficient waters represent a net source for DOP. Whether accumulated DOP stimulates growth of diazotrophic phytoplankton is presently unknown.

These results are corroborated by in situ observations along an east–west transect at 10° S stretching from the upwelling region above the narrow continental shelf to the well-stratified oceanic section of the eastern boundary regime (Franz et al., 2012a). New production from 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 and showed intermediate N : P ratios close to Redfield proportions. High PON : POP ($> 20 : 1$) ratios were observed in the stratified open ocean section, coinciding with the abundance of the pico-cyanobacterium *Prochlorococcus*. Excess phosphate present along the entire transect did not appear to stimulate growth of nitrogen-fixing phytoplankton, as pigment fingerprinting did not indicate the presence of diazotrophic cyanobacteria at any of our sampling stations. Instead, a large fraction of the excess phosphate generated within the OMZ was consumed by non-Redfield stoichiometry and likely by large phytoplankton found in shelf surface waters.

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 eficiency 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. While, higher surface nutrient concentrations would 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) is that the competitive advantage of diazotrophs is most pronounced under conditions of low DIN and DIP availability, because diazotrophy increases the competitive ability for DIP when DIN is limiting (Houlton et al., 2008). The competitive ability for DIP is less important than for high DIP, however, high phosphate concentration above the ETSP OMZ might actually reduce the selective advantage of diazotrophs compared to ordinary phytoplankton. This could in part be an explanation for why diazotrophy was apparently not stimulated by excess phosphate in the abovementioned transect.

If fixed-nitrogen removal exceeds the lateral supply of nitrate into the OMZ region, the OMZ will be completely void of fixed inorganic nitrogen and the OMZ will become sulfidic. The transition to sulfidic conditions marks an important tipping point, as most higher life forms, including fish, cannot tolerate sulfide. That this is not the case 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.

However, widening and intensifying of tropical OMZs over the recent decades has been observed (Stramma et al., 2008), which could also indicate a strengthening of the fixed-nitrogen 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 oxygen and nitrogen may be triggered once a certain tipping point is reached. The positive feedbacks appear to be linked to a spatial coupling of N_2 fixation and N loss (Deutsch et al., 2007) and several mechanisms have been suggested to weaken the positive feedback via spatial uncoupling, e.g., by redirecting of primary production to semi-labile or refractory dissolved organic matter (Landolfi et al., 2013). Still, too little is currently known about the interactions among the stoichiometry of inorganic nutrient supply, primary production, N_2 fixation, end remineralization under anoxic conditions, to allow a definite characterization of the conditions leading to fixed-nitrogen exhaustion in the OMZs.

7 Oceanic sulfidic events and detoxification by sulfide-oxidizers in the Peruvian upwelling: open questions

7.1 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). To date sulfide 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 the 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 the Saanich Inlet in Canada (Tebo and Emerson, 1986; Walsh et al., 2009). Oceanic events are understood to originate from sulfide containing sediments (Fig. 3). Here, the sulfide accumulates to milli-molar concentrations under oxygen and nitrate-free conditions and is released by a diffuse 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 reoxidize 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 ($\mathrm{mmol\,m^{-2}\,d^{-1}}$) 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 oxygen minimum zones in both the Atlantic and Pacific (Stramma et al., 2008), sulfidic events are expected to become more frequent.

7.2 Sulfidic events off Peru

The first quantitative measurements and detailed profiles of 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 $\mathrm{km^2}$ and contained approximately 2.2×10^4 t 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 $\mathrm{\mu mol\,L^{-1}}$), nitrate (< 1 $\mathrm{\mu mol\,L^{-1}}$) and nitrite (2 $\mathrm{\mu mol\,L^{-1}}$) 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 epsilonsuch 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., 2012; Walsh et al., 2009; Swan et al., 2011). Both gamma- and epsilon-proteobacteria members are known chemolithoautotrophs, which assimilate carbon dioxide into organics 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. Emphasizing that while chemolithoautotrophic driven CO_2-fixation was 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.

While the bulk sulfide production is likely to originate from the sediments it has been suggested that pelagic sulfate reduction may also contribute to sulfide production. 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. In situ incubation experiments done in the Chilean upwelling have even shown the capacity for sulfate reduction. However, measured rates of sulfide oxidation were larger, indicating that any produced sulfide is immediately re-oxidized (Canfield et al., 2010). The authors had suggested an active but cryptic sulfur cycle linked to nitrogen cycling in the pelagic OMZ. However, it is still not fully known if and how sulfide could accumulate under these conditions and how this may contribute to the formation of sulfidic events.

8 Trace gases

8.1 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 our 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 (Santoro et al., 2011). The production of N_2O by archaea (and bacteria) depends on dissolved O_2 concentrations and is thought to be increasing with decreasing O_2 concentrations (Frame and Casciotti, 2010; Löscher et al., 2012). Denitrifying bacteria do not produce N_2O under oxygenated conditions classically described as $< 10 \mu\text{mol}\,\text{L}^{-1}$; however, when O_2 concentrations are approaching $0\,\mu\text{mol}\,\text{L}^{-1}$, N_2O is consumed during denitrification. There is no N_2O production under full anoxic conditions (i.e. when no O_2 is detectable using standard techniques). The significance of an oceanic N_2O production during anammox and DNRA (see Sect. 5), which can occur in OMZs as well, 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 indeed two facts (Ryabenko et al., 2012): (i) The lower O_2 concentrations found in the core of the OMZ of the ETSP ($< 5\,\mu mol\,L^{-1}$) favor N_2O consumption by denitrification which is not observed in the ETNA because of its comparably higher 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–$10\,\mu mol\,L^{-1}$) 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 nitrogenous or even 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, Sect. 7). Figure 4 shows the distribution of N_2O, water temperature, nutrients and H_2S during the anoxic 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 (sulfidic) 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 conditions) N_2O production turns into N_2O consumption. Similar N_2O distributions during anoxic events were found off the west coast of India and in the Gotland Deep (central Baltic Sea) (Brettar and Rheinheimer, 1991; Naqvi et al., 2000). 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 the recent findings from the anoxic event off Peru by Schunck et al. (2013) and the recent hypothesis proposed by Canfield et al. (2010).

8.2 The role of OMZs in trace gas emissions

The upper 1000 m of the ocean (incl. the euphotic zone and the so-called subsurface layer) 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) occur (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 in the subsurface layer (i.e. OMZ) where the O_2 concentrations are depleted due to the remineralisation of organic matter. 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.

In OMZs below 20 $\mu mol\, O_2\, L^{-1}$, N_2O production does not take place in the core. Instead, N_2O production is found at the oxycline. Exceptionally high N_2O concentrations have so far only been found in seasonally occurring anoxic (O_2 below the detection limit of conventional methods) regions off Peru and West India (Naqvi et al., 2010). Stagnant anoxic systems such as in the Baltic and Black Seas as well as the Cariaco Basin, have only shown slightly enhanced N_2O concentrations at the oxic/anoxic interfaces (Bange et al., 2010, and references therein). This implied that significant pulses of N_2O emissions to the atmosphere occur only when a shallow coastal system rapidly shifts from oxic to anoxic 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,

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albeit that 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).

DMS is not normally produced under low O_2 concentrations. 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).

8.3 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).

9 Summary and outlook

In the following, the predominant processes and biogeochemical interplays are summarized for the ETNA and ETSP, respectively (Fig. 5). 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 throughout the OMZ as a core community. 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 classical 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 most 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 and ETSP OMZs is still missing. It remains unclear how much of the POM is solubilized or hydrolyzed within the OMZ and how much is exported to deeper waters and the benthos.

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; Codispoti et al., 1986; 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 this production 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, a quantification of microbial production and respiration, particularly at ultra-low O_2 levels, is still missing. Further unresolved is the role of particulate organic matter that could act as microniches for microbes and thus host certain processes such as the 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 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.

10 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, (2) the sensitivities of heterotrophic plankton abundance and activity to low oxygen conditions, and (3) biogeochemical feed-back processes in oxygen minimum zones and their impacts on the local to global scale.

In detail, we aim to answer the following key questions in the future:

1. 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?
2. How do the rates of nutrient cycling and loss in OMZs relate to particles and associated microniches?
3. How does nutrient stoichiometry influence phytoplankton production and succession and what is the ultimate fate of excess phosphate?
4. What are the rates of oxygen supply and consumption in the upper OMZ? And what is regulating respiration rates?
5. Do small-scale processes affect fluxes on larger scales? And how can models represent these important processes?

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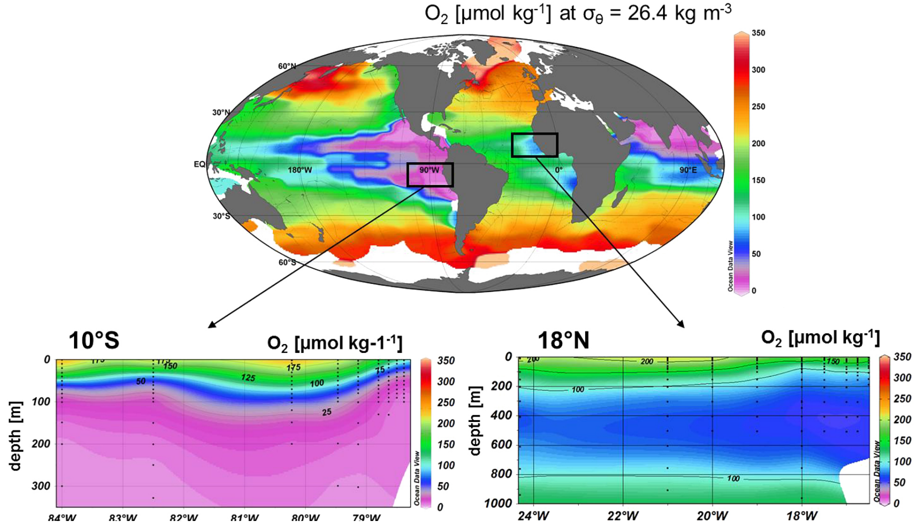

Figure 1. Global distribution of O_2 at $\sigma_\Theta = 26.4\,\mathrm{kg\,m^{-3}}$ (∼ 400 m depth): the major regions of low oxygen in the world ocean are all located in the tropical oceans, at shallow to intermediate depths. The area off Peru represents one of the most pronounced OMZs. The investigated 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.

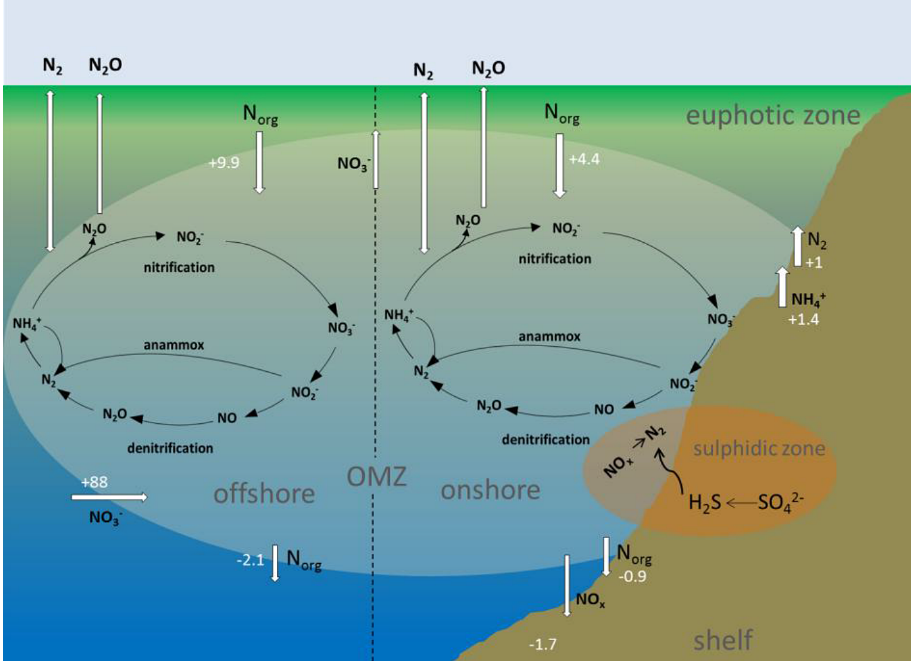

Figure 2. The marine nitrogen (N) cycle with the major onshore and offshore processes in the ETSP OMZ, modified from Kalvelage et al. (2013). Numbers indicate fluxes of N [Tg y^{-1}].

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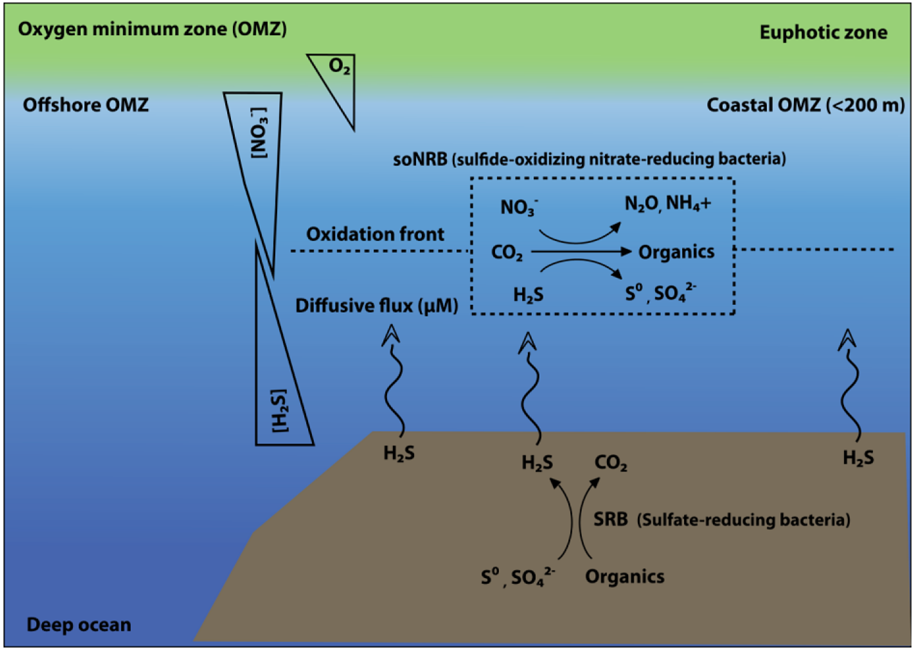

Figure 3. Schematic representation of the dynamics of a sulfidic event occurring in an oxygen minimum zone. The sulfide and nitrate fluxes are shown in steady state. Sulfate-reducing bacteria produce sulfide from the sediment while the complementary detoxification process occurs in the water column at overlapping profiles.

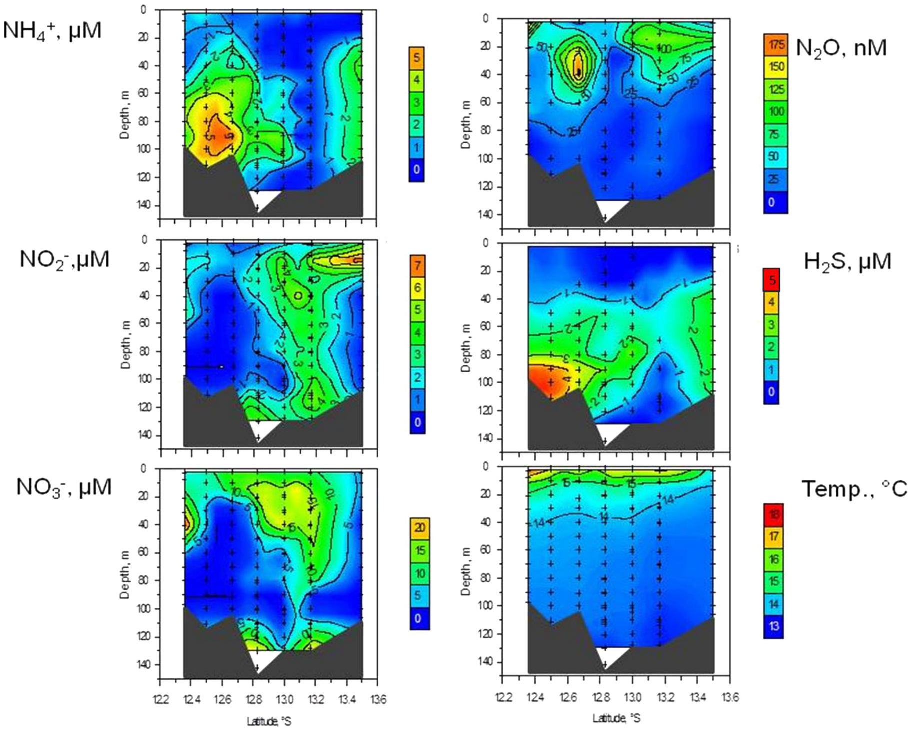

Figure 4. Distributions of N$_2$O, NH$_4^-$, NO$_2^-$, NO$_3^-$, H$_2$S, and water temperature during December 2008/January 2009 (R/V *Meteor* cruise M77/3) on the shelf along the coast of Peru. Max. N$_2$O concentrations have been detected right above the sulphidic zone, where a sharp oxycline is present and ammonia and nitrate are available.

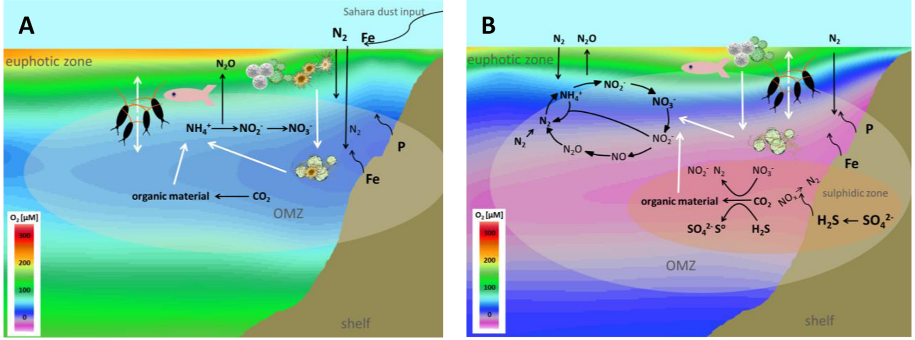

Figure 5. Scheme of the **(A)** ETNA and **(B)** ETSP OMZs with major processes identified. TheO$_2$ background is taken from the SOPRAN cruise P399, along 18° N in the ETNA and from the SFB754 cruise M77/3, along 10° S in the ETSP.

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