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Present past and future of the OMZ in the northern Indian Ocean

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Abstract. Decreasing concentrations of dissolved oxygen and the resulting expansion of anaerobic ecosystems is a major threat to marine ecosystem services because it favors the formation of greenhouse gases such as methane, endangers the growth of economically important species, and increases the loss nitrate. Nitrate is one of the potential primary nutrients, which availability controls the marine productivity. The Arabian Sea and the Bay of Bengal are home to ~59% of the Earth's marine sediments exposed to severe oxygen depletion and approximately 21% of the total volume of oxygen-depleted waters (oxygen minimum zones, OMZs). The balance between physical oxygen supply and the biological oxygen consumption controlled the oxygen concentrations. In the Arabian Sea and most likely also in the Bay of Bengal the supply of oxygen sustained by mixing and advection associated with mesoscale eddies compensated the biological oxygen consumption. These steady states maintain low (hypoxic) oxygen concentrations allowing the competition between anaerobic and aerobic processes. However, due to slightly higher oxygen concentrations, the aerobic nitrite oxidization inhibits the anaerobic nitrite reduction and thus denitrification (the reduction of nitrate to N_2) to become significant in the Bay of Bengal. A feedback mechanism caused by the negative influence of decreasing oxygen concentrations on the biological oxygen demand helped to maintain these steady states. Furthermore, it might have also counteracted a reduced physical oxygen supply into the Arabian Sea caused by climate-driven changes in the ocean's circulation during the last 6000 years. However, due to human-induced global changes, the OMZs in Arabian Sea and the Bay of Bengal intensified and expanded, which included also the occurrence of anoxic events on the Indian shelf. This affects benthic ecosystems, and in the Arabian Sea it seems to have initiated a regime shift within the pelagic ecosystem structure. Consequences for biogeochemical cycles are unknown, which, in addition to the poor representation of mesoscale features reduces the reliability of predictions of the future OMZ development in the northern Indian Ocean.

1. Introduction

The rise of oxygen at about 600 Million years ago initiated a revolution by facilitating aerobic live forms to displace anaerobic ecosystems from the Earth's surface (Canfield, 2014 ; Lenton et al., 2011; Lyons et al., 2014). Albeit it seems that today anaerobic microorganisms do not emerge from their shadow existence in guts of animals, wetlands and marine sediments, yet they strongly influence the productivity of aerobic ecosystems and the Earth's climate as they reduce nitrate to N_2 and produce methane. Nitrate limits the productivity in many of the aerobic ecosystems and methane is the most important greenhouse gas in the Earths' atmosphere after water vapor and CO_2 (Gruber et al., 2008; Kirschke et al., 2013; Myhre et al., 2013; Nisbet et al., 2016).

The transition from solely aerobic to anaerobic ecosystems occurs in steps at which microorganisms utilize oxygen bound to nitrogen (e.g. nitrate and nitrite) as well as to sulfur (e.g. sulfate) to decompose organic matter. Heterotrophic organisms use the resulting energy for running their metabolism whereas autotrophic life forms oxidize reduced metabolites to gain energy which additionally sustains the build-up of new biomass (e.g. Middelburg, 2011). The absence of elementary oxygen (anoxia) and oxygen bound to nitrogen and sulfur inhibits this chemosynthesis, and organic matter is decomposed to carbon dioxide, methane, ammonia, and hydrogen sulfide. At anoxic conditions and in the presence oxygen

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bound to sulfur methane is oxidized to carbon dioxide by the reduction of sulfate to hydrogen sulfide. The occurrence of hydrogen sulfide is considered as an indicator of anoxia while oxygen detection limits of classical seabird sensors (0.09 µM) and the newly developed STOX sensors (0.01 µM) is too high to prove anoxia (Thamdrup et al., 2012). At low levels of dissolved oxygen (hypoxia) and in the presence of sulfate and nitrate, organic matter is decomposed to carbon dioxide, sulfate, and N_2. The heterotrophic denitrification and the autotrophic anammox (anaerobic oxidation of ammonia) are the two main processes reducing nitrate and nitrite to N_2 at such conditions. The relative importance of denitrification and anammox reveals spatial and temporal variability and is difficult to constrain (Jensen et al., 2011; Ward et al., 2009). Hence, and since finally both processes produce N_2 at the expanse of nitrate we use the term denitrification as synonym for both processes in the following discussion if anommox is not specifically mentioned.

Oxygen threshold concentrations below which anaerobic processes start to dominate over aerobic processes are poorly constrained. According to experiments and *in situ* observations anammox sets in if oxygen concentrations drop below 20 µM while decreasing oxygen concentrations progressively reduce the inhibition of denitrification at oxygen concentrations of < 1 µM (Dalsgaard et al., 2014; Kalvelage et al., 2011). Hence, 20 µM is often considered as an upper threshold of hypoxia and to define hypoxic OMZ (e.g. Acharya et al., 2016). This differs, however, from other definition resting on the impact of low oxygen concentrations on the performance of higher organisms. Some fish species start e.g. to suffer from oxygen deficiency at oxygen concentrations of already < 133 µM and an oxygen concentration of 60 µM is suggested as threshold defining the upper limit of hypoxia in fisheries (Ekau et al., 2010). Since this paper focuses on biogeochemical processes we consider 20 µM as upper threshold of hypoxia and the occurrence of hydrogen sulfide as indicator of anoxia.

Since hyp- and anoxic conditions inhibits or prevents the growth of all life forms that depend on oxygen their occurrence is often associated with mass mortality of commercially important species (e.g. Weeks et al., 2002). Thus, the spatial expansion of hyp- and anoxia, which is an increasingly common feature in coastal waters, is called the "spreading of dead zones" (Altieri et al., 2017; Diaz et al., 2008). Although this term ignores the existence anaerobic microbes, it expresses the threat of oxygen-depletion to marine ecosystem services. Decreasing concentrations of dissolved oxygen as observed in the open ocean during the last 50 years give also rise to concerns and are considered as one of the main threats to pelagic ecosystems and fisheries (Breitburg et al., 2018; Stramma et al., 2010a; Stramma et al., 2008; Stramma et al., 2010b).

Based on data obtained from the World Ocean Atlas, the total volume of hyoxic waters in the global ocean is approximately 15 10^6 km^3 of which 21% (3.13 10^6 km^3) is located in the northern Indian Ocean (Fig.1, Acharya & Panigrahi, 2016; Garcia et al., 2010). The majority of this oxygen-poor water is in the Arabian Sea (2.5 10^6 km^3), with a much smaller proportion is located in the Bay of Bengal (0.6 10^6 km^3). In regions where these OMZs impinge on continental margin, sediments and benthic communities are also exposed to semi-permanent bottom-water hypoxia. The Arabian Sea and the Bay of Bengal together are currently home to ~59% of the Earth's marine sediments exposed to hypoxia (Helly et al., 2004).

Denitrification, within the OMZs and sediments, is by far the largest sink of nitrate in the ocean (Gruber, 2004). Estimates of denitrification rates in sediments and OMZs are fraught with large uncertainties and range between 65 and 300 Tg N year^{-1} and 80 and 270 Tg N year^{-1}, respectively (Gruber, 2004; Somes et al., 2013). So far there are only very few measurements in Arabian Sea sediments but according to this data the sedimentary denitrification at the Pakistan continental margin amounts to up to 10.5 Tg N year^{-1}(Schwartz et al., 2009; Somes et al., 2013). This represents 6.5 % of the global mean sedimentary denitrification rate of 160 Tg N year^{-1}. Mid-water denitrification in the OMZ of the Arabian Sea contributes approximately 20% to the global mid-water denitrification rate of 147 Tg N year^{-1} (Bange et al., 2000; Bristow et al., 2017; Codispoti, 2007; Codispoti et al., 2001; Deuser et al., 1978; Gaye et al., 2013; Howell et al., 1997; Naqvi et al., 1982; Somasundar et al., 1990). This further emphasizes the role of the OMZ in the northern Indian Ocean for the marine nitrogen cycle, which on the other hand is one of least understood OMZs in the world's ocean (Schmidt et al., 2020). The aim of this paper is to provide a short background on the development of OMZs and recent trends in the Indian Ocean as well as to discuss drivers, ecosystem responses and the future development of the OMZ in the Indian Ocean.

2. Background

2.1 Oxygen Minimum Zones (OMZ)

The first large ocean going oceanographic expeditions discovered OMZs in Pacific, Atlantic, and Indian Ocean already between the end of the 19th and the first third of the 20th century (Sewell et al., 1948 and references therein). Their occurrence was explained by a sluggish horizontal renewal of water within the OMZ and the consumption of oxygen during the respiration of organic matter exported from the sunlit surface ocean (Dietrich, 1936; Seiwell, 1937). Sverdrup (1938) presented a first model showing that oxygen concentrations within the OMZ represent the balance between biological oxygen consumption and oxygen supply. Primary production and fluxes of oxygen across the air sea interface are the sources of dissolved oxygen. Vertical mixing and subduction of oxygen-enriched surface waters during the deep and mode water formation at high latitudes are in turn the main processes ventilating the interior of the ocean (McCartney, 1977; Sverdrup, 1938). OMZ emerged at intermediate depths because the majority of the exported organic matter is respired at water-depths between ca. 100 and 1000 m (Suess, 1980; Sverdrup, 1938).

Dissolved oxygen concentrations within OMZs strongly depend on the age of the water mass (Karstensen et al., 2008). The older it is, the more organic matter has been respired and the lower are the dissolved oxygen concentrations. Due to the accumulation of aged water masses in so-called 'shadow zones', pronounced OMZs occur in the eastern tropical and subtropical Atlantic and Pacific Ocean (Karstensen et al., 2008). The Indian Ocean differs from these ocean basins as the OMZ occurs in the north, where the Indian subcontinent splits the northern part of the Indian Ocean into two semi enclosed basins: the Arabian Sea and the Bay of Bengal.

2.2 OMZ and upwelling

In the Atlantic and Pacific Oceans, hypoxic OMZs are associated with major eastern boundary current upwelling systems. In the Indian Ocean, the geographic setting prevents the development of a strong

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eastern boundary current upwelling system but a major monsoon-driven seasonal upwelling system emerges in the western Arabian Sea off the Arabian Peninsula. Schott (1935) already described this upwelling system (Böhnecke, 1935), which thereafter was subject to intense studies. This includes the International Indian Ocean Expedition (IIOE) between 1959 and 1965 and the Joint Global Ocean Flux Study (JGOFS) in the Arabian Sea with its field phase between 1994 and 1997 (e.g. Bauer et al., 1991; Brock et al., 1991; Bruce, 1974; Currie et al., 1973; Sastry et al., 1972; Wyrtki, 1973).

The high upwelling-driven productivity sustains a high export of organic matter into the deep sea (Haake et al., 1993; Rixen et al., 1996) but in contrast to the obvious expectation, the OMZ is most intense in the eastern Arabian Sea and not in western Arabian Sea where the upwelling-driven productivity is highest (Fig. 1, Antoine et al., 1996; Naqvi, 1991). The seasonal monsoon-driven reversal of the surface circulation in combination with the strong inflow of oxygen-enriched Indian Ocean Central Water (ICW) into the western Arabian Sea is assumed to cause this eastwards displacement of the OMZ in the Arabian Sea (Rixen et al., 2005; Sen Gupta et al., 1984; Swallow, 1984). The ICW originates by convective mixing as Subantarctic Mode Water (SAMW) in the southern Indian Ocean (McCartney, 1977; Sverdrup et al., 1942) and enters the western Arabian Sea along with Timor Sea Water and the Subtropical Subsurface Water via the Somali Current (Schott et al., 2001; Stramma et al., 1996; You, 1997).

In addition to the strong upwelling off the Arabian Peninsula a weaker summer monsoon-driven upwelling develops along the Indian southwest coast (Schott, 1935; Sharma, 1978; Shetye et al., 1990). Here an undercurrent emerged, which compensates the poleward flowing West Indian Coastal Current and carried also ICW northwards into the eastern Arabian Sea (Schmidt et al., 2020; Shenoy et al., 2020; Shetye et al., 1990). Despite the inflow of ICW, in this region the OMZ expands southwards during the summer monsoon and retreats northwards during the winter monsoons (Shenoy et al., 2020). In contrast to the eastern Arabian Sea, the OMZ retreats eastwards in summer and expands westwards in winter in the western Arabian Sea (Rixen et al., 2014). This opposing behavior discloses a seesaw billowing of the OMZ due to the seasonal reversal of the surface ocean circulation - anticlockwise during the winter monsoon and clockwise during summer monsoon. However, on average the OMZ reveals its lowest areal extension in summer which is also associated with low oxygen concentrations (Fig. 2, Acharya & Panigrahi, 2016). The low areal extension appears to be a consequence of the inflow of ICW because it favors the eastward retreat of the OMZ in the western Arabian Sea while it attenuates the influence of the clockwise circulation and the associated southwards expansion of the OMZ in the eastern Arabian Sea. The summer-monsoon-driven upwelling and the resulting offshore advection of blooms along filaments increase the carbon export in the central Arabian Sea (Rixen et al., 2006a) which in turn explains the low oxygen concentrations during the summer monsoon.

Similar to the Arabian Sea, upwelling favorable winds occur also in the Bay of Bengal during the summer monsoon season (Hood et al., 2017; Shetye et al., 1988). However, high freshwater fluxes from both river runoff and precipitation form a buoyant low salinity surface layer that isolates nutrient-enriched subsurface water and increases stratification (Kumar et al., 1996). This weakens upwelling and vertical mixing and lowers nutrient concentrations in subsurface water entrained into the euphotic zone by these processes (Rixen et al., 2006b). Hence, productivity in the Bay of Bengal is lower than in

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the Arabian Sea (Fig. 1). Nevertheless, sediment trap studies have shown that, despite a lower productivity, organic carbon fluxes into the deep Bay of Bengal are almost as high as those in the central and eastern Arabian Sea, due to a ballast-effect associated with high loadings of lithogenic mineral material (Rao et al., 1994; Rixen et al., 2019b). Ballast minerals supplied from land via rivers or as dust protect organic matter against bacterial attacks by adsorbing organic molecules to atomic lattices (Armstrong et al., 2002) and accelerate the sinking speed of particles (Haake et al., 1990; Hamm, 2002; Ramaswamy et al., 1991). Enhanced sinking speeds reduce respiration in shallower waters and thereby increase the flux of organic matter to deeper waters (Banse, 1990; Ittekkot, 1993). The ballast-effect and the resulting deeper remineralization depth in the Bay of Bengal in comparison to the Arabian Sea is assumed to cause differences between the intensity of the OMZ in the Arabian Sea and the Bay of Bengal (Al Azhar et al., 2017; Rao et al., 1994).

2.3 Recent trends in the Bay of Bengal and the Arabian Sea

Carruthers et al (1959) described mass mortality of fish along the Arabian and Indian coast as well as in the central Arabian Sea at around 62.5°E and 9 °N. Such events indicate a severe perturbation of the pelagic ecosystem but the underlying processes were unclear. The development of harmful algae blooms were discussed but oxygen depletion was preferred as the more likely mechanism explaining these mass mortalities. This view was supported by a report on the occurrence of anoxia from the north-eastern Arabian Sea (Ivanenkov et al., 1961). However, this was so far the only report on the occurrence of hydrogen sulfide in Arabian Sea (Naqvi et al., 2000; Swallow, 1984) until Naqvi et al. (2000) discovered an anoxic event that developed along the western Indian coast off Mumbay during the late summer and autumn in 1999. Such strong events seem to emerge not every year (Gupta et al., 2016; Sudheesh et al., 2016) but mass mortalities occur, in between, also along the eastern Indian coast in the Bay of Bengal (Altieri et al., 2017). The spreading of 'dead zones' in coastal regions is apparently a global phenomenon that does not spare the Indian coast in the Arabian Sea and the Bay of Bengal (Altieri et al., 2017; Diaz & Rosenberg, 2008).

During the last 50 years also an intensification of OMZs in open waters beyond conational shelves and slopes were observed (Stramma et al., 2008). In comparison to the South Atlantic Ocean and the Pacific Ocean, global syntheses reveal only a weak decrease of dissolved oxygen concentrations in the OMZ of the northern Indian Ocean (Ito et al., 2017; Schmidtko et al., 2017). However, even a small decline in oxygen concentrations has significant biogeochemical implications. For example, Bristow et al (2017) showed that the low oxygen concentration enables anaerobic microbial processes within the OMZ of the Bay of Bengal even though a constant physical oxygen supply (Johnson et al., 2019) maintained a oxygen levels of 0.01 – 0.2 µM. This suffices to support nitrite oxidization and the resulting lack of nitrite strongly reduced, but probably did not prevent, denitrification. Based on a measured excess N_2 and a residence time of water within the OMZ of 12 years, Bristow et al (2017) calculated a potential denitrification rate of 1.7 Tg N year^{-1}. In the hypoxic Arabian Sea OMZ the re-oxidation of nitrite to nitrate plays also an important role and reduced the formation of N_2 by 50 to 60% (Gaye et al., 2013). In the core of the Arabian Sea OMZ oxygen concentrations drop below 0.09 µM (Jensen et al., 2011) which matches results from the eastern Pacific Ocean where oxygen concentrations of < ~0.05 µM characterize sites where denitrification is pronounced (Thamdrup et al.,

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2012). Accordingly, ~0.05 µM seems to be a threshold oxygen concentration below which nitrate reduction outcompete nitrite oxidation and supplies nitrite for the further reduction to N_2. Incubation experiments also suggest a threshold oxygen concentration below which nitrate reduction outcompete nitrite oxidation even though this is with about 0.7 µM much higher (Bristow et al., 2016). However, the in comparison to the Arabian Sea low denitrification rate implies a less intense hypoxic OMZ in the Bay of Bengal as in the Arabian Sea.

A detailed analysis of all data available from the central Arabian Sea in the depth range between 100 and 500 m displayed that changes of the intensity of OMZ revealed a pronounced spatial variability between 1959 and 2004 (Banse et al., 2014). Whereas within this depth range oxygen concentrations increased in the southern part of the Arabian Sea, they decline in the central part of the Arabian Sea. Following studies reported also from decreasing oxygen concentrations in the western and northern Arabian Sea (Piontkovski et al., 2015; Queste et al., 2018). In the northern Arabian Sea dissolved oxygen concentrations in the surface mixed layer largely reflect the trend seen in the OMZ as indicated by a compilation of dissolved oxygen data covering the period from the 1960s to 2010 (do Rosário Gomes et al., 2014). However, periodic outbreaks of hydrogen sulfide as seen in the upwelling systems off Peru (Schunck et al., 2013) and Namibia (Weeks et al., 2002) have so far not been reported in the northern Indian Ocean during the last 50 years other than in bottom waters on the Indian shelf as mentioned before. This implies that the physical oxygen supply and the biological oxygen consumption reached a steady state that largely maintained hypoxic conditions and prevented anoxia in the Arabian Sea and Bay of Bengal OMZ.

3. Export production and its controlling effect on the intensity of the OMZ

3.1 Biological oxygen consumption

The apparent oxygen utilization (AOU) represents the oxygen deficit caused by the biological oxygen consumption. It is calculated by subtracting the measured oxygen concentration from the temperature and salinity dependent oxygen saturation concentration. This approach rests on the assumption that the regarded water mass was saturated with respect to oxygen during its formation and since than, the respiration of exported organic matter consumed oxygen within this water mass. The OMZs in the northern Indian Ocean are melting pots collecting the influence of a variety of water masses revealing different origins and histories (e.g. Hupe et al., 2000; You, 1997). Mixing analyses indicate that in the Arabian Sea the inflow of oxygen-rich Indian Ocean Deep Water affects the lower OMZ (water-depth > 500 m). In addition to the formation of the Arabian Sea Surface Water (ASW), the intrusion of water masses from the central Indian Ocean (ICW), the Persian Gulf and Red Sea strongly influenced the upper OMZ (Acharya & Panigrahi, 2016; Rixen & Ittekkot, 2005 and references therein). Based on data measured during JGOFS in 1994/95 oxygen-deficits inherited from these water masses contribute approximate 25% to the AOU which implies that the respiration of organic matter produced in the Arabian Sea largely (to 75%) causes the low oxygen concentrations in the Arabian Sea OMZ (Rixen & Ittekkot, 2005). However, satellite-derived export production rates were much too low to sustain such a high biological oxygen consumption during the residence time of water within the OMZ (10 years, Olson et al., 1993; Rixen & Ittekkot, 2005). The mismatch between oxygen deficits and the biological

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oxygen consumption reflects uncertainties caused by the poorly constrained physical oxygen supply and export production rates (Rixen et al., 2019b; Rixen & Ittekkot, 2005). Nevertheless, these two processes are linked to each other if the seasonal thermocline is hypoxic.

3.2 Interplay between the intensity of the OMZ and export production

The seasonal thermocline is the subsurface layer from which water is introduced into the euphotic zone via physical processes such as upwelling and vertical mixing on a seasonal timescale. Nutrient supplied by these mechanisms largely sustain the productivity of pelagic ecosystems and the associated export production (Eppley et al., 1979). Hence, the seasonal thermocline is the main nutrient reservoir of pelagic ecosystems and to fulfill this role the vast majority of the exported organic matter must be respired within the seasonal thermocline. Accordingly, the season thermoclines represents the main zone of respiration and similar to soils on land, accommodates the nutrient recycling machinery of the pelagic ecosystem. Nutrient losses from the seasonal thermocline via particle fluxes into the deep sea, denitrification, and lateral advection must be compensated by nutrient inputs in order to maintain the productivity (Rixen et al., 2019a). Nitrogen fixation, river discharges, and atmospheric deposition can be important nutrient sources but in the Arabian Sea lateral inflow of water masses from the south are the main source balancing nutrient losses from the season thermocline (Bange et al., 2000; Gaye et al., 2013). In contrast to the Bay of Bengal nitrite accumulates in the seasonal thermocline of the Arabian Sea (Fig. 3).

The accumulation of nitrite in the upper part seasonal thermocline, which was first described during John Murray expedition of 1933 - 34 (Gilson, 1937), is assumed to indicate active denitrification and is called the secondary nitrite maximum (SNM, Naqvi, 1991). The role of the SNM as indicator of active denitrification is further supported by stabile isotopic ratio of nitrogen in nitrate ($\delta^{15}N_{NO3}$) and nitrate (NO_3^-) concentration profiles (Gaye et al., 2013; Rixen et al., 2014). Since denitrification increases $\delta^{15}N_{NO3}$ in the water column due to the preferential uptake of the lighter $^{14}NO_3^-$ (Cline et al., 1975; Mariotti et al., 1981) low nitrate concentrations correspond to high $\delta^{15}N_{NO3}$ within the SNM.

In the Arabian Sea the SNM indicates the core of the OMZ (Fig. 1 c) and during the last decades it expanded towards the south and west due to the decreasing oxygen concentrations in these regions (Banse et al., 2014; Rixen et al., 2014). The SNM occurs at water depths between 200 and 400 m in the central Arabian Sea (Fig. 3a) and as deep as 500 m in the eastern Arabian Sea. It divides the main respiration zone in an aerobic upper part at water depths between ~40 and 200 m and an anaerobic lower part down to the base of SNM (Fig. 3a). The base of the SNM is still located in the hypoxic OMZ but, in contrast to the SNM, associated with increasing nitrate concentrations. Therefore anaerobic processes including also the sulfate/nitrate based respiration (Canfield et al., 2010) are assumed to be negligible so that the base of the SNN seems to represent also the base of the main respiration zone.

Even though nitrate concentrations decrease within the SNM they remain above 10 µM, which suggest that not nitrate but the supply of decomposable organic matter limits denitrification. A substrate limitation at a water depth of 400 to 500 m and the arrival of organic matter at sediment traps deployed in the deep sea at a water depth of 3000 m support the concept of export production that is divided between free (reactive) and protected (low contribution of reactive) organic matter (Armstrong et al., 2002). This partition is based on the assumption that ballast-associated, protected organic matter is preferentially exported to deeper waters as fast sinking particles, whereas the slow sinking free organic matter is preferentially respired with the main respiration zone (Fig. 3). Therewith the ballast-effect is a prime factor controlling the nutrient supply to the seasonal thermocline and therewith the export production and the intensity of the OMZ.

Although the ballast effect is not specifically addressed in numerical models used to study the OMZ in the northern Indian Ocean, there are models that account to some extent for the concept of protected and free organic matter by considering the formation of fast and slow sinking particles (Aumont et al., 2015; Lachkar et al., 2019; Lachkar et al., 2016; McCreary et al., 2013; Resplandy et al., 2012). These models indicate that organic matter is mostly remineralized within in the upper 300 m of the water column (Resplandy et al., 2012) which nearly encompasses the depth range of the SNM. It also covers approximately the depth range of vertical migrating zooplankton during the large summer bloom in the Arabian Sea (Smith, 2001), and roughly matches the water depth range from where subsurface water is introduced via upwelling into the euphotic zone in the western Arabian Sea (Brock et al., 1992; Rixen et al., 2000).

In addition to the ballast-effect also concentrations of dissolved oxygen influence the organic matter export into the deep sea as decreasing oxygen concentrations are assumed to slow down the respiration (Aumont et al., 2015; Laufkötter et al., 2017; Thamdrup et al., 2012; Van Mooy et al., 2002). Consequences of a reduced respiration within the seasonal thermocline are enhanced fluxes of organic matter into the deep sea and a deepening of the respiration zone. Data presented by Acharya and Panigrahi (2016) support the hypothesis by showing that decreasing oxygen concentrations within the OMZ correlate with a deepening of the OMZ on a seasonal time scale (Fig. 4). On the other hand an increased export of organic matter and nutrients out of the seasonal thermocline lowers the productivity and the associated export production, which in turn reduces the oxygen consumption within the OMZ.

3.3 Implications

If decreasing oxygen concentrations within the seasonal thermocline lower the export production, the resulting lower biological oxygen demand could mitigate or even prevent an intensification of the OMZ caused by weaker ballast-effect and or a reduced physical oxygen supply. This feedback mechanism might have played an important role in maintaining the hypoxic conditions within the Arabian Sea and Bay of Bengal OMZ by preventing the development of anoxic conditions. As discussed in the following chapters this also agrees with model and paleoceanographic results suggesting that variations of the physical oxygen supply rather than changes in the biological oxygen demand are drivers controlling the intensity of the OMZ in both the Arabian Sea and the Bay of Bengal (Gaye et al., 2018; McCreary Jr et al., 2013; Resplandy et al., 2012).

4. The role of mesoscale eddy activity as a driver of OMZ ventilation

Mesoscale eddies, in the form of coherent vortices and filaments, are ubiquitous in the ocean. They develop from baroclinic and barotrophic instabilities related to the shear of horizontal currents. As they transport heat, salt, nutrients and oxygen across large distances in the ocean, eddies affect both climate and large-scale marine biogeochemistry. Previous studies have also shown that eddies generally

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enhance biological production in oligotrophic environments through nutrient pumping (e.g., Oschlies et al., 1998) and suppress productivity in biologically active eastern boundary upwelling systems as they cause subduction of incompletely consumed nutrients offshore below the euphotic zone (e.g., Gruber et al., 2011). More recent work has highlighted the role of eddies in enhancing ocean mixing in regions of sluggish circulation in the eastern tropical Atlantic and Pacific, thus contributing to the ventilation of the OMZ located there (Bettencourt et al., 2015; Brandt et al., 2015; Gnanadesikan et al., 2013). In particular, stirring of oxygen by eddies along isopycnal surfaces has been suggested to modulate the intensity and distribution of low-oxygen waters in the ocean (Fig. 5, Gnanadesikan et al., 2012).

4.1. Effects of eddies on the Arabian Sea OMZ

In the Arabian Sea, numerical model studies have shown that eddies play an important role in the transport of nutrients and oxygen (Lachkar et al., 2016; McCreary Jr et al., 2013; Resplandy et al., 2012; Resplandy et al., 2011). For instance, Resplandy et al., (2011) emphasized the role of mesoscale eddies in spreading nutrients vertically and horizontally in the Arabian Sea (Fig. 5). Furthermore, mesoscale eddies and filaments were shown to dominate the supply of oxygen to the OMZ in the Arabian Sea on an annual timescale due to the semiannual reversal of the mean circulation and a resulting reduced oxygen supply (Resplandy et al., 2012). This study also showed that eddy-driven advection enhances the vertical supply of oxygen along the western coast of the Arabian Sea and contributes to the lateral transport of ventilated waters offshore into the central Arabian Sea. In a process study aiming to explore the dynamics of the Indian Ocean OMZs, McCreary et al (2013) highlighted the important role of vertical eddy mixing in the ventilation of the western Arabian Sea in addition to the inflow of ICW. Their work suggests that this mechanism strongly contributes to the eastward shift of the upper OMZ relative to the region of highest productivity located along the western part of the Arabian Sea.

Using a suite of regional model simulations with increasing horizontal resolution, Lachkar et al (2016) found that isopycnal eddy transport of oxygen to the Arabian Sea OMZ strongly limits the extent of its suboxic core. Within the model this leads to a suppression of denitrification and in turn to an increase in biological productivity driven by an increase of nitrate availability in the subsurface. As more organic matter is produced near the surface, more remineralization and oxygen consumption occur at depth. This in turn results in an expansion of the volume of hypoxia and a compression of habitats of O_2-sensitive species. Thus, eddies affect the Arabian Sea marine biogeochemistry and living organisms both at lower (e.g., plankton) and higher trophic levels (e.g., fish).

Finally, eddies have also been shown to control the transport and the spreading of the Persian Gulf Water (PGW) into the Gulf of Oman (Queste et al., 2018; Vic et al., 2015). These dense waters, relatively rich in O_2, subduct in the northern Arabian Sea and strongly contribute to the ventilation of the upper OMZ there (Lachkar et al., 2019; Rixen & Ittekkot, 2005; Schmidt et al., 2020). Using a series of computer simulations, it could be shown that a warming driven decrease in the sinking of oxygen-saturated dense waters formed in the Persian Gulf contributes to a drop in oxygen at depths between 200 and 300 m in the northern Arabian Sea (Lachkar et al., 2019).

4.2. Eddies and the ventilation of the Bay of Bengal

In the Bay of Bengal, previous studies have highlighted the role of eddy pumping of nutrients in enhancing biological productivity during all seasons (Kumar et al., 2007; Prasanna Kumar et al., 2004; Singh et al., 2015). Eddies have also been shown to affect the ventilation of the Bay of Bengal and subsequently the intensity of its OMZ. For instance, Sarma et al (2018a) showed that while cyclonic eddies inject nutrients into the euphotic zone, thus enhancing productivity and oxygen consumption at depth, anticyclonic eddies supply oxygen to the subsurface layer and hence weaken the OMZ. Sarma and Baskhar (2018b) focused on anticyclonic eddies sampled by bio-Argo floats between 2012 and 2016 in the Bay of Bengal and found these to form in the eastern side of the basin and propagate westward, ventilating the layer between 150 and 300 m and weakening the OMZ. The frequent episodic injection of oxygen, likely by mesoscale eddies, could be the physical oxygen supply mechanism that inhibited denitrification and/or prevent it from becoming significant.

4.3 Implications

The variability of eddy activity in space and time can modulate the intensity of OMZs between different regions and across time, thus contributing to the observed variability of dissolved O_2. In this context, previous work has linked long-term changes in oxygen to changes in the intensity of eddy activity. For instance, Brandt et al (2010) have shown that a reduction in filamentation and the strength of alternating zonal jets associated with mesoscale eddies between the periods 1972-1985 and 1999-2008 in the tropical north Atlantic has contributed to a reduction in the ventilation of the OMZ located there and hence contributed to its deoxygenation. In the Bay of Bengal, strong interannual variations in the intensity of the eddy activity have been reported (Chen et al., 2012). These are expected to cause strong variations in the subsurface ventilation that may eventually lead to deoxygenation and onset of denitrification at the core of the OMZ (Johnson et al., 2019).

The fact that eddies affect both the supply of O_2 (through ventilation) and its consumption (through biological productivity) in a non-trivial manner can explain the fundamental difficulty to adequately parameterize the effects of eddies on dissolved oxygen in coarse resolution models. An additional potential source of error in the currently used parameterizations is their underlying assumption that the eddy-driven isopycnal tracer mixing and isopycnal flattening occur at similar rates (Griffies, 1998). Yet, recent studies (e.g., Gnanadesikan et al., 2013) suggest that the two can be substantially different. In the Arabian Sea, Lachkar et al (2016) show that the eddy driven transport of O_2 is mostly driven by enhanced mixing along the isopycnal surfaces with very little change in the slope of the isopycnals. However in the Arabian Sea, both Resplandy et al. (2012) and McCreary et al. (2013) found that the biological oxygen consumption is counterbalanced by the supply of oxygen sustained by mixing and advection associated with mesoscale eddies and filaments. This in turn agrees with paleoceanographic studies, implying that remotely-forced changes in physical oxygen supply cause long-term changes to the intensity of the OMZ.

5. Holocene records

5.1. The $\delta^{15}N$ as an indicator of OMZ strength in sediments

Changes in OMZ oxygenation were shown to be reflected by the $\delta^{15}N$ of nitrogen in sediments (Altabet et al., 1995; Ganeshram et al., 1995). The average $\delta^{15}N_{NO3}$ value of oceanic deep water is ~5‰ (Sigman et al., 2005) but $\delta^{15}N_{NO3}$ in OMZs can be much higher during periods of denitrification as this process has an isotopic effect of 20-30 ‰ and resulting $\delta^{15}N_{NO3}$ can exceed 20‰ (Altabet et al., 1999; Brandes et al., 1998). Convective mixing and especially upwelling force nitrate-deficient water masses to the surface, so that the nitrate with high $\delta^{15}N$ values is transported into the euphotic zone. After assimilation into biomass by phytoplankton, ^{15}N-enriched particulate matter sinks through the water column to the seafloor where the signal of denitrification and OMZ intensity is preserved in sediments (Altabet et al., 1995; Gaye-Haake et al., 2005; Naqvi et al., 1998; Suthhof et al., 2001). Early diagenesis may raise sedimentary $\delta^{15}N$ values by 2-5 ‰ and the diagenetic effect increases with water depth (Altabet, 2006; Tesdal et al., 2013). Nevertheless, the relative changes of $\delta^{15}N$ in deep-sea sediments record variations in the OMZ intensity while records from the continental slopes are subjected to negligible diagenetic enrichments so that they retain the signal of the nitrogen source (Altabet et al., 1999; Gaye et al., 2018).

5.2. OMZ Fluctuations in the Holocene

A core from the northern Bay of Bengal, which at present has the lowest oxygen concentrations of the basin shows a range of $\delta^{15}N$ between 4.4 and 5.0 ‰ during the Holocene and even slightly lower $\delta^{15}N$ during the last glacial maximum so that denitrification can be ruled out from a paleoceanographic perspective (Contreras-Rosales et al., 2016). The $\delta^{15}N$ values at the core top of 4.6 ‰ were similar to values in sediment trap materials of 3.7-4.5 ‰, and were explained by a mixture of nutrients or suspended matter from the Ganges-Brahmaputra-Meghna river system with nitrate from subsurface water (Contreras-Rosales et al., 2016; Gaye-Haake et al., 2005; Unger et al., 2006). Enhanced $\delta^{15}N$ values in the early Holocene to 6000 years BP (BP = before present, whereas present means 1950) coincide with a stronger monsoon and were attributed to enhanced supply of nitrate from the subsurface which has elevated $\delta^{15}N$ compared to the depleted values of the riverine endmember (Sarkar et al., 2009). Nevertheless, to our knowledge there is only one published record from the Bay of Bengal spanning the entire Holocene (Contreras-Rosales et al., 2016) so that we know nothing about the spatial variability within the basin. However, the available data imply so far that results presented by Bristow et al. (2017) and discussed before indicate a recent onset of denitrification within the Bay of Bengal.

In contrast to the Bay of Bengal denitrification has prevailed in the Arabian Sea during the warm interstadials of the Pleistocene and during the entire Holocene as can be discerned from $\delta^{15}N$ >6 ‰ with maxima of >11 ‰ (Agnihotri et al., 2003; Higginson et al., 2004; Kessarkar et al., 2018; Möbius et al., 2011; Pichevin et al., 2007). Productivity increased with the onset of the Holocene as the summer monsoon strengthened and monsoonal upwelling off Somalia and Oman commenced and became a permanent feature of the Holocene Arabian Sea (Böning et al., 2009; Gaye et al., 2018). A rise of $\delta^{15}N$ by at least 2 ‰ shows that onset of upwelling immediately strengthened the OMZ and led to

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denitrification in the entire basin (Böll et al., 2015; Gaye et al., 2018). Furthermore, production of the oxygen- enriched ICW was reduced by the southward retreat of the Antarctic Sea Ice, so that ventilation of the Arabian Sea OMZ from the south was in turn reduced (Böning & Bard, 2009; Naidu et al., 2010).

A decline in $\delta^{15}N$ by about 1 ‰ is found in the early Holocene until 6000 years BP in high- resolution sediment cores from the western, northern and eastern Arabian Sea and indicates that the OMZ weakened and became less persistent during this period (Fig. 6a). A possible explanation may be the enhanced input of surface derived and therefore oxygen enriched water from the Red Sea and Persian Gulf due to prolonged sea level rise until about 6000 years BP (Siddall et al., 2003). More vigorous upwelling during this period, discernible from benthic foraminifera, also led to a better ventilation of the basin by Indian Central Water (ICW) from south during this period (Das et al., 2017). After 6000 years BP increasing $\delta^{15}N$ values indicate a strengthening of the OMZ across the entire basin, which is still ongoing (Fig 6a). It is assumed that a weaker ventilation is responsible for decreasing oxygen concentrations and it could be due to reduced inflow of ICW as it is blocked by the enhanced inflow of PGW and Red Sea Water (RSW) since the sea level high stand at 6000 years BP (Pichevin et al., 2007). Ventilation of the eastern Arabian Sea by the West Indian Coastal Current also declined and was shifted southward (Mahesh et al., 2014). An associated weakening of the northward propagation of the ICW within the poleward countercurrent might have reduced ventilation and prolonged the residence time of water within the OMZ. These are further explanations for the observed strengthening of the OMZ and its shift to the NE part of the basin and matches results from the Kiel Climate Model. It indicates a decline of oxygen concentrations since about 6000 years BP and an increase in the age of the OMZ water mass.

5.3 Holocene model simulations

In order to give an additional model-based estimate of the OMZ evolution in the Indian Ocean, transient model simulations over the Holocene were performed with the global atmosphere-ocean Kiel Climate Model (KCM, Park et al., 2009) and the marine biogeochemistry model PISCES (Aumont et al., 2003). In a first step, KCM was forced with transient orbital parameters and greenhouse gas concentrations from 9500 years BP to present. In a second step, the PISCES model was forced with the ocean physical fields from the above KCM experiment in so-called off-line mode (see Segschneider et al. (2018) for a more detailed description of the model components and experiment setup). While the oceanic 2°x2° grid in this setup is refined to a meridional resolution of 0.5° near the equator to allow a better representation of equatorial waves, the long integrations (9500 model years) require a coarse model resolution that is far from eddy resolving and also neglects the lithogenic ballast effect.

From these model experiments, temperature and oxygen fields in the Arabian Sea and the Bay of Bengal are analyzed here and compared to the sedimentary records where possible. For the Arabian Sea the model results were subdivided into areas corresponding to the binned sediment core regions specified in Gaye et al (2018) (North: 62°E-68°E, 20°N-25°N; East: 68°E-78°E, 9°N-20°N; West: 50°E-60°E, 13°N-18°N; South: 40°E-51°E, 0°N-5°N).

The simulated oxygen concentrations are generally somewhat too high at the surface due to a cold bias of KCM, but the observed near-surface gradient is very well matched, while in the deeper layers the model overestimates oxygen concentrations (not shown, see supplementary figures in (Segschneider et al., 2018). As a result, oxygen concentrations in the model Arabian Sea are nowhere low enough for denitrification to occur (below 5 µM would be required). Moreover, no nitrogen isotopes are simulated in the current model version. Comparison to the $\delta^{15}N$ data from the sediment cores is, therefore, restricted to a qualitative assessment.

The simulated oxygen concentrations (averaged between 200 m and 800 m depth) show the lowest concentrations in the northern Arabian Sea (initially around 80 µM in the early Holocene, yellow curve in Fig. 6.1b). The concentrations are 10 µM higher in the western Arabian Sea (blue line), and a further 5 µM higher in the eastern Arabian Sea (red line), while they are much higher in the southern Arabian Sea (starting at 155 µM, grey line). O_2 concentrations are fairly constant over the first 2.5 thousand years, and then gradually decrease until the late Holocene. This decrease is strongest in the northern Arabian Sea (-20 µM) and quite similar in the western and eastern Arabian Sea (-10 µM). This is in qualitative agreement with the Holocene trends of $\delta^{15}N$ data (Fig. 6.1) that show highest $\delta^{15}N$ values (indicating strong denitrification and thus low oxygen) for the shallow northern core, and lower $\delta^{15}N$ for the western and the eastern core.

5.4 Implications

The $\delta^{15}N$ records from the Arabian Sea and Bay of Bengal reveal the difference in late Pleistocene and Holocene history of denitrification. Oxygen concentrations in the Bay of Bengal never declined below the threshold of denitrification whereas denitrification prevailed in the Arabian Sea during the warm interstadials and the entire Holocene. A data-model comparison shows that the age of the OMZ water mass increased after 6000 years BP in both basins coinciding with a strengthening of the OMZ and denitrification in the Arabian Sea which is still ongoing. It is assumed that a reduced ventilation is responsible for decreasing oxygen concentrations and it could be due to less inflow of ICW as it is blocked by the enhanced inflow of PGW and RSW since the sea level high stand at 6000 years BP (Pichevin et al., 2007). Ventilation of the eastern Arabian Sea by the West Indian Coastal Current and the associated counter current also declined and was shifted southward (Mahesh & Banakar, 2014). The similar temporal evolution of observed OMZ intensity and modelled O_2 concentration in the Arabian Sea thus indicates that the mid- to late Holocene OMZ intensification may be related to oceanic circulation rather than to local processes in the Northern Indian Ocean. The progressive oxygen loss may thus be the result of orbital and greenhouse gas forcing.

6. Model predictions

6.1 Global models

For future climate predictions we rely on earth system models (ESM). Although these models reproduce large-scale features and global trends they suffer from considerable mismatches between measured and model oxygen concentrations in the ocean (Bopp et al., 2013; Cabré et al., 2015; Oschlies et al., 2018; Oschlies et al., 2008). In comparison to observational data, they underestimate oxygen losses significantly (e.g. Oschlies et al., 2018 and references therein) and simulated volumes of OMZs differ considerably. Unresolved physical oxygen supply mechanisms, poorly constrained biological oxygen consumption rates and their hardly known responses to global change cause these

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uncertainties (e.g., Oschlies et al., 2018; Segschneider et al., 2013). Furthermore, feedbacks caused by the strong coupling of the marine oxygen and nitrogen cycles complicate long-term predictions (Fu et al., 2018; Oschlies et al., 2019).

Especially in the Indian Ocean, global coupled biogeochemical ESMs struggle to represent the OMZs (Fig. 7, Oschlies et al., 2008). In most ESMs the east – west contrast between the Arabian Sea and Bay of Bengal is backward, with most global models producing lower oxygen values in the Bay of Bengal than in the Arabian Sea. To some degree this problem may be attributed to the fact that ESMs are not tuned for the northern Indian Ocean. In addition, global models generally have coarser resolution to reduce computational costs, thus they are not able to resolve mesoscale processes, which are important for both the ventilation of the OMZ and for resolving upwelling that generates high rates of primary production and biological oxygen demand. These processes are parameterized in the ESMs but the question remains, why do they still fail to represent the OMZs in the northern Indian Ocean? We conclude that more care should be dedicated to the representation of the eddy-driven isopycnal mixing in the global ocean models for a more accurate representation of OMZs and O_2 in general, and an enhanced ability to predict future global oxygen distributions and climate.

6.2 Future prediction

The poor representation of the OMZs in the northern Indian ocean in ESMs reduces the reliability of future predictions of potential changes in the OMZs related to natural and anthropogenic forcing, and thus their ecological impacts and possible feedbacks to climate change. Global models suggest a general decline of oxygen for the entire ocean, but there is no clear trend visible in the Indian Ocean (Oschlies et al., 2017). However, an older set of ESMs analyzed in Cocco et al. (2013) suggest a future decrease in oxygen in the subtropical Indian Ocean in the upper mixed layer and a small increase in the western tropical Indian Ocean. This increasing oxygen concentration is also seen in response to climate change in the RCP8.5 and RCP2.6 scenarios of the 5th coupled model intercomparison project (CMIP5, Bopp et al., 2013). Specifically, Bopp et al. (2013) showed that a decrease in productivity is consistently simulated across all CMIP5 models and scenarios in the tropical Indian Ocean and that, by 2100, all models project an increase in the volume of waters below 80 µM, relative to 1990–1999. This response is more consistent than that of the previous generation of ESMs, i.e., changes varying from −26 to +16% over 1870 to 2099 under the SRES-A2 scenario (Cocco et al., 2013).

However, for lower oxygen levels, there is less agreement among the CMIP5 models and also compared to observations regarding the volume of the OMZ (Bopp et al., 2013). Specifically, for the volume of waters below 50 µM, four models project an expansion of 2 to 16% (both GFDL-ESMs, HadGEM2-ES and CESM1-BGC), whereas two other models project a slight contraction of 2% (NorESM1-ME and MPI-ESMMR). For the volume of waters below 5 µM, only one model (IPSL-CM5A-MR) is close to the volume estimated from observations and simulates a large expansion of this volume (+30% in the 2090s). These results for low oxygen waters (5 and 50 µM) agree with those of Cocco et al. (2013), with large model–data and model–model discrepancies and simulated responses varying in sign for the evolution of these volumes under climate change (Bopp et al., 2013). Thus, future trends in the northern Indian Ocean OMZs derived from the ESMs are highly uncertain, with

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predicted potential increases or decreases in the volume of low oxygen waters, depending on the model and the oxygen levels under consideration (Bopp et al., 2013; Cocco et al., 2013).

6.3 Implications

The OMZ in the Indian Ocean is the one we know least about but it may also be the OMZ with the most complex dynamics in terms of forcing and variability. Regional modelling studies have been able to reproduce the OMZs and thus they have helped us to understand the interplay between physical and biogeochemical drivers (Lachkar et al., 2019; McCreary Jr et al., 2013; Resplandy et al., 2012; Resplandy et al., 2011). However, there is still very little known about the interannual variability of the Indian Ocean OMZs, as there are limited long term observational data and the influence of the remote forcing processes that drive this variability (e.g., IOD and ENSO) is not fully understood. Global models still struggle to reproduce the Indian Ocean OMZ. One explanation for this is the coarse resolution of these models, i.e., they cannot resolve the mesoscale processes that ventilate the subsurface waters and they underestimate coastal upwelling during the monsoon seasons and, therefore, also primary production and biological oxygen demand. As a result, the oxygen trend in the tropical Indian Ocean remains unclear. However, in addition poor representation of mesocale features in global models large uncertainties stem also from largely unknown ecosystem responses to global changes.

7. Ecosystem responses

7.1 Pelagic ecosystems

Dissolved oxygen concentrations in seawater are crucial for the successful development of many pelagic organisms, particularly marine animals both planktonic vertebrates, and invertebrates whose metabolism, life cycle performance, growth capacity, reproductive success and longevity are intimately linked to oxygen availability (Ekau et al., 2010 and references therein). However, hypoxia tolerance and threshold values vary enormously among species, and even within the same species, and the growth stage of animals, the differences can be very large (Miller et al., 2002). Many fish larvae present in the pelagic realm are incapable of further growth and development at oxygen values <134 μM, while organisms such as euphausiids can survive to 4.5 μM. Thus a change in the average or the range of dissolved oxygen concentrations in the water column could have significant impacts on the survival of certain species and consequently the species composition in the ecosystem. As compared to marine vertebrates and invertebrates, the impacts of hypoxia on phytoplankton physiology and growth are less known. What is well known is that large phytoplankton blooms promote oxygen loss following their demise and export into the OMZ.

7.1.1. *Noctiluca* blooms

Since the end of JGOFS-India field studies (1997 to present), the pelagic ecosystem of the Arabian Sea has undergone considerable change, as is evident from the nearly four-fold increase in summer-time phytoplankton biomass in the northern Arabian Sea (Goes et al., in review). This increase in biomass has been attributed to intensification of summer monsoonal wind intensities and wind-driven coastal upwelling along the coasts of Somalia, Yemen and Oman, fuelled by the warming trend and the loss of snow in the Himalayan-Tibetan mountain range (Goes et al., 2005; Goes et al., in review).

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Since upwelling is fed by waters from the seasonal thermocline that are in close proximity to the upper OMZ, the postulated intensification of upwelling and the expansion of the OMZ agrees with the observed declining oxygen concentrations in the surface mixed layer during the period of convective mixing in the western Arabian Sea (do Rosário Gomes et al., 2014). However, when the summer monsoon winds die down and upwelling along the coast ceases, the coast of Oman continues to experiences episodic on-shore influxes of sub-oxic waters (Al-Hashmi et al., 2015). Gomes et al (2009) have shown that immediately following the end of the summer monsoon in September/October, the western boundary of the northern Arabian Sea begins to become populated with large, long-lived cyclonic and anti-cyclonic meso-scale eddies. These eddies continue to uplift oxygen-poor and nutrient-enriched waters subsurface waters into the euphotic zone and promote large blooms, in particular that of the mixotrophic dinoflagellate *Noctiluca scintillans* (hereafter referred to as *Noctiluca*) (Gomes et al., 2009). In the Sea of Oman, the appearance of *Noctiluca* as surface blooms begins around the month of November (Al-Azri et al., 2015; Al-Hashmi et al., 2015), in association with a large cyclonic eddy that facilitates the upshoaling of low oxygen, high-nutrient waters to the surface (Fig. 8, Gomes et al., 2009; Harrison et al., 2017). Altimetry data show furthermore that this semi-permanent cyclonic and mesoscale eddy is responsible for sustaining this bloom for a prolonged period resulting in thick blooms along the coasts of Oman and Iran by the month of February. By mid-February the activity of both cyclonic and anticyclonic eddies are responsible for the dispersal of this seed population of *Noctiluca* eastwards into the central and eastern Arabian Sea, ultimately engulfing the entire northern Arabian Sea (Gomes et al., 2009; Yan et al., 2019). First discovered in the early 2000's (Prakash et al., 2008; Prakash et al., 2017), these *Noctiluca* blooms have since become increasingly pervasive and widespread in the Arabian Sea, occurring with predictable regularity every year from December to mid of March (do Rosário Gomes et al., 2014; Goes et al., 2016; Lotliker et al., 2018; Prakash et al., 2017; Werdell et al., 2014). At the time the main sediment trap work and the JGOFS-India field studies were carried out (1989 – 1997), cyanobacteria dominated the phytoplakton community in the Arabian Sea except during the peak of the upwelling seasons in the western Arabian Sea and during the winter bloom in the northern Arabain Sea (Garrison et al., 1998; Garrison et al., 2000). During these two periods large diatom dominated blooms occurred. However, despite the emergence of *Noctiluca* blooms in the northern Arabian Sea, high rates of N_2 fixation occur in the Arabian Sea during spring and fall seasons associated with *Trichodesmium* blooms in the eastern Arabian Sea (Gandhi et al., 2011; Singh et al., 2019).

An on-board experimental study conducted by Gomes et al. (2014)in the central and western Arabian Sea during the winter monsoons of 2009, 2010 and 2011, provided the first conclusive evidence that the growth of green *Noctiluca* blooms were being facilitated by hypoxia. Additionally, prior to their appearance as surface blooms, *Noctiluca* were observed in large numbers at depth in association with the oxycline (Goes & Gomes, 2016). In their study, Piontkovski et al. (2017) were able to show a gradual descent of *Noctiluca* cells into the water column towards the oxycline following peak blooms at the surface. More recently based on observations that showed that *Noctiluca* blooms of the eastern Arabian Sea were not associated with hypoxic waters Lotliker et al. (2018) argued that low oxygen waters were not the cause of *Noctiluca* blooms. Their conclusions were not backed by any

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experimental data and their oxygen data were from Bio-ARGO floats that were located south of where Noctiluca blooms occur. Furthermore, in a recent study, Yan et al. (2019) showed that *Noctiluca* blooms of the eastern Arabian Sea were largely the result of advection by coherent eddy structures, filaments and streamers and not actively growing as in the western and central Arabian Sea. Gomes et al. (2014) posited that the capacity of the of endosymbionts *Protoeuglena noctilucae* present within *Noctiluca* to photosynthesize more efficiently at low oxygen concentrations was probably linked to their primitive origin when oxygen levels in Earth's atmosphere and in the oceans were much lower.

The exact role of *Noctiluca's* endosymbionts is not clearly understood, but preliminary evidence suggests that when the host cell is actively grazing on other phytoplankton, microzooplankton, detritus and fish eggs, the endosymbionts help reduce excessive build-up of ammonia within the central cytoplasm of *Noctiluca* (Goes & Gomes, 2016). In addition, oxygen produced by the endosymbionts helps to maintain the balance of oxygen within *Noctiluca* cells.

Noctiluca is not a preferred food for most micro- and meso- zooplankton (do Rosário Gomes et al., 2014). Instead, its major consumers are salps and jellyfish. Respiration rates of gelatinous zooplankton in gelatinous plankton are rather low and most species belonging to this group are capable of regulating their oxygen consumption allowing them to grow and survive under low-oxygen conditions.

7.1.2 Zooplankton migration

Knowledge of the concentrations of dissolved oxygen within the water column is also important, because these concentrations can also set limits to horizontal and vertical distribution of zooplankton (Saltzman et al., 1997; Wishner et al., 2008). In general, most zooplankton taxa show minimum abundances in the core of the OMZ, and higher abundances in well-oxygenated waters above or beneath the OMZ (Böttger-Schnack, 1996; Saltzman & Wishner, 1997; Wishner et al., 1995). There are indications that several copepods are highly susceptible to low-oxygen waters that can at times lead to their death (Elliott et al., 2013; Jagadeesan et al., 2013). Certain zooplankton, however, have developed vertical migration strategies that enable them to pass through or even live within the OMZ (Gonzalez et al., 2002; Herring et al., 1998; Longhurst, 1967). The ability to do so has been linked to the presence and activity of lactic dehydrogenase (LDH), an enzyme associated with anaerobic metabolism (Escribano, 2006; Gonzalez & Quiñones, 2002). Gonzalez and Quinones (2002) were also able to show that the specific LDH activity within *Euphausia mucronata* a species capable of conducting daily vertical migrations through the OMZ in the Humboldt Current upwelling system, was roughly two orders higher than *Calanus chilensis,* a zooplankton species which restricts itself to the oxygenated waters above the OMZ. In Escribano (2006), bulk zooplankton samples from within the OMZ, were seen to contain very high amounts of LDH.

In the Arabian Sea, almost 85% of the epipelagic mesozooplankton biomass are found within the upper 100 m within the upper aerobic part of the seasonal thermocline. Nevertheless, the mesozooplankton biomass is roughly only half of that found in areas without a pronounced OMZ (Vinogradov et al., 1962). Below 100 m within the anaerobic part of the seasonal thermocline zooplankton concentrations decline sharply (Banse, 1994; Böttger-Schnack, 1996; Smith et al., 2005; Wishner et al., 1998).

Comparisons of day versus night hauls revealed that the permanent OMZ of the Arabian Sea does indeed strongly suppress vertical migration of zooplankton (Smith et al., 1998), on account of their inability to swim across the OMZ. At locations where the OMZ was forced upwards due to physical processes, mesozooplankton communities were observed as narrow aggregates within the surface layer (Morrison et al., 1999), where they became easily accessible to predators.

In the Arabian Sea there appears to be only one species, *Pleuromamma indica,* that has displayed the ability to survive and thrive in hypoxic waters. This species is not only observed in high numbers in hypoxic waters (Goswami et al., 1992; Haq et al., 1973; Saraswathy et al., 1986; Vinogradov & Voronina, 1962), but is also capable of migrating daily through the well-oxygen surface layer (Saraswathy & Iyer, 1986). There are also indications that the increased abundance of *P. indica* being witnessed in recent years may be tied to the geographically more widespread oxygen depletion.

7.1.3. Implications

In comparison to the Arabian Sea, little is known about the plankton dynamics in the Bay of Bengal. Limited data from the Bay of Bengal Process Studies (BOBPS) program suggested a diatom-dominated community that contained more genera compared to the Arabian Sea (Madhupratap et al., 2003). However, the regular occurrence of *Noctiluca* blooms and the increase in salps and jellyfish being witnessed in the Arabian Sea in recent years is consistent with the idea of an ecosystem shift associated with decreasing concentrations of dissolved oxygen. The emerging trophic structure fundamentally differs from the traditional planktonic food web, with a reduced transfer of biomass to larger size classes and fishes (Mitra et al., 2014). Similar to diatom blooms, senescent salp blooms are also exported efficiently into the deep sea (Martin et al., 2017). Impacts on the export production are still difficult to predict but it is likely that this will have implications for the cycling nutrients and oxygen within the seasonal thermocline and the benthic community (Billett et al., 2006; Lebrato et al., 2012).

7.2 Benthic ecosystems

7.2.1 Benthic communities

Hypoxia has major consequences at the sea floor, for benthic communities and for the biogeochemical processes they drive. Benthic communities and processes in the Bay of Bengal have thus far received less study than those of the Arabian Sea. It is however clear that oxygen exerts an important control on benthic communities across the margins of both basins (e.g, Ingole et al., 2010; Raman et al., 2015). There are grain-size related contrasts in communities across the shelves, but also clear oxygen-related patterns across the upper slope depth ranges where mid-water oxygen minima impinge on the sea floor (Fig. 9). In the Arabian Sea, the degree to which this oxygen effect is expressed varies between margins due to differing degrees of bottom-water ventilation. On the Pakistan margin, where ventilation and bottom-water oxygen levels are lowest, hypoxia-resistant foraminifera are the only fauna to persist at the core of the OMZ, and macro- and megafauna are totally absent (Gooday et al., 2009). By contrast, on the Indian margin, and even off Oman, where upwelling-driven productivity and delivery of organic matter to sediments are particularly high, macrofauna generally persist across the entire margin, albeit in reduced numbers and diversity at the OMZ core (e.g., Ingole et al., 2010; Levin et al., 2000). Further, across the OMZ boundaries, clear "edge effects" have been observed; sharp changes in community composition and faunal abundance linked to different oxygen thresholds (e.g.,

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Levin et al., 2009b), as has also been observed on other hypoxia-impacted margins in the eastern Pacific and off SW Africa (e.g., Levin et al., 1991).

7.2.2 Benthic ecosystem function

The strong but variable cross-OMZ gradients in bottom-water oxygen and benthic communities translate to contrasts in benthic ecosystem function, which also varies between margins. For example, the numbers, size and depth of faunal burrows, and the extent of bioturbation and bio-irrigation, change across the OMZ boundaries (e.g., Cowie et al., 2009a; Smith et al., 2000). In the extreme case, this leads to total absence of bioturbation and bio-irrigation at the core of the OMZ off Pakistan, and the resulting presence of annually laminated (varved) sediments, which are not observed on the better ventilated margins of the Arabian Sea or in the Bay of Bengal. In the Arabian Sea, there are also clear oxygen-dependent differences in benthic community organic matter processing, as have been revealed by tracer incubation experiments. For example, a threshold oxygen concentration occurs, above which macrofauna dominate short-term OM processing, and below which meiofauna and bacteria dominate. This was illustrated on the Pakistan margin both at sites that spanned the lower OMZ boundary and at a shelf-edge site that underwent strong seasonal change in bottom-water oxygen levels, from fully oxygenated (intermonsoon) to hypoxic (summer monsoon) (e.g., Andersson et al., 2008; Pozzato et al., 2013; Woulds et al., 2009; Woulds et al., 2007).

Further, the "edge effect" seen in benthic community composition also has been observed in faunal OM processing. At sites in the lower OMZ transition zone, the polychaete *Linopherus sp.* showed clear morphological adaptation to low oxygen levels, and overwhelmingly dominated both the benthic community and also the uptake and processing of organic matter (Jeffreys et al., 2012). These results, and those of other experiments (e.g., Hunter et al., 2012; White et al., 2019), illustrate that faunal assemblage composition may represent an important factor determining the pattern of seafloor processing, but also the composition, bioavailability and fate of residual organic matter. It is certainly clear that faunal digestive processes are recorded in the composition of organic matter deposited across the margins (e.g., Jeffreys et al., 2009; Smallwood et al., 1999). In summary, oxygen-dependent cross-margin variability in benthic communities and ecosystem function (feeding, bioturbation and bio-irrigation etc) may be important contributors to the role that oxygen exposure plays in controlling organic carbon distribution and burial across Arabian Sea margins, although other factors, most notably hydrodynamic processes, are also important (e.g., Cowie, 2005; Cowie et al., 2009b; Koho et al., 2013; Kurian et al., 2018).

7.2.3 Sediment redox conditions and microbial processes

Alongside the contrasts in faunal communities, bioturbation and irrigation, there are cross-OMZ differences in sediment redox conditions and microbial processes. Again, these are expressed to varying degree on the different margins of the Arabian Sea (Cowie, 2005), and will be less apparent in the Bay of Bengal due to the less intense oxygen depletion at the OMZ core. In the Arabian Sea, sulfate reduction has generally been shown to be surprisingly limited in near-surface sediments (top ~50 cm) (e.g., Cowie, 2005; Law et al., 2009), and redox conditions overall to be only moderately reducing (e.g., Crusius et al., 1996) relative to rates observed on upwelling/OMZ margins in other basins.

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Nonetheless, Pakistan margin sediments, and possibly those on other Arabian Sea margins, are home to significant rates of denitrification and anammox (e.g., Schwartz et al., 2009; Sokoll et al., 2012) and authigenic phosphorous (P) burial (e.g., Filippelli GM, 2017; Kraal et al., 2012). These phenomena represent important sink terms in the N and P biogeochemical cycles, and along with sediment-water nutrient fluxes that vary in direction, magnitude and N:P stoichiometry across the OMZ, serve as potential controls on pelagic nutrient inventories.

Finally, there is evidence that Pakistan margin sediments (and possibly OMZ sediments on other margins), sequester important amounts of "dark" carbon arising from anammox and possibly other chemoautrophic processes occurring in overlying waters or within the sediments (e.g., Cowie et al., 1999; Cowie et al., 2009b; Lengger et al., in press). It is a term that is currently underestimated or ignored in carbon budgets and biogeochemical models. On the Pakistan margin, there are also chemosynthetic bacterial mats associated with methane seeps (Himmler et al., 2018)

7.2.4 Implications

As mentioned above, the coastal hypoxia on the western Indian shelf can reach the extreme of fully sulfidic conditions in nearshore bottom waters (e.g. Naqvi et al., 2000). Apart from mortality of benthic (as well as pelagic) fauna under extreme conditions, details of the effects of seasonal hypoxia on benthic communities in the shelf and coastal waters of Arabian Sea and Bay of Bengal are not well documented. Thus, while seasonal contrasts in benthic community organic matter processing were reported on the Pakistan shelf (see above), it is not otherwise clear if or how benthic communities have adapted to the recurring, possibly intensifying, hypoxia. What is clear is that wholesale seasonal changes occur in benthic microbial processes and in the magnitudes and directions of sediment-water nutrient fluxes (e.g., Pratihary et al., 2014).

Potential benthic ecosystem and biogeochemical consequences of projected intensification and expansion of hypoxia have been the subject of multiple reviews (e.g., Levin et al., 2009a; Middelburg et al., 2009; Stramma et al., 2008). Intensification of hypoxia within the Arabian Sea and Bay of Bengal OMZs would predictably drive distributions in benthic communities, sediment characteristics and biogeochemical processes towards those currently observed off Pakistan. This would result in potentially expanded depth ranges devoid of macro- and megafauna (and thus bioturbation and irrigation), but also shifts in the locations and composition of "edge" populations associated with oxygen gradients at OMZ boundaries. Other hypoxia-related phenomena might also impact on benthic ecosystems. These include the increasing prevalence of *Noctiluca* and jellyfish and their potential impacts on food webs and organic matter export to depth. Mass deposition of jelly fish on the seafloor off Oman (Billett et al., 2006) have major impacts on seafloor communities and processes (Sweetman et al., 2016).

It is not yet clear what the net effect of such changes would be on carbon burial, but changes in faunal populations and transition from hypoxic to fully anoxic conditions could have major impacts on benthic N and P cycling and sediment-water nutrient fluxes (and N:P ratios), as has been observed with expanding hypoxia in the Baltic (Jilbert et al., 2011; Karlson et al., 2007). Intensification of existing seasonal coastal hypoxic zones, or shoaling of upper OMZ boundaries (currently close to shelf edge depth) into shelf waters, could have particularly pronounced impacts on benthic (and pelagic) fauna –

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with direct implications in terms of food security for large human populations - and on biogeochemical processes.

Intensification or increased duration of coastal hypoxia could lead to increasing occurrence of mass mortality or to reduced ability of faunal populations to recover between hypoxic events. It would also result in expanded areas of reducing sediments and potential changes to carbon sequestration, N and P cycling and N_2O emissions (Middelburg & Levin, 2009). Further, the magnitudes and the dramatic intermonsoon/monsoon (oxic/hypoxic) changes in benthic processes and nutrient fluxes seen at sites on the western Indian shelf (Pratihary et al., 2014), imply that expanded or intensified hypoxia could, through benthic-pelagic coupling, have major influences on nutrient inventories and processes occurring in shallow overlying waters.

8. Conclusion

Hypoxic conditions prevail in the Arabian Sea and Bay of Bengal OMZ, which allowed anaerobic microorganisms to thrive and to compete against aerobic organisms. However, in contrast to the Arabian Sea, in the Bay of Bengal the low oxygen concentrations suffice to support nitrite oxidization to a degree that is prevented denitrification to become significant. The in comparison to the Arabian Sea high freshwater fluxes and lithogenic matter supply into the Bay of Bengal might have caused this difference as they influence the balance between biological oxygen consumption and physical oxygen supply. Nevertheless, in the Arabian Sea and probably also the Bay of Bengal the supply of oxygen sustained by mixing and advection associated with mesoscale eddies compensated the biological oxygen consumption. The negative influence of decreasing oxygen concentrations on the respiration of organic matter might have helped to establish these balances and counteracted a reduced oxygen supply in the Arabian Sea during the last 6000 years. This was caused by climate-driven changes in the ocean's circulations. Due to human induced global changes, the OMZ is expanding in the Arabian Sea, and the Bay of Bengal, and hyp- as well as anoxic events occurred on the Indian shelf in both basins. These trends significantly affect benthic and pelagic ecosystems. The regular occurrence *Noctiluca* is e.g. a new phenomenon, which is assumed to herald a regime shift within the pelagic ecosystem of the Arabian Sea in response to declining concentrations of dissolved oxygen. These recent changes augment the problems to represent the Indian Ocean OMZ in models and thus to predict the impact of the changing monsoon system on productivity and OMZ development under global change scenarios.

9 Author contribution

The paper was written jointly by all co-authors whereas Tim Rixen coordinated the writing processes and co-authors focused on specific sections as listed in the following: Sections 1 – 3 (Tim Rixen), section 4 (Zouhair Lachkar), section 5 (Birgit Gaye and Joachim Segschneider), section 6 (Henrike Schmidt and Raleigh R. Hood), section 7.1 (Joaquim Goes, Helga do Rosário Gomes and Arvind Singh), and section 7.3 (Greg Cowie).

10 Competing interests

The authors declare that they have no conflict of interest.

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Figure Captions:

Figure 1: (a, b) Monthly mean primary production rates (Behrenfeld et al., 1997) covering the periods between 2002 and 2014.(c) Minimum oxygen concentration in the water column of the Indian Ocean. Oxygen concentrations > 20 µM are indicated by white color. The data was obtained from the World Ocean Atlas 2013 (Boyer et al., 2013). The black line indicates the extent of the secondary nitrate maximum (SNM) in 1997 (Rixen et al., 2014). The maps were produced with Generic Mapping Tool.

Figure 2: (a) The seasonal mean areal extension of the Arabian Sea OMZ and the mean seasonal oxygen concentration within the Arabian Sea OMZ. Data are obtained from Table 5 in Acharya and Panigrahi (2016). (b) Monthly mean organic carbon fluxes measured by sediment trap moored at water-depth of approximately 3000 m in the western (WAST), central (CAST) and eastern Arabian Sea (EAST) between 1986 and 1997. For more detailed information see Rixen et al. (2019a).

Figure 3: Fluxes of protected and free particulate organic carbon versus water (black line) calculated according to the equation introduced by Armstrong et al. 2002 and data measured by a sediment trap in the central Arabian Sea. The black circle in (b) shows the long-term mean organic carbon fluxes measured by sediment trap in the central Arabian Sea. The blue and broken black lines indicates the concentrations of dissolved oxygen and nitrite measured during the cruise with RV Meteor (M74) in 2007 in the central Arabian Sea (Station 450). The red line represents the variation of dissolved oxygen (oxygen consumption) with depth versus water-depth. Rixen al. 2019 a,b and Rixen et al. (2014) provide further information about the sediment trap study and the RV Meteor cruise M74.

Figure 4: The mean seasonal oxygen concentration within the Arabian Sea OMZ versus the thickness of the Arabian Sea OMZ. Data are obtained from Table 5 in Acharya and Panigrahi (2016).

Figure 5: Schematic sketch illustrating role of mesoscale eddies in spreading nutrients and oxygen vertically (diapycnical) and horizontally (isopycnical) in comparisons to a situation without these processes.

Figure 6: (a) Increasing δ^{15}N values in high resolution cores from the Arabian Sea (note inverted scale) show increasing denitrification since about 6000 – 8000 years BP; data from the northern (yellow; light brown), eastern (red), western (blue) and southwestern (black) Arabian Sea. Sediment cores: SO9090-63KA (Burdanowitz et al., 2019), RC27-23 (Altabet et al., 2002), NIOP-905P (Ivanochko et al., 2005), SK148-55 (Kessarkar et al., 2018), MD04-2876 (Pichevin et al., 2007) parallel with (b) sinking oxygen concentrations in biogeochemical model simulations driven by the Kiel Climate/PISCES Model in the northern (yellow), eastern (red), western (blue) and southern Arabian Sea (dark grey). See text for definition of regions. Model results are 20 yr running means.

Figure 7: Thickness of the OMZ (oxygen concentration <20 µM) in 10 ESM from the 5th coupled model intercomparison project (CMIP5; Taylor et al., 2012) and in observations from oxygen climatologies of the World Ocean Atlas 2013 (Garcia et al., 2013; bottom right). The model data cover the period from 1900-1999 and are taken from the 'historical' experiment. For more information on the models see Cabré et al. 2015 (Table A1). The maps were produced with MATLALB.

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Figure 8: (a) NOAA Suomi-VIIRS derived Chl *a* on 6th of Feb. 2018 showing *Noctiluca* blooms in the Sea of Oman in association with a cyclonic eddy. For projecting the Chl a concentrations the google earth low-resolution land elevation map was used © Google Earth (b) *Noctiluca* blooms along the coast of Muscat on 6th Feb. 2018.

Figure 9: A summary of water-column conditions, sediment properties, benthic communities and processes influencing C cycling across the OMZ on the Indus margin of the Arabian Sea (modified from Cowie and Levin (2009a) and reprinted with the permission of Elsevier). Water-column dissolved oxygen (DO) concentration profiles are shown for intermonsoon (April)-May and late-to-postmonsoon (September-October) periods. Organic carbon (C_{org}) concentrations (weight percent) are for surficial (0-2 cm) sediments. Vertical shaded zone indicates OMZ boundaries as defined by DO ≤ 0.5 ml/l. Shaded depth ranges denote the OMZ core (~250-750 m, near-uniform DO of ≤0.1 ml/l), a lower OMZ transition zone (~750-1300 m) in which DO and the numbers of and activity of macrofauna increase with station depth, and a seasonally hypoxic zone (~100-250 m) in which the upper OMZ boundary shoals during the summer monsoon season. Faunal classes are as defined by Gooday et al (2009).

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Figure 1

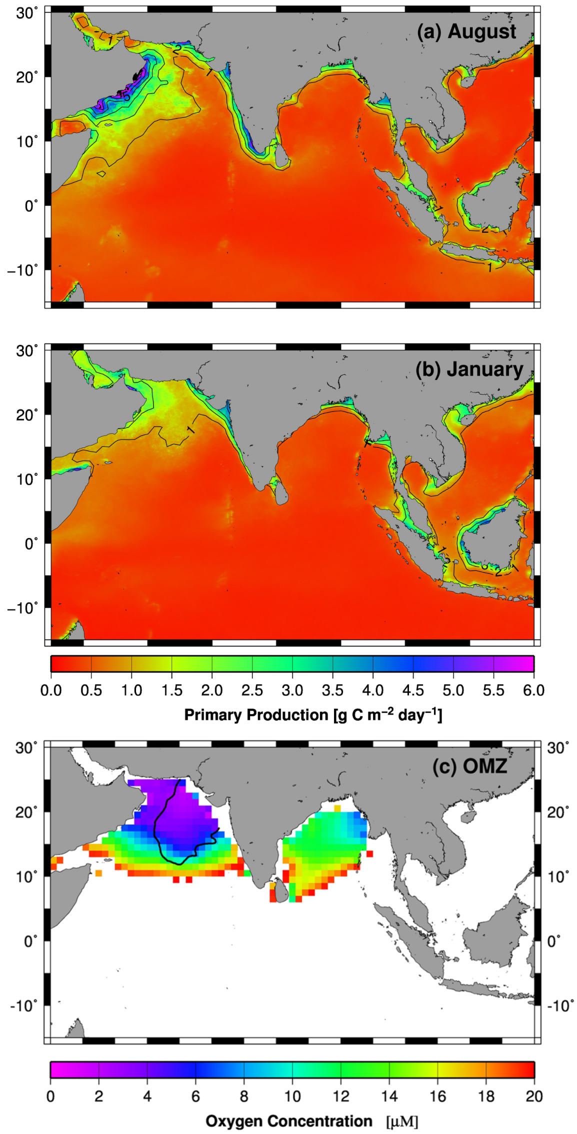

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Figure 2

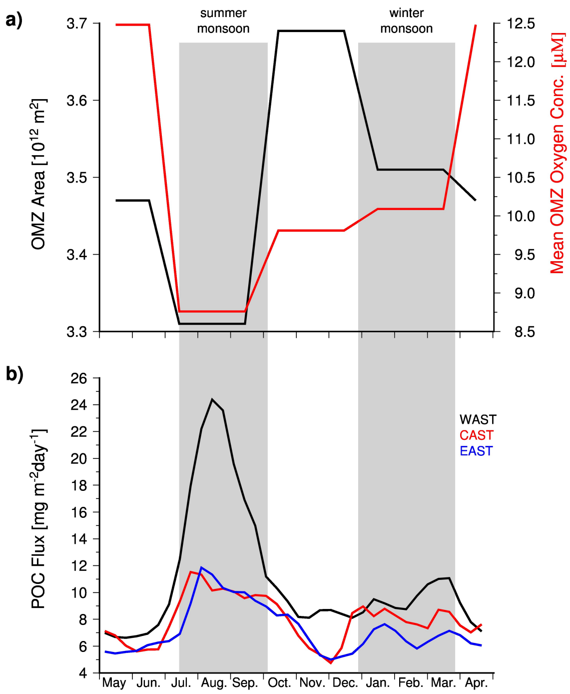

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Figure 3

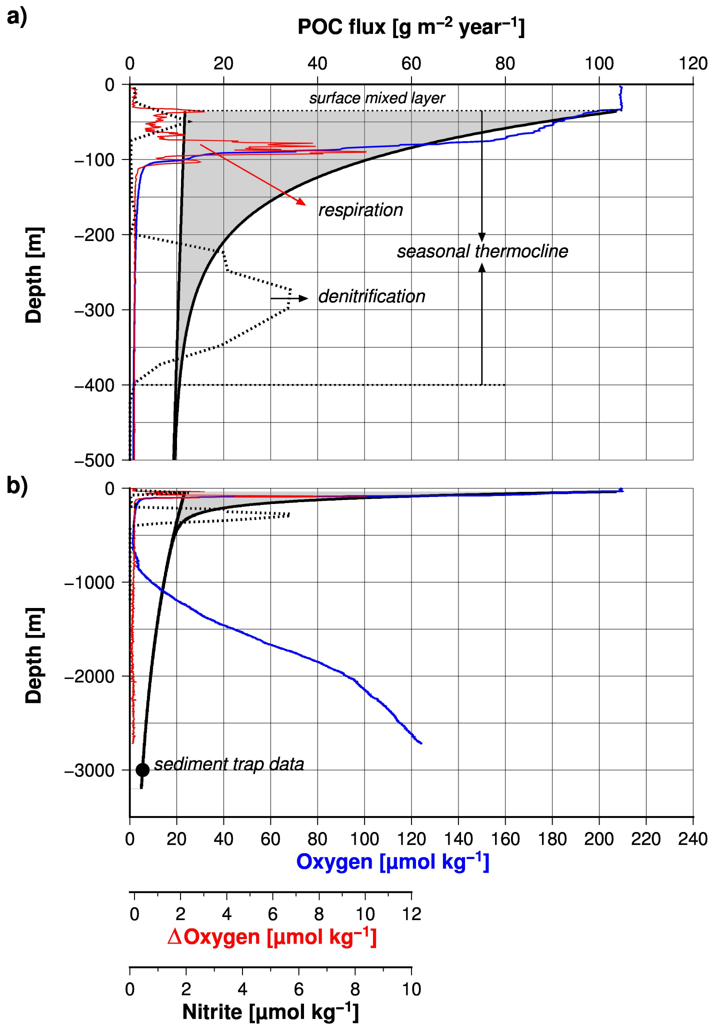

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Figure 4

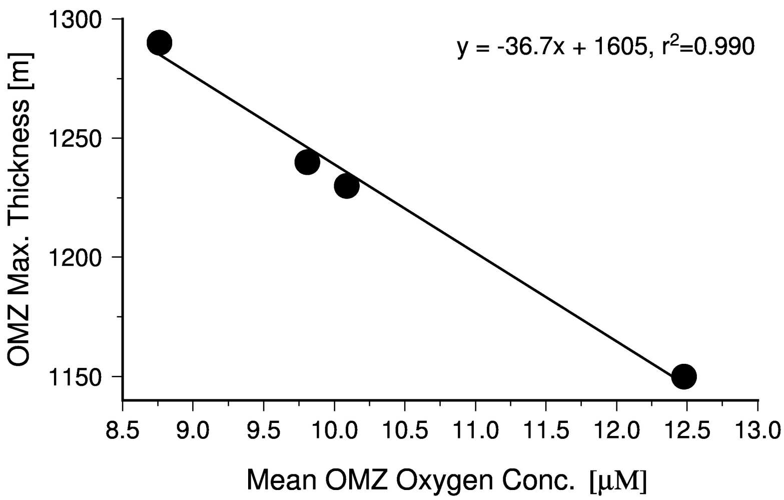

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Figure 5

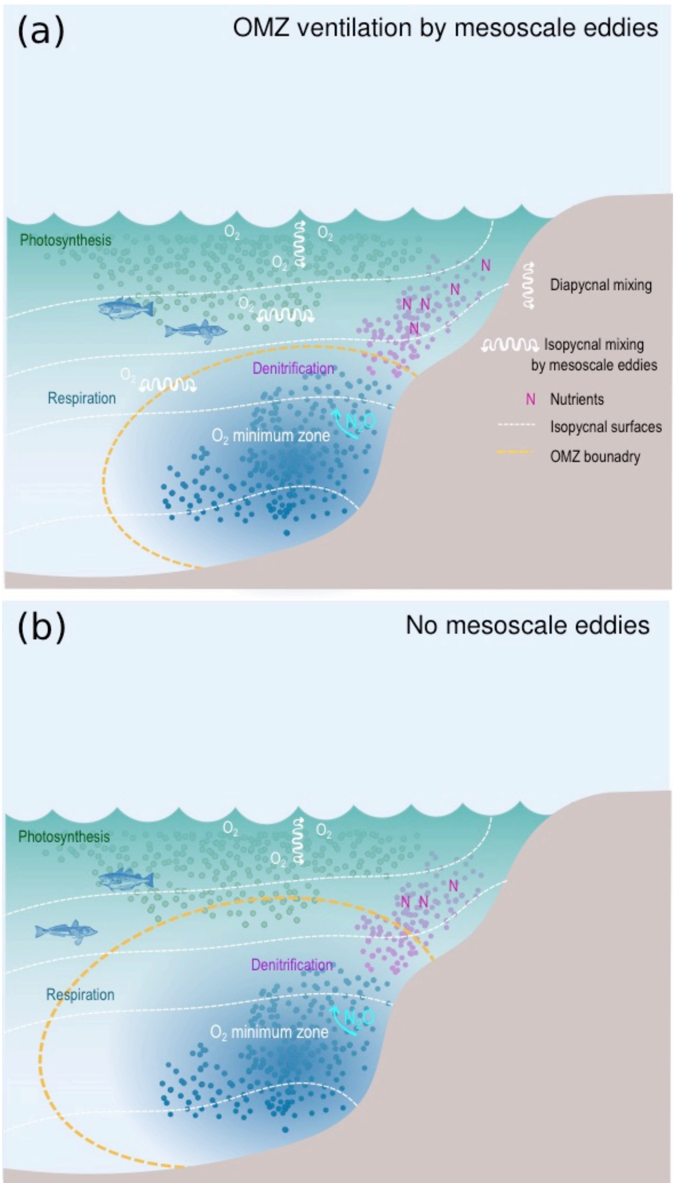

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Figure 6

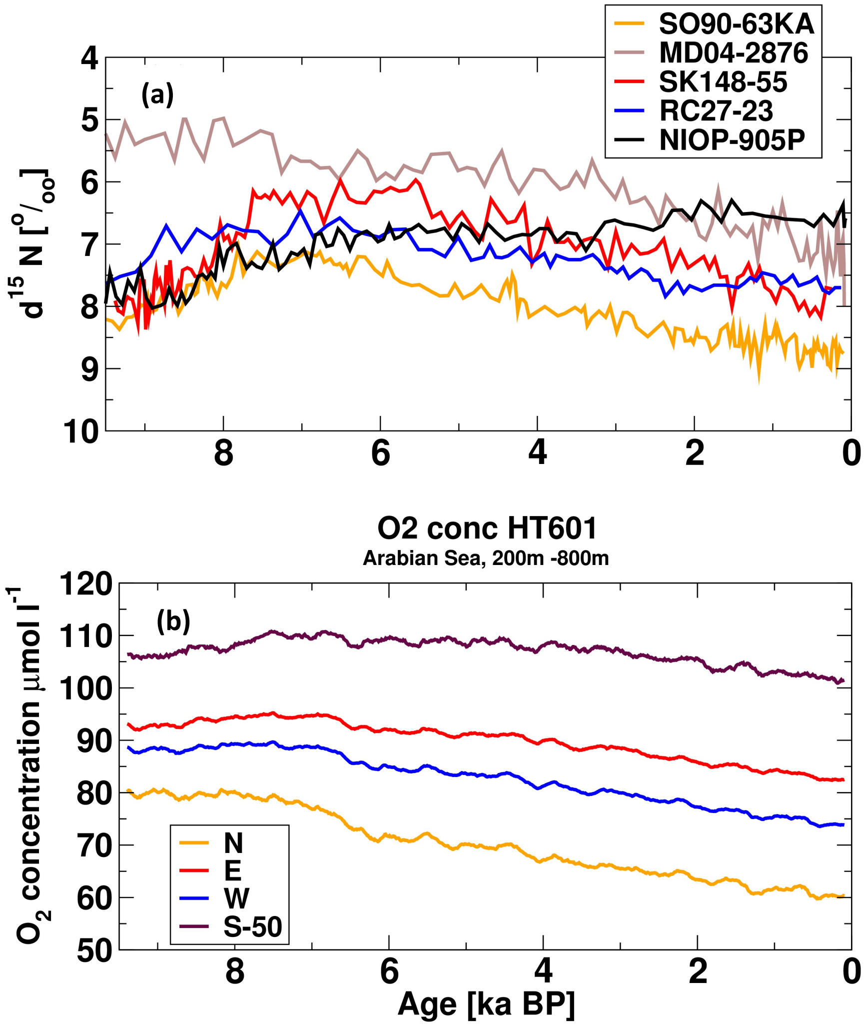

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Figure 7

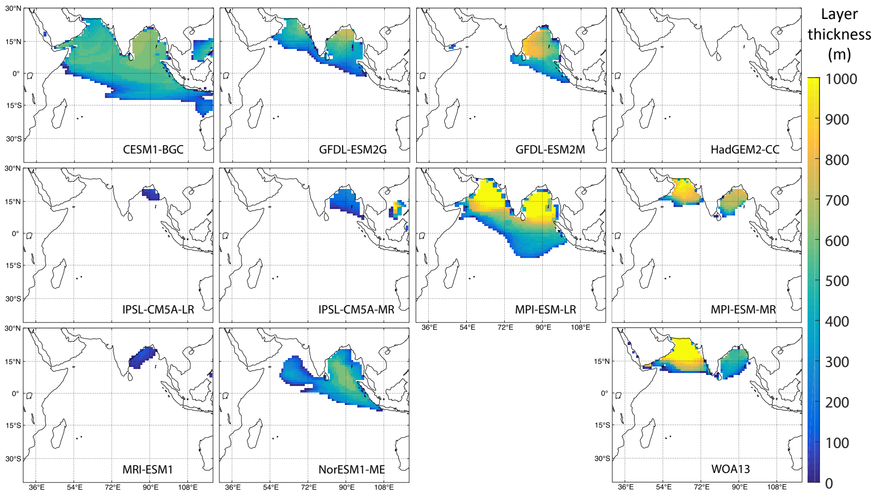

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Figure 8

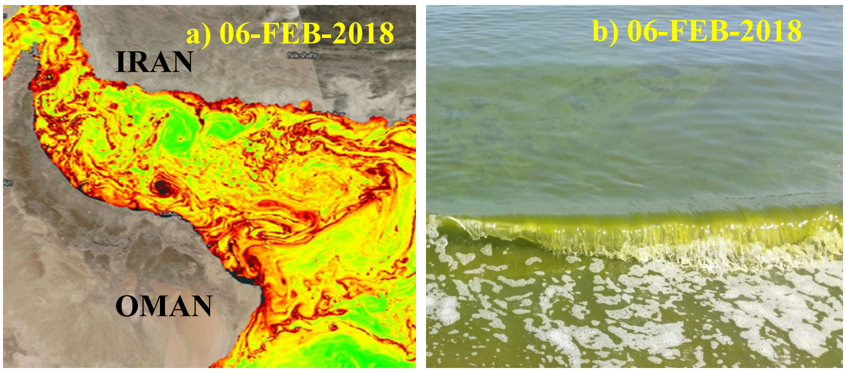

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Figure 9