Present, past, and future of the oxygen minimum zone in the northern Indian Ocean

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1 **Abstract.**

2 Decreasing concentrations of dissolved oxygen in the ocean are considered as one

3 of the main threats to marine ecosystems as they jeopardize the growth of higher

4 organisms. They also alter the marine nitrogen cycle, which is strongly bound to the

5 carbon cycle and climate. While higher organisms in general start to suffer from

6 oxygen concentrations < ~63 µM (hypoxia), the marine nitrogen cycle responds to

7 oxygen concentration below a threshold of about 20 µM (microbial hypoxia), whereas

8 anoxic processes dominate the nitrogen cycle at oxygen concentrations of < ~0.05

9 µM (functional anoxia). The Arabian Sea and the Bay of Bengal are home to

10 approximately 21% of the total volume of ocean waters revealing microbial hypoxia.

11 While in the Arabian Sea this oxygen minimum zone (OMZ) is also functionally

12 anoxic, the Bay of Bengal OMZ seems to be on the verge of becoming so. Even

13 though there are a few isolated reports on the occurrence of anoxia prior to 1960,

14 anoxic events have so far not been reported from the open northern Indian Ocean

15 (i.e. other than on shelves) during the last 60 years. Maintenance of functional anoxia

16 in the Arabian Sea OMZ with oxygen concentrations ranging between > 0 and ~0.05

17 µM is highly extraordinary considering that the monsoon reverses the surface ocean

18 circulation twice a year and turns vast areas of the Arabian Sea from an oligotrophic

19 oceanic desert into one of the most productive regions of the oceans within a few

20 weeks. Thus, the comparably low variability of oxygen concentration in the OMZ

21 implies stable balances between the physical oxygen supply and the biological

22 oxygen consumption, which includes negative feedback mechanisms such as

23 reducing oxygen consumption at decreasing oxygen concentrations (e.g., reduced

24 respiration). Lower biological oxygen consumption is also assumed to be responsible

25 for a less intense OMZ in the Bay of Bengal. According to numerical model results, a

26 decreasing physical oxygen supply via the inflow of water masses from the south

27 intensified the Arabian Sea OMZ during the last 6000 years, whereas a reduced

28 oxygen supply via the inflow of Persian Gulf Water from the north intensifies the OMZ

29 today in response to global warming. The first is supported by data derived from the

30 sedimentary records, and the latter concurs with observations of decreasing oxygen

31 concentrations and a spreading of functional anoxia during the last decades in the

32 Arabian Sea. In the Arabian Sea decreasing oxygen concentrations seem to have

33 initiated a regime shift within the pelagic ecosystem structure, and this trend is also

34 seen in benthic ecosystems. Consequences for biogeochemical cycles are as yet

35 unknown, which, in addition to the poor representation of mesoscale features in

36 global Earth System Models, reduces the reliability of estimates of the future OMZ

37 development in the northern Indian Ocean.

1. Introduction

The rise of atmospheric oxygen concentrations to nearly present-day levels was a precondition for the evolution of complex life forms and accompanied the appearance of algae and planktonic cyanobacteria at about 800 to 500 million years ago (Brocks et al., 2017; Canfield, 2014 ; Lenton et al., 2011; Lyons et al., 2014; Sánchez-Baracaldo, 2015). Numerically, planktonic cyanobacteria are still the most abundant plankton clade in the ocean and exert a strong control on the energy transfer into the marine biosphere by transforming nitrogen gas (N_2) into ammonium (NH_4^+) (nitrogen fixation, Fig. 1, Falkowski et al., 2004). Since algae, which in addition to cyanobacteria comprise marine primary producers, cannot fix nitrogen gas, they rely on the supply of fixed nitrogen (NH_4^+, NO_2^-, NO_3^-) for the production of organic matter. Energy yielded by the respiration of organic matter produced by cyanobacteria and algae sustains heterotrophic life in the ocean, while chemoautotrophic organisms oxidize degradation products such as methane and ammonium to gain energy for running their metabolisms (Dalsgaard et al., 2003; Kuypers et al., 2001; Middelburg, 2011). In the absence of elementary oxygen, oxygen bound to sulfur (e.g. sulfate) or nitrogen (nitrate and nitrite), can also be utilized to oxidize organic matter and its degradation products. Since nitrate and nitrite are (like ammonium) accessible to algae, their use as oxidizing agents reduces the availability of fixed nitrogen in the ocean. Accordingly, decreasing oxygen concentrations could exert a negative feedback on marine primary production by lowering the availability of fixed nitrogen for algal production (Canfield et al., 2019; McElroy, 1983).

Anoxic conditions emerge only rarely in the ocean, but appear to be common in microenvironments within particles via which organic matter, which is produced in the sunlit surface ocean, is exported into the deep sea (e.g. Bianchi et al., 2018; Naqvi et al., 2000; Weeks et al., 2002). However, already at low levels of dissolved oxygen, aerobic and anaerobic processes occur simultaneously and compete against each other (Bristow et al., 2017; Gaye et al., 2013). Chemoautotrophic microbes use the available elementary oxygen to oxidize ammonium to nitrite and further to nitrate (nitrification: NH_4^+ -> NO_2^- –> NO_3^-), while microbes carrying out anaerobic processes transform ammonium as well as nitrate and nitrite into N_2 (Fig. 1). Among these anaerobic processes heterotrophic denitrification and the chemoautotrophic anaerobic oxidation of ammonium (anammox) are the most relevant. Denitrification reduces nitrate in a sequence of several steps via nitrite to N_2 (NO_3^- -> NO_2^- -> N_2), whereas anammox bacteria utilize nitrite to oxidize ammonium (NO_2^- + NH_4^+ -> N_2).

74   Thus, nitrite plays an import role in the competition between these anaerobic and
75   aerobic processes because, independent of its formation via nitrification and
76   denitrification, it can either be oxidized to nitrate or reduced to N_2. Concentrations of
77   dissolved oxygen strongly influence the fate of nitrite and thereby exert a control on
78   the availability of fixed nitrogen in the ocean (Bristow et al., 2016; Gaye et al., 2013).
79   According to experiments and *in situ* observations, anammox sets in when oxygen
80   concentrations drop below ~20 µM, while denitrification occurs at oxygen
81   concentrations of approximately < 6 µM (Fig. 2, Bristow et al., 2016; Dalsgaard et al.,
82   2014; Kalvelage et al., 2011). Consequently, anammox competes with nitrification for
83   nitrite at oxygen level between 6 and 10 µM, and additionally with denitrification at
84   oxygen level < 6 µM. Decreasing oxygen concentrations favor anammox and
85   denitrification while, in addition to the influence of oxygen, the quality of the supplied
86   organic matter appears to also control the relative importance of denitrification vs.
87   anammox for the reduction of nitrite to N_2 (Babbin et al., 2014; Bristow et al., 2016;
88   Ward et al., 2009). However, since denitrification and anammox ultimately produce
89   N_2 at the expense of fixed nitrogen, the term denitrification is used as a synonym for
90   both processes in the following discussion if anammox is not specifically mentioned.
91   Hypoxia, which means 'low oxygen concentrations', describes oxygen concentrations
92   below which higher organisms start to suffer from the lack of oxygen (Ekau et al.,
93   2010; Vaquer-Sunyer et al., 2008). Accordingly, an oxygen concentration of 60 – 63
94   µM is commonly applied as upper limit of hypoxia in fisheries and ecology. Since
95   such high threshold values do not reflect oxygen-dependent changes in the nitrogen
96   cycle, it is suggested to subdivide hypoxia into microbial hypoxia and functional
97   anoxia (Fig. 2). Functional anoxia was defined already in other works (Canfield et al.,
98   2019; Thamdrup et al., 2012) and covers oxygen levels below which denitrification
99   dominates the nitrogen cycle. Microbial hypoxia is suggested here as the range at
100   which decreasing oxygen levels progressively offset the oxygen-inhibition of
101   denitrification. Since this starts with the occurrence of anammox, we consider 20 µM
102   as the upper threshold of microbial hypoxia whereas anoxia (zero oxygen) terminates
103   hypoxia and therewith also functional anoxia and microbial hypoxia. Because oxygen
104   detection limits of classical Winkler titration (~1 µM), seabird sensors (~0.09 µM) and
105   the newly developed switchable trace oxygen sensors (STOX, ~0.01 µM) are too
106   high to prove anoxia (Thamdrup et al., 2012; Ulloa et al., 2012) the appearance of
107   hydrogen sulfide is generally considered as an indicator of anoxia.
108   Based on data obtained from the World Ocean Atlas, the total volume of waters
109   characterized by oxygen concentrations < 20 µM in the global ocean is
110   approximately 15 x 10^{15} m^3, of which 21% (3.13 x 10^{15} m^3) is located in the northern

111 Indian Ocean (Fig. 3c, Acharya et al., 2016; Garcia et al., 2010). The largest
112 proportion of this oxygen-poor water body is in the Arabian Sea ($2.5 \times 10^{15}\,m^3$) and
113 only a small fraction in the Bay of Bengal ($0.6 \times 10^{15}\,m^3$). In comparison to the Bay of
114 Bengal OMZ, with a mean concentration of dissolved oxygen of 14.51 ± 4 µM, the
115 Arabian Sea OMZ is more intense, as indicated by mean concentration of dissolved
116 oxygen of 10.45 ± 3 µM (Acharya & Panigrahi, 2016). Notably, in regions where
117 these OMZs impinge on continental margins, sediments and benthic communities
118 are exposed to semi-permanent bottom-water hypoxia. The Arabian Sea and the Bay
119 of Bengal together are currently home to ~59% of the Earth's marine sediments
120 exposed to hypoxia (Helly et al., 2004).

121 Denitrification, within sediments (benthic denitrification) and under hypoxic conditions
122 in the water column, is by far the largest sink of nitrate in the ocean (Gruber, 2004).
123 Estimates of benthic and water column denitrification rates are still fraught with large
124 uncertainties on global as well as on regional scales. Global scale estimates of
125 benthic and water-column denitrification range between 65 and 300 Tg N year^{-1} and
126 39 and 270 Tg N year^{-1}, respectively (Eugster et al., 2012; Gruber, 2004; Somes et
127 al., 2013). Although denitrification in the Arabian Sea has been much more
128 intensively studied than in the Bay of Bengal, estimates of benthic (1 to 6.8 Tg N
129 year^{-1}) and water column (1 to 33 Tg N year^{-1}) denitrification in the Arabian still reveal
130 a wide range (Bange et al., 2000; Bristow et al., 2017; Deuser et al., 1978; Gaye et
131 al., 2013; Howell et al., 1997; Naqvi et al., 1982; Somasundar et al., 1990).
132 However, these estimates imply that on average the Arabian Sea contributes
133 approximately 2 % and 11 % to the global mean benthic and water column
134 denitrification, respectively, although published data indicate that the estimated
135 benthic denitrification rates might be too low. According to these more recent data,
136 the benthic denitrification at the Pakistan continental margin amounts to up to 10.5
137 Tg N year^{-1} (Schwartz et al., 2009; Somes et al., 2013), which exceeds the former
138 budget (6.8 Tg N year^{-1}) of the entire Arabian Sea sediments (Bange et al., 2000). In
139 line with a severe depletion of nitrate in bottom waters on the Indian shelf (Naqvi et
140 al., 2010) this implies that benthic denitrification rates contribute > 2% to the global
141 mean benthic denitrification rate. This further emphasizes the role of the northern
142 Indian Ocean OMZ for the marine nitrogen cycle, which was considered as one of
143 the least understood OMZs in the world's ocean (Schmidt et al., 2020; Segschneider
144 et al., 2018). The aim of this paper is to provide a short background on the
145 development of OMZs and recent trends in the OMZs of the Indian Ocean as well as
146 to discuss biological and physical drivers, the past and future development, and

ecosystem responses to changes in the intensity of OMZs in the northern Indian Ocean.

2. Background

2.1 Oxygen Minimum Zones

The first large ocean-going oceanographic expeditions discovered OMZs in the Pacific, Atlantic, and Indian Ocean 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 the consumption of oxygen during the respiration of organic matter exported from the sunlit surface ocean and a sluggish horizontal renewal of water within the OMZ (Dietrich, 1936; Seiwell, 1937). Due to the main respiration depth of exported organic matter, OMZs mostly develop at water-depths between approximately 100 and 1000 m (Suess, 1980) and oxygen concentrations within OMZs generally decrease with an increasing age of the water mass within the OMZ (Karstensen et al., 2008).

Sverdrup (1938) presented the first OMZ-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 in surface waters. 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). Accordingly, Broecker and Peng (1982) introduced a model in which upwelling of oxygen-enriched deep water at the lower boundary and vertical mixing at the upper boundary serve to ventilate the OMZ, whereas the respiration of exported organic matter decreases oxygen concentrations.

More recent studies emphasize the influence of mesoscale eddies on the development of OMZ (e.g. Chelton et al., 2011; Fassbender et al., 2018; Lachkar et al., 2016; Oschlies et al., 1998; Resplandy et al., 2019). Mesoscale eddies emerge from baroclinic and barotropic instabilities related to the shear of horizontal currents and affect the vertical and lateral transport of water. This results in a patchiness of environmental conditions with complex and non-linear impacts on the OMZ (Fassbender et al., 2018; McGillicuddy, 2016). For instance, upward movements of water can increase the biological oxygen consumption by increasing nutrient inputs into the surface waters and thereby the biological production. Vice versa, downward water movements could lower the biological production (Gruber et al., 2011) and increase oxygen concentrations in the OMZ additionally by increasing the supply of

oxygen-enriched surface waters into the OMZ. 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 (Gnanadesikan et al., 2013; Gnanadesikan et al., 2012). In the eastern tropical Atlantic and Pacific Ocean, recent work has highlighted the role of eddies in enhancing ocean mixing in regions of sluggish large scale circulation, thus contributing to the ventilation of OMZs located there (Bettencourt et al., 2015; Brandt et al., 2015; Gnanadesikan et al., 2013). In this context, long-term changes in oxygen concentrations have been linked 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 has contributed to a reduction in the ventilation of the OMZ located in the tropical north Atlantic. Eddy trapping in turn maintains properties of the trapped fluid over relatively long time periods. This favors the development of localized OMZs, which propagate laterally along with eddies as seen e.g. in the open North Atlantic Ocean and off Peru in the Pacific Ocean (Bourbonnais et al., 2015; d'Ovidio et al., 2013; Fiedler et al., 2016; Karstensen et al., 2017; Schütte et al., 2016).

2.2 Spatial and temporal variability of the Arabian Sea OMZ

In the Atlantic and Pacific Oceans, hypoxic OMZs are associated with highly productive major eastern boundary current upwelling systems. In the Indian Ocean, the geographic setting prevents the development of such an upwelling system. However, a major monsoon-driven upwelling system emerges in the western Arabian Sea off the Arabian Peninsula and a smaller one develops along the Indian southwest coast during the northern hemispheric summer (Fig. 3a). Initially described by Schott (1935), the upwelling system in the western Arabian Sea was subject to intense studies including the International Indian Ocean Expedition (IIOE) between 1959 and 1965 and the Joint Global Ocean Flux Study (JGOFS) 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). However, contrary to expectations, the OMZ is most intense in the central and eastern Arabian Sea and not in the western Arabian Sea where the productivity is highest (Fig. 3c, Antoine et al., 1996; Naqvi, 1991). The offshore advetion of upwelling–driven blooms, which increases the organic carbon export into the central Arabian Sea (Rixen et al., 2006) contribute to this eastward displacement of the OMZ but monsoon-driven and seasonally varying physical oxygen supply mechanisms are assumed to be the main processes causing it.

220 Numerical model studies have shown that, on an annual timescale, mesoscale
221 eddies and filaments dominate the vertical supply of oxygen to the OMZ and the
222 lateral transport of ventilated waters into the central and northern Arabian Sea
223 (Resplandy et al., 2012; Resplandy et al., 2011). In line with these numerical model
224 studies and previous field work (Rixen et al., 2005; Sen Gupta et al., 1984; Swallow,
225 1984) McCreary et al (2013) also highlighted the important role of vertical eddy
226 mixing in the ventilation of the western Arabian Sea in addition to the inflow of
227 oxygen-enriched Indian Ocean Central Water (ICW).

228 The ICW originates from convective mixing as Subantarctic Mode Water (SAMW) in
229 the southern Indian Ocean (McCartney, 1977; Sverdrup et al., 1942). It enters the
230 western Arabian Sea along with Timor Sea Water and the Subtropical Subsurface
231 Water via the Somali Current (Schott et al., 2001; Stramma et al., 1996; You, 1997).
232 To lesser extent, it is also carried into the eastern Arabian Sea along with an
233 undercurrent, which compensates the poleward flowing West Indian Coastal Current
234 (WICC, Fig. 4a, Schmidt et al., 2020; Shenoy et al., 2020; Shetye et al., 1990). Due
235 to the much stronger inflow of ICW in the western Arabian Sea, the OMZ retreats
236 eastwards in summer (Rixen et al., 2014). In winter the OMZ expands westwards
237 due to weaker inflow of ICW and the seasonal reversal of the surface ocean
238 circulation - anticlockwise during the winter monsoon and clockwise during summer
239 monsoon.

240 Data compiled by Acharya and Panigrahi (2016) indicate the response of the OMZ to
241 the monsoon-driven seasonality in the Arabian Sea in more detail. These authors
242 analyzed the Word Ocean Atlas 2013 (WOA13) and data obtained from the Global
243 Ocean Data Analysis Project. Thereby, they took methodical biases into account,
244 corrected the WOA13 data, and applied a 20 µM threshold to define the OMZ. Based
245 on the corrected data set, these authors determined the areal extension and
246 maximum thickness of the OMZ and calculated the mean oxygen concentration
247 within the OMZ. According to their data, the OMZ has its lowest areal extension in
248 summer (Fig. 5a) due to the inflow of ICW. However, since the shrinking horizontal
249 extension of the OMZ is associated with a thickening, the OMZ also has its largest
250 volume in summer, which in turn is accompanied by the lowest concentration of
251 oxygen within the OMZ (Fig. 5b). The summer thickening of the OMZ is favored by
252 the negative wind stress curl and the associated downwelling in the central Arabian
253 Sea (Brock et al., 1991; Rao et al., 1989), and is coincident with the confluence of
254 ICW that enters the Arabian Sea in the west and east as mentioned before. The low
255 oxygen concentrations reflect in turn impacts of the enhanced upwelling-driven
256 productivity and the associated increased oxygen consumption in the OMZ, which

257   apparently exceeds the increased physical oxygen supply via eddy stirring and the

258   inflow of ICW.

259   In order to test whether the monsoon controls the intensity of the OMZ via its impact

260   on the biological production, satellite-derived primary production values were

261   obtained from ocean primary production website

262   (http://www.science.oregonstate.edu/ocean.productivity/). The data cover the period

263   between 2002 and 2019 and were averaged seasonally for the Arabian Sea north of

264   10°. In general, the obtained mean primary production rates were inversely linked to

265   the OMZ oxygen concentrations (Fig. 6a), which supports the hypothesis that

266   monsoon-driven changes in the biological carbon production and export exert a

267   strong control on the intensity of the OMZ on a seasonal time scale.However, the

268   autumn season appears to be an exception. During this season the OMZ oxygen

269   concentrations were lower than expected from the low primary production rate,

270   indicating an even lower physical oxygen supply. One explanation could be the

271   strongly reduced inflow of ICW in combination with a low air-sea oxygen supply in

272   response to the warming and the resulting enhanced stratification of surface waters

273   after the upwelling season.

274

275   **2.3 The Bay of Bengal OMZ**

276   Similar to the Arabian Sea, upwelling-favorable winds also occur in the Bay of Bengal

277   during the summer monsoon (Hood et al., 2017; Shetye et al., 1988). However, the

278   productivity in the Bay of Bengal is lower than in the Arabian Sea and shows only a

279   weakly pronounced seasonality (Fig. 3a,b). Nevertheless, sediment trap studies have

280   shown that, despite a lower productivity, organic carbon fluxes into the deep Bay of

281   Bengal are almost as high as those in the central and eastern Arabian Sea, due to a

282   ballast effect associated with high loadings of lithogenic mineral material (Rao et al.,

283   1994; Rixen et al., 2019b). Ballast minerals, supplied from land via rivers or as dust,

284   protect organic matter against bacterial attacks by adsorbing organic molecules to

285   atomic lattices (Armstrong et al., 2002) and accelerate the sinking speed of particles

286   (Haake et al., 1990; Hamm, 2002; Ramaswamy et al., 1991). Enhanced sinking

287   speeds reduce respiration in shallower waters and thereby increase the flux of

288   organic matter to deeper waters (Banse, 1990; Ittekkot, 1993). A stronger ballast

289   effect, in addition to the lower primary production, was assumed to lower the oxygen

290   consumption in the Bay of Bengal in comparison to that in the Arabian Sea OMZ (Al

291   Azhar et al., 2017; Rao et al., 1994). High freshwater fluxes largely cause the lower

292   oxygen consumption in the Bay of Bengal and also reduce the physical oxygen

293   supply.

In addition to their role as supplier of ballast minerals, high freshwater fluxes from river runoff, but also from precipitation, form a buoyant low-salinity surface layer that isolates nutrient-enriched subsurface water and increases stratification (Kumar et al., 1996). The increased stratification weakens vertical mixing as well as upwelling and thereby the biological productivity and the physical oxygen supply. Furthermore, in addition to the reduced vertical oxygen supply, the inflow of oxygen-poor Arabian Sea Water also lowers the lateral oxygen supply into the Bay of Bengal OMZ. The inflow of Arabian Sea Water into the Bay of Bengal is marked by a broad salinity maximum that occurs below the low-salinity surface layer, to a water depth of approximately 1000 m (Rao et al., 1994 and references thereine).

The influence of eddies on the OMZ has been studied (Kumar et al., 2007; Prasanna Kumar et al., 2004; 2018a; Singh et al., 2015) but due to the pronounced interannual variability (Chen et al., 2012; Johnson et al., 2019) and the eddies non-linear behavior, impacts of eddies on the Bay of Bengal OMZ are difficult to quantify. For instance, Sarma and Baskhar (2018b) focused on anticyclonic eddies sampled by bio-Argo floats between 2012 and 2016 in the Bay of Bengal and showed that anticyclonic eddies are formed on the eastern side of the basin and propagate westward. They ventilate the layer between 150 and 300 m and weaken the OMZ. Such episodic injection of oxygen could be a mechanism that enhances the oxygen supply by reducing impacts of the strong stratification on vertical mixing. On the other hand, Sarma et al (2018a) showed that while anticyclonic eddies supply oxygen to the subsurface layer and hence weaken the OMZ, cyclonic eddies inject nutrients into the euphotic zone and thus enhance productivity and oxygen consumption at depth.

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

Today, the balance between physical oxygen supply and biological oxygen consumption is disturbed as indicated by the expansion of hypoxia, which is an increasingly common feature in coastal waters (Altieri et al., 2017; Diaz et al., 2008). It is called the "spreading of dead zones" because their occurrence is often associated with mass mortality of fish and invertebrates (e.g. Weeks et al., 2002). Eutrophication and global warming mainly cause the spreading of dead zones by enhancing the production of organic matter and decreasing the oxygen supply due to a reduced solubility of oxygen in warmer surface waters. Since decreasing concentrations of dissolved oxygen have also been widely observed in the open ocean (i.e. beyond coastal systems) during the last 50 years, deoxygenation of the ocean is considered as one of the main threats to pelagic ecosystems (Breitburg et

331 al., 2018; Keeling et al., 2009; Schmidtko et al., 2017; Stramma et al., 2010a;
332 Stramma et al., 2008; Stramma et al., 2010b).

333 However, there are indications that the Arabian Sea and apparently also the Bay of
334 Bengal OMZ was more intense in the recent past, i.e. prior to the Indian Ocean
335 Expedition (IIOE, 1959 - 1965), than thereafter. For instance, Carruthers et al (1959)
336 described mass mortality of fish along the Arabian and Indian coast as well as in the
337 central Arabian Sea at around 62.5°E and 9 °N and identified oxygen depletion as
338 the most likely trigger (Carruthers et al., 1959). This view was supported by a report
339 on the occurrence of hydrogen sulfide from the north-eastern Arabian Sea and off
340 Oman at Ras-al-Hadd (Ivanenkov et al., 1961). Furthermore, hydrogen sulfide was
341 also detected in the north-western Bay of Bengal (Ivanenkov & Rozanov, 1961).,
342 These were the only reports on the occurrence of hydrogen sulfide in northern Indian
343 Ocean until Naqvi et al. (2000) discovered an anoxic event that developed along the
344 western Indian coast off Mumbai in the late summer of 1999. Such strong events do
345 not evolve every year (Gupta et al., 2016; Sudheesh et al., 2016), but their
346 appearance shows that the spreading of 'dead zones' in coastal regions does not
347 spare the Indian shelf (Altieri et al., 2017; Diaz & Rosenberg, 2008; Diaz et al.,
348 2019).

349 In contrast to these shelf processes, global, observation based syntheses of OMZs
350 (beyond continental shelves) reveal only a weak decrease of dissolved oxygen
351 concentrations in the OMZs of the Arabian Sea and the Bay of Bengal in comparison
352 to OMZs of the South Atlantic Ocean and the Pacific Ocean (Ito et al., 2017; Naqvi,
353 2019; Schmidtko et al., 2017; Stramma et al., 2008). The detailed analysis of all
354 oxygen data available from the central Arabian Sea by Banse et al. (2014) ascribes
355 this to opposing regional trends within the Arabian Sea. The authors analyzed
356 oxygen data, which were measured between 1959 and 2004 in the Arabian Sea and
357 in the depth range between 100 and 500 m. Biases caused by different analytical
358 procedures were taken into account and oxygen data were compiled for sub-regions
359 within the Arabian Sea. The results showed that oxygen concentrations increased in
360 the southern part of the Arabian Sea and declined in the central Arabian Sea. Follow-
361 up studies also reported decreasing oxygen concentrations in the western and
362 northern Arabian Sea (Piontkovski et al., 2015; Queste et al., 2018). In the northern
363 Arabian Sea, dissolved oxygen concentrations in the surface mixed layer largely
364 reflect the trend seen in the OMZ, as indicated by a compilation of dissolved oxygen
365 data covering the period from the 1960s to 2010 (Gomes et al., 2014).

366 Since STOX data for the Arabian Sea were unavailable prior to 2007, the data
367 compiled by Banse et al. (2014) do not resolve any changes in the oxygen

368 concentrations below 0.09 µM (Fig. 2). Such low oxygen concentrations have

369 recently been measured in the Arabian Sea and in the Bay of Bengal as well as in

370 OMZ of the eastern Pacific Ocean (Bristow et al., 2017; Jensen et al., 2011;

371 Thamdrup et al., 2012). In the latter study, it was shown that nitrite accumulates in

372 the water column at oxygen concentrations of < 0.05 µM. In the Arabian Sea OMZ,

373 the accumulation of nitrite was first described during the John Murray expedition of

374 1933 - 34 (Gilson, 1937). It is called the secondary nitrite maximum (SNM) and

375 assumed to indicate active denitrification (Naqvi, 1991). The role of the SNM as

376 indicator of active denitrification is further supported by profiles of stable isotope

377 ratios of nitrogen in nitrate ($\delta^{15}N_{NO3}$) and nitrate (NO_3^-) concentration profiles (Fig. 7,

378 Gaye et al., 2013; Rixen et al., 2014). Since denitrification increases $\delta^{15}N_{NO3}$ in the

379 water column due to the preferential uptake of the lighter $^{14}NO_3^-$ (Cline et al., 1975;

380 Mariotti et al., 1981), low nitrate concentrations correspond to high $\delta^{15}N_{NO3}$ within the

381 SNM. Assuming a similar response of the nitrogen cycle to low oxygen concentration

382 in the Arabian Sea as in the eastern Pacific Ocean suggests that the Arabian Sea

383 SNM is characterized by oxygen concentrations of about ~0.05 µM, and in turn that

384 denitrification dominates the nitrogen cycle at such low oxygen concentrations.

385 Nevertheless, an isotope tracer study indicated that the re-oxidation of nitrite to

386 nitrate reduced the formation of N_2 by 50 to 60% (Gaye et al., 2013), which implies

387 an active competition between aerobic and anaerobic processes even at such low

388 oxygen concentrations. However, since anaerobic denitrification dominates the

389 competition, as indicated by the accumulation of nitrite, the depletion of nitrate and

390 the $\delta^{15}N_{NO3}$ maxima, an oxygen concentration of ~0.05 µM is seen as a threshold

391 below which functional anoxia occurs (Fig. 2).

392 Naqvi (1991) was the first to use the SNM to map the spatial extent of functional

393 anoxia in the Arabian Sea. His analysis was based on data obtained during the

394 International Indian Ocean Expeditions between 1959 and 1965 and cruises

395 thereafter but did not include data from Ivanenkov and Rozanov (1961) and JGOFS.

396 The data of Ivanenkov and Rozanov (1961) indicate a more intense OMZ, including

397 the occurrence of hydrogen sulfide as mentioned earlier and a larger extent of the

398 SNM than calculated by Naqvi (1991), although there are doubts regarding the

399 reliability of the older data (Sen Gupta & Naqvi, 1984). Comparison of JGOFS data,

400 collected in 1994/95, with those compiled by Naqvi (1991), shows that the SNM has

401 expanded south- and westwards (Rixen et al., 2014). This implies, in accordance

402 with decreasing oxygen concentrations, an expansion of the OMZ in the Arabian

403 Sea, which might have started in the early 1990s. However, the reliability of this trend

404 has been questioned by Naqvi (2019). While it is acknowledged that the data are too

405 sparse to have unquestionable confidence in this trend, it is difficult to assess the
406 doubts raised by Naqvi (2019), as these are based on data derived from sediment
407 cores that do not cover the most recent past.

408 In the Bay of Bengal, a pronounced SNM has not yet been detected, although a
409 recent study presented data from 7 stations in the northern Bay of Bengal and
410 revealed oxygen concentrations which partly drop below 0.05 ~µM at four sites
411 (Bristow et al., 2017). Incubation experiments were carried but with, one exception,
412 these failed to prove denitrification. At the one exceptional station, a denitrification
413 rate of 0.9 nmol L^{-1} day^{-1} was measured, which falls much below denitrification rates
414 of > 20 nmol L^{-1} day^{-1} as measured by Ward et al. (2009) in the Arabian Sea.
415 However, these results indicate that the Bay of Bengal OMZ is on the verge of
416 functional anoxia, with re-oxidation of nitrite to nitrate as yet preventing significant
417 denitrification (Bristow et al., 2017). However, outbreaks of hydrogen sulfide as seen
418 in the upwelling systems off Peru (Schunck et al., 2013) and Namibia (Weeks et al.,
419 2002) have so far not been reported in the northern Indian Ocean during the last 50
420 years, other than in bottom waters on the Indian shelf as mentioned earlier. This
421 implies that the physical oxygen supply and the biological oxygen consumption
422 maintained hypoxic conditions and prevented persistent anoxia in the Arabian Sea
423 and functional anoxia in the Bay of Bengal OMZ.

424 **3. The role of biological and physical drivers for the OMZ development**

425 Maintenance of functional anoxia in the Arabian Sea OMZ with oxygen
426 concentrations ranging between > 0 and ~0.05 µM is highly extraordinary considering
427 that the monsoon-driven seasonality reverses the surface ocean currents and turns
428 the Arabian Sea from an oligotrophic oceanic desert into one of the most productive
429 regions in the world's ocean within weeks. This, on the one hand, suggests that there
430 are feedback mechanisms counteracting impacts of the monsoon on the intensity of
431 the OMZ. On the other hand, the recent expansion of the OMZ in the Arabian Sea,
432 and the first indication of denitrification in the Bay of Bengal OMZ, indicate that there
433 are also processes overriding effects of these feedback mechanisms.

434

435 **3.1 Biological feedback mechanism**

436 Based on the growing evidence that low concentrations of dissolved oxygen slow
437 down the respiration of organic matter in the water column and thereby the biological
438 oxygen consumption (Aumont et al., 2015; Cavan et al., 2017; Laufkötter et al., 2017;
439 Thamdrup et al., 2012; Van Mooy et al., 2002), it has been hypothesized that an
440 oxygen–related feedback mechanism stabilizes the Arabian Sea OMZ (Rixen et al.,

441 2019a). This mechanism operates in the upper part of the OMZ, which hosts the
442 seasonal thermocline but also affects the base of the OMZ and thereby its thickness
443 as discussed before (Fig. 8).

444 The seasonal thermocline is the subsurface layer from which water is introduced into
445 the euphotic zone via physical processes such as upwelling, vertical mixing and
446 eddy-driven transports on a seasonal timescale. Nutrients supplied by these
447 mechanisms largely sustain the productivity of pelagic ecosystems and the
448 associated export production (Eppley et al., 1979). Hence, the seasonal thermocline
449 is the main nutrient reservoir of pelagic ecosystems, and to fulfill this role the vast
450 majority of the exported organic matter must be respired within the seasonal
451 thermocline. Accordingly, the seasonal thermocline represents the main zone of
452 respiration and, similar to soils on land, accommodates the nutrient recycling
453 machinery of the pelagic ecosystem. Nutrient losses from the seasonal thermocline,
454 via particle fluxes into the deep sea, denitrification, and lateral advection, must be
455 compensated by nutrient inputs in order to maintain the productivity (Rixen et al.,
456 2019a). Nitrogen fixation, river discharges, and atmospheric deposition can be
457 important nutrient sources, but in the Arabian Sea lateral inflow of water masses from
458 the south via the cross-equatorial cell are the main source balancing nutrient losses
459 from the seasonal thermocline (Bange et al., 2000; Gaye et al., 2013). Accordingly, a
460 significant negative impact of denitrification on primary and export production and the
461 associated oxygen consumption appear to be unlikely on seasonal to centennial time
462 scales in the Arabian Sea.

463 The SNM, which occurs at water depths between 200 and 400 m in the central
464 Arabian Sea and as deep as 500 m in the eastern Arabian Sea, divides the seasonal
465 thermocline into an aerobic part at water depths between ~40 and 200 m and an
466 anaerobic part down to the base of the SNM (Fig. 8). The depth of the seasonal
467 thermocline of approximately 300 – 400 m corresponds to the depth range of
468 vertically migrating zooplankton as observed during the large summer bloom in the
469 Arabian Sea (Smith, 2001), and roughly matches the water depth range from where
470 subsurface water is introduced via upwelling into the euphotic zone in the western
471 Arabian Sea (Brock et al., 1992; Rixen et al., 2000). Furthermore, nitrate
472 concentrations, which decrease within the SNM, remain above 10 µM (Fig. 7),
473 suggesting that supply of decomposable organic matter (rather than nitrate
474 availability) limits denitrification, as also suggested by other studies (Bristow et al.,
475 2016; Ward et al., 2009). A substrate limitation at a water depth of 400 to 500 m, and
476 the arrival of organic matter at sediment traps deployed in the deep sea at a water
477 depth of 3000 m, support the concept of export production that is divided between

free (reactive) and protected (low reactivity) 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 within the seasonal thermocline. If decreasing oxygen concentrations reduce the respiration of free organic matter, this prevents a further depletion of oxygen and the development of anoxia by reducing the oxygen consumption within the seasonal thermocline. Consequences are an increasing export of free organic matter out of the seasonal thermocline, which could enhance the oxygen consumption at the base of the OMZ. This would imply that low oxygen concentrations within the OMZ are accompanied by a thickening of the OMZ, which can be seen on a seasonal time scale by the negative correlation between mean OMZ oxygen concentrations and the maximum thickness of the OMZ (Fig. 6b).

3.2 Biological oxygen consumption

The role of an oxygen-dependent, biologically driven feedback mechanism, counteracting impacts of the monsoon on the intensity of the OMZ, depends on the local oxygen consumption. If this is too low, remote processes instead of the local monsoon-driven carbon export rates need to be considered as forces controlling the intensity of the OMZ. The apparent oxygen utilization (AOU), in addition to mixing analyses, provides information that helps to estimate the role of the local oxygen consumption for maintaining the intensity of the OMZ in the Arabian Sea. The AOU represents the oxygen deficit caused by biological oxygen consumption and is calculated by subtracting the measured oxygen concentration from the temperature- and salinity-dependent oxygen saturation concentration. This approach is based on the assumption that the water mass of interest was saturated with respect to oxygen during its formation at the surface and, since then, the respiration of exported organic matter consumed oxygen within the water mass.

A mixing analysis based on data measured during JGOFS in 1994/95 reveals that oxygen-deficits inherited from ICW contribute approximately 25% to the AOU determined in the Arabian Sea OMZ (Rixen & Ittekkot, 2005). Accordingly, the respiration of organic matter produced in the Arabian Sea largely causes the low oxygen concentration in the Arabian Sea OMZ, which emphasizes the role of the monsoon-driven productivity in the Arabian Sea and the oxygen-dependent biologically driven feedback mechanism as local drivers for the OMZ development. However, it should be noted that in the Arabian Sea, mean satellite-derived export production rates were too low to explain a high biological oxygen consumption

515 considering a residence time of water within the OMZ of 10 years (Rixen & Ittekkot,
516 2005). The mismatch reflects uncertainties caused by the poorly constrained
517 residence time of water within the OMZ and export production rates. Even though
518 residence times of water within the Arabian Sea and Bay of Bengal OMZ of 10 and
519 12 years seems to be well accepted (Bristow et al., 2017; Olson et al., 1993), there
520 are also estimates ranging from 1 to 51 years for the Arabian Sea OMZ (Naqvi et al.,
521 1993; Sen Gupta & Naqvi, 1984). In the Arabian Sea, satellite-derived export
522 production rates vary by a factor of 10 (Rixen et al., 2019b) and an even larger
523 variability can be seen on a global scale. Global export production rates derived from
524 satellite-data, numerical models, extrapolated from sediment trap data and based on
525 estimates of the biological oxygen demand vary approximately between 1.8 and 27.5
526 Pg C yr^{-1}. In general estimates based on the biological oxygen demand, in line with
527 inverse modeling studies, call for higher export production rates (Burd et al., 2010;
528 del Giorgio et al., 2002; Schlitzer, 2000; Schlitzer, 2002), whereas satellite and
529 sediment trap data, as well as numerical model studies, suggest lower export
530 production rates (Emerson, 2014). Nevertheless, considering estimates within the
531 upper range (higher carbon export and longer residence times of water in the OMZ),
532 the AOU determined in the Arabian Sea could be explained (Rixen & Ittekkot, 2005).
533

534 **3.3 Physical oxygen supply mechanisms as driver of OMZ changes**
535 The OMZs in the northern Indian Ocean are melting pots collecting the influence of a
536 variety of water masses with different origins and histories (e.g. Morcos et al., 2012;
537 Schott & McCreary, 2001; You, 1997). Mixing analyses indicate that the Arabian Sea
538 OMZ contains in addition to ICW also Arabian Sea Water (ASW) as well as Persian
539 Gulf and Red Sea Water (Acharya & Panigrahi, 2016; Hupe et al., 2000; Rixen &
540 Ittekkot, 2005). The Persian Gulf Water (PGW) is a dense and oxygen-rich surface
541 water that subducts in the northern Arabian Sea and strongly contributes to the
542 ventilation of the upper OMZ (Lachkar et al., 2019; Schmidt et al., 2020). Regional
543 model simulations have shown that eddies control the transport and the spreading of
544 the PGW into the Gulf of Oman (Lachkar et al., 2019; Queste et al., 2018; Vic et al.,
545 2015). Projected future warming of the Persian Gulf can, in turn, lower the oxygen
546 concentrations of the PGW and its sinking in the Gulf of Oman. Consequences are a
547 drop of oxygen concentrations at depths between 200 and 300 m in the northern
548 Arabian Sea (Lachkar et al., 2019). Such a reduced physical oxygen supply could
549 explain the observed intensification of the Arabian Sea OMZ and the expansion of
550 the SNM (see above). Furthermore, it implies that global warming impacts on the
551 physical oxygen supply override effects of the biologically driven feedback

554

555 3.4 Implications

556 Understanding the processes controlling oxygen consumption within OMZs, such as

557 export production and the residence time of water, is still fraught with large

558 uncertainties. Nevertheless, it seems that there are oxygen-dependent, biologically

559 driven feedback mechanisms counteracting impacts of the monsoon on the intensity

560 of the OMZ. This could explain the absence of persistent anoxia and functional

561 anoxia in the Arabian Sea and Bay of Bengal OMZs. However, the recent expansion

562 of the OMZ in the Arabian Sea, and the first indication of denitrification in the Bay of

563 Bengal OMZ, indicate that there are other processes overriding effects of these

564 feedback mechanisms. The postulated decrease in the physical oxygen supply

565 caused by the inflow of warmer and hence more oxygen-depleted PGW agrees with

566 the observed decreasing oxygen concentrations and expansion of the SNM in the

567 Arabian Sea. In the Bay of Bengal, a response to global warming is more difficult to

568 establish due to strong interannual variations in the intensity of the eddy activity. The

569 fact that eddies affect both the supply of oxygen (through ventilation) and its

570 consumption (through biological productivity) in a non-trivial manner increases the

571 difficulties to adequately parameterize the effects of eddies on dissolved oxygen in

572 coarse resolution models.

573 4. Holocene records

574 4.1. Sediment δ^{15}N records of OMZ strength

575 On millennial and even longer timescales, sedimentary records have been used to

576 trace changes in OMZ intensities. The δ^{15}N values of particulate nitrogen in

577 sediments are often used as tracers of OMZ intensity because they reflect major

578 shifts in the pool of fixed nitrogen due to denitrification, as discussed before (Altabet

579 et al., 1995; Altabet et al., 1999; Brandes et al., 1998; Ganeshram et al., 1995).

580 Locally, eolian and riverine nitrogen supply affect δ^{15}N values (Kendall et al., 2007;

581 Voss et al., 2006), but in the Indian Ocean sedimentary records of δ^{15}N reflects the

582 balance between denitrification vs. nitrogen fixation. Deep water nitrate has an

583 average δ^{15}N value of ~5‰ (Sigman et al., 2005) but, due to denitrification, the δ^{15}N

584 of nitrate in the Arabian Sea increases to values > 17 ‰ (Fig. 7). Convective mixing,

585 eddy pumping, and especially upwelling, move nitrate-deficient water masses from

586 the OMZ to the surface, so that nitrate with high δ^{15}N values is transported into the

587 euphotic zone. After assimilation into biomass by phytoplankton, ^{15}N-enriched

588 particulate matter sinks through the water column to the seafloor where the signal of
589 denitrification, and hence OMZ intensity, is preserved in sediments (Altabet et al.,
590 1995; Gaye-Haake et al., 2005; Naqvi et al., 1998; Suthhof et al., 2001). Early
591 diagenesis may raise sedimentary $\delta^{15}N$ values by 2 - 5 ‰, and the diagenetic effect
592 increases with water depth (Altabet, 2006; Tesdal et al., 2013). Nevertheless, the
593 relative changes of $\delta^{15}N$ in deep-sea sediments record variations in the OMZ
594 intensity while records from the continental slopes are subjected to negligible
595 diagenetic enrichments so that they retain the signal of the nitrogen source (Altabet
596 et al., 1999; Gaye et al., 2018).
597
598 **4.2. OMZ Fluctuations during the Holocene**
599 A sediment core from the northern Bay of Bengal (Contreras-Rosales et al., 2016)
600 indicates that the highest $\delta^{15}N$ values (and thus the lowest OMZ oxygen
601 concentrations) recorded in the core prevailed during the Holocene and the last
602 glacial maximum, with a $\delta^{15}N$ range between 4.4 and 5.0 ‰ (i.e., in the range of the
603 average value of deep ocean waters, see above). Therefore, denitrification in the
604 past 21,000 years can be ruled out in the Bay of Bengal from a paleoceanographic
605 perspective (Contreras-Rosales et al., 2016). The $\delta^{15}N$ values at the core top (4.6 ‰)
606 were similar to values in sediment trap materials (3.7 - 4.5 ‰), and were explained
607 by a mixture of nutrients or suspended matter from the Ganges-Brahmaputra-
608 Meghna river system with nitrate from subsurface water (Contreras-Rosales et al.,
609 2016; Gaye-Haake et al., 2005; Unger et al., 2006). Enhanced $\delta^{15}N$ values in the
610 early Holocene to 6000 years BP (BP = before present, where present means 1950)
611 coincide with a stronger monsoon and were attributed to enhanced supply of nitrate
612 from the subsurface, which has elevated $\delta^{15}N$ compared to the depleted values of the
613 riverine end-member (Sarkar et al., 2009). However, to our knowledge there is only
614 one published sediment record from the Bay of Bengal spanning the entire Holocene
615 (Contreras-Rosales et al., 2016) so that we know nothing about the spatial variability
616 within the basin.
617 In contrast to the Bay of Bengal, denitrification in the Arabian Sea has prevailed
618 during the warm interstadials of the Pleistocene and during the entire Holocene, as
619 can be discerned from sedimentary $\delta^{15}N$ values > 6 ‰, with maxima of > 11 ‰
620 (Agnihotri et al., 2003; Higginson et al., 2004; Kessarkar et al., 2018; Möbius et al.,
621 2011; Pichevin et al., 2007). Productivity increased with the onset of the Holocene as
622 the summer monsoon strengthened and monsoonal upwelling off Somalia and Oman
623 commenced and became a permanent feature of the Holocene Arabian Sea (Böning

624 et al., 2009; Gaye et al., 2018). A rise of δ^{15}N by at least 2 ‰ shows that an onset of
625 upwelling immediately strengthened the OMZ and led to denitrification across the
626 entire basin in the beginning of the Holocene (Böll et al., 2015; Gaye et al., 2018).
627 Furthermore, southward retreat of Antarctic Sea Ice is assumed to have reduced
628 ventilation of the Arabian Sea OMZ through its influences on the formation of the
629 oxygen-enriched ICW and associated meridional overturning circulation of the upper
630 Indian Ocean (Böning & Bard, 2009; Naidu et al., 2010). A decline in δ^{15}N by about 1
631 ‰ is found in the early Holocene until 6000 years BP in high-resolution sediment
632 cores from the western, northern and eastern Arabian Sea, and indicates that the
633 OMZ weakened and became less persistent during this period (Fig. 9a,b). More
634 vigorous upwelling, discernible from benthic foraminifera, may have led to a better
635 ventilation of the basin as it is associated with an increased inflow of ICW from the
636 south (Das et al., 2017). As discussed before, the inflow of ICW increases the
637 physical oxygen supply and, furthermore, reduces the residence time of OMZ waters
638 (Böning & Bard, 2009; Pichevin et al., 2007).

639 After 6000 years BP, increasing δ^{15}N values indicate a strengthening of the OMZ
640 across the entire basin (Fig. 9a,b). It is hypothesized that a weaker ventilation is
641 responsible for decreasing oxygen concentrations and that this could be due to
642 reduced inflow of ICW, as it was blocked by the enhanced inflow of PGW and RSW
643 since the sea level high stand at 6000 years BP (Pichevin et al., 2007). Furthermore,
644 a southward shift of the West Indian Coastal Current and the associated poleward
645 undercurrent lowered the inflow of ICW and thereby the ventilation of the OMZ in the
646 eastern Arabian Sea (Mahesh et al., 2014).

647

4.3 Holocene model simulations

649 In order to give an additional, model-based estimate of the OMZ evolution in the
650 Indian Ocean, transient model simulations over the Holocene were performed with
651 the global atmosphere-ocean Kiel Climate Model (KCM, Park et al., 2009) and the
652 marine biogeochemistry model PISCES (Aumont et al., 2003).

653 In a first step, KCM was forced with transient orbital parameters and greenhouse gas
654 concentrations from 9500 years BP to present. In a second step, the PISCES model
655 was forced with the ocean physical fields from the above KCM experiment in so-
656 called off-line mode. This model set-up comprised a ventilation age tracer of the
657 water masses (see Segschneider et al. (2018) for a more detailed description of the
658 model components and experiment set-up). While the oceanic 2° x 2° grid in this set-
659 up was refined to a meridional resolution of 0.5^o near the equator to allow a better

660 representation of equatorial waves, the long integrations (9500 model years) required
661 a coarse model resolution that is far from eddy resolving. The ballast scheme for the
662 export of POC also neglected the lithogenic ballast effect, which is important in the
663 Arabian Sea and Bay of Bengal as discussed before.

664 From these model experiments, temperature and oxygen fields have been analyzed
665 and compared to sedimentary records mainly in the Arabian Sea. Here the model
666 results were subdivided into areas corresponding to the binned sediment core
667 regions specified in Gaye et al (2018) (Fig. 9 a; North: 62°E-68°E, 20°N-25°N; East:
668 68°E-75°E, 13°N-20°N; West: 54°E-60°E, 15°N-20°N; South: 48°E-55°E, 7°N-12°N).
669 The simulated oxygen concentrations in the Arabian Sea are generally somewhat too
670 high at the surface due to a cold bias of the KCM, but the observed near-surface
671 gradients of oxygen concentrations are very well matched. However, in the deeper
672 layers the model overestimates oxygen concentrations (not shown, see
673 supplementary Figure A.1c in Segschneider et al. (2018)). As a result, simulated
674 oxygen concentrations in the model Arabian Sea are nowhere low enough for
675 denitrification to occur (denitrification sets in at 6 µM in the PISCES model, with a
676 transition phase to full denitrification at lower oxygen concentrations). Moreover, no
677 nitrogen isotopes are simulated in the current model version. Comparison to the δ^{15}N
678 data from the sediment cores is, therefore, restricted to a qualitative assessment.

679 The simulated oxygen concentrations (averaged between 200 m and 800 m depth)
680 show the lowest concentrations in the northern Arabian Sea (initially around 80 µM in
681 the early Holocene, yellow curve in Fig. 9c). The concentrations are 10 µM higher in
682 the western Arabian Sea (blue line), and a further 5 µM higher in the eastern Arabian
683 Sea (red line), while they are much higher in the southern Arabian Sea (starting at
684 155 µM, grey line). Oxygen concentrations are fairly constant over the first 2.5
685 thousand years, and then gradually decrease until the late Holocene. This decrease
686 is strongest in the northern Arabian Sea (-20 µM) and quite similar in the western and
687 eastern Arabian Sea (-10 µM). This is in qualitative agreement with the Holocene
688 trends of δ^{15}N data (Fig. 9b) that show highest δ^{15}N values (indicating strong
689 denitrification and thus low oxygen) for the shallow northern core, and lower δ^{15}N for
690 the western and eastern cores.

691 Simulated export production and water mass age in the Arabian Sea have been
692 discussed for an earlier model experiment with the same model set-up (but
693 accelerated forcing) by Gaye et al. (2018), and in more detail for the global OMZs
694 including the Indian Ocean for the model experiment analyzed here by Segschneider
695 et al. (2018). While simulated export production in the Arabian Sea is fairly constant
696 throughout the Holocene (Fig. 7 in Gaye et al. 2018), ventilation age is increasing

697 throughout the Holocene concurrent with decreasing oxygen concentrations (Fig. 15
698 in Segschneider et al., 2018). This implies that changes in the ocean circulation and
699 the associated inflow of oxygen-enriched ICW largely influenced the OMZ during the
700 Holocene after the onset of upwelling at the beginning of Holocene.
701

4.4 Implications
703 The δ^{15}N sedimentary records reveal the difference in the late Pleistocene and
704 Holocene history of denitrification in the Arabian Sea and Bay of Bengal. Oxygen
705 concentrations in the Bay of Bengal never declined below the threshold of
706 denitrification, whereas denitrification prevailed in the Arabian Sea during the warm
707 interstadials and the entire Holocene. A data-model comparison shows that the age
708 of the OMZ water mass increased after 6000 years BP in both basins (not shown for
709 BoB), coinciding with a strengthening of the OMZ and denitrification in the Arabian
710 Sea. Based on the model results of constant export production and increasing water
711 mass age, it is concluded that a reduced ventilation is responsible for decreasing
712 oxygen concentration. The similar temporal evolution of observed OMZ intensity and
713 modeled oxygen concentration in the Arabian Sea under orbital and greenhouse gas
714 forcing thus indicates that the mid- to late Holocene OMZ intensification may be
715 related to oceanic circulation rather than to local processes in the Northern Indian
716 Ocean. The progressive oxygen loss over the Holocene may thus be the result of
717 orbital and greenhouse gas forcing in a qualitatively similar way to the much stronger
718 variations simulated for LGM to mid-Holocene changes (Bopp et al. 2017).
719

5. Model projections

5.1 Global models
722 For future climate projections we rely on earth system models (ESM). Although these
723 models reproduce large-scale features and global OMZ trends, they suffer from
724 considerable mismatches between measured and model oxygen concentrations in
725 the ocean (Bopp et al., 2013; Cabré et al., 2015; Oschlies et al., 2018; Oschlies et
726 al., 2008). In comparison to observational data, they underestimate oxygen losses
727 significantly (e.g. Oschlies et al., 2018 and references therein), and simulated
728 volumes of OMZs differ considerably. Unresolved physical oxygen supply
729 mechanisms, poorly constrained biological oxygen consumption rates, and their
730 hardly known responses to global change, cause these uncertainties (e.g., Oschlies
731 et al., 2018; Segschneider et al., 2013). Furthermore, feedbacks caused by the

732 strong coupling of the marine oxygen and nitrogen cycles complicate long-term
733 predictions (Fu et al., 2018; Oschlies et al., 2019).
734 Especially in the Indian Ocean, global coupled biogeochemical ESMs struggle to
735 represent the OMZs (Fig. 10, Oschlies et al., 2008). In most ESMs the east – west
736 contrast between the Arabian Sea and Bay of Bengal is opposite to what
737 observations show, with most global models producing lower oxygen concentrations
738 in the Bay of Bengal than in the Arabian Sea. Furthermore, half of the models cannot
739 simulate hypoxic conditions in the Arabian Sea at all. A comparison of the thickness
740 of the hypoxic layer in the northern Indian Ocean shows a disagreement among all
741 models (Fig. 10). The maximum simulated volume (8.2 x 10^{15} m^3, CESM1-BGC) is
742 more than twice the hypoxic volume found from observations (3.1 x 10^{15} m^3,
743 WOA13). Moreover, this volume extends too far horizontally and does not cover the
744 thickness of the observed OMZ in the Arabian Sea (Fig.10).
745 To some degree, this problem may be attributed to the fact that ESMs are not tuned
746 for the northern Indian Ocean. In addition, global models generally have coarser
747 resolution to reduce computational costs, and thus are far from eddy resolving, as for
748 the KCM (results discussed in the previous section). Eddy transport is parameterized
749 in the ESMs, but these still fail to represent the OMZs in the northern Indian Ocean.
750 Even though the next generation of ESMs already targeted this problem, by providing
751 high-resolution options including mesoscale processes in models used in the
752 Coupled Model Intercomparison Project phase 6 (CMIP6), there are only moderate
753 improvements in subsurface oxygen representation (Kwiatkowski et al., 2020). The
754 CMIP6 models still tend to overestimate oxygen concentrations in the Arabian Sea
755 (Séférian et al., 2020).

756

757 **5.2 Future projections**
758 The poor representation of the OMZs of the northern Indian Ocean in ESMs reduces
759 the reliability of future projections of potential changes in the OMZs related to natural
760 and anthropogenic forcing, and thus their ecological impacts and possible feedbacks
761 to climate change. Global models suggest a general decline of oxygen for the entire
762 ocean, but there is no clear trend visible in the Indian Ocean (Oschlies et al., 2017).
763 However, an older set of ESMs analyzed in Cocco et al. (2013) suggests a future
764 decrease in oxygen in the subtropical Indian Ocean in the upper mixed layer, and a
765 small increase in the western tropical Indian Ocean. This increasing oxygen
766 concentration is also seen in response to climate change in the RCP8.5 and RCP2.6
767 scenarios of the Coupled Model Intercomparison Project phase 5 (CMIP5, Bopp et
768 al., 2013). Specifically, Bopp et al. (2013) showed that a decrease in productivity is

769   consistently simulated across all CMIP5 models and scenarios in the tropical Indian
770   Ocean and that, by 2100, all models project an increase in the volume of waters with
771   an oxygen concentration below 80 µM, relative to 1990–1999. This response is more
772   consistent than that of the previous generation of ESMs, i.e., changes varying from
773   −26 to +16% over 1870 to 2099 under the SRES-A2 scenario (Cocco et al., 2013).
774   However, for lower oxygen levels, there is less agreement among the CMIP5 models
775   and also compared to observations regarding the volume of the OMZ (Bopp et al.,
776   2013).   Specifically, for the volume of waters < 50 µM, four models project an
777   expansion of 2 to 16% (both GFDL-ESMs, HadGEM2-ES and CESM1-BGC),
778   whereas two other models project a slight contraction of 2% (NorESM1-ME and MPI-
779   ESM-MR). For the volume of waters with an oxygen concentration < 5 µM, only one
780   model (IPSL-CM5A-MR) is close to the volume estimated from observations, and
781   projects a large expansion of this volume (+30% in the 2090s). These results for low
782   oxygen waters (oxygen concentrations of 5 - 50 µM) agree with those of Cocco et al.
783   (2013), with large model–data and model–model discrepancies, and simulated
784   responses varying in sign for the evolution of these volumes under climate change
785   (Bopp et al., 2013).
786   Globally, the models agree on a negative oxygen trend over the 21st century driven
787   by declining solubility of oxygen in surface waters through global warming
788   (Resplandy, 2018; Schmidtko et al., 2017) and a reduced ventilation by changes in
789   the ocean's circulation (Bopp et al., 2017). This holds true even though these models
790   take into consideration the negative feedback caused by reduced tropical export
791   production due to increased stratification of the upper water column (Fu et al., 2018;
792   Palter et al., 2018). Uncertainties and disagreements among the models arise from
793   subtle differences in timing and magnitude of these opposing trends (Bopp et al.,
794   2017). Waters with low oxygen saturation are particularly sensitive to impacts of
795   climate warming (Fu et al., 2018) as well as vertical diffusivity that is parameterized
796   by the mixing coefficient in the models (Duteil et al., 2012) and also mesoscale eddy
797   transport and the lateral mixing coefficient (Bahl et al., 2019; Lachkar et al., 2016).
798   Globally, reduced mixing across the mixed layer explains 75% of the reduced
799   subduction, but regionally changes in wind patterns that cause modulations in Ekman
800   pumping and subduction are more important (Couespel et al., 2019). Thus, future
801   trends in the northern Indian Ocean OMZs derived from the ESMs are highly
802   uncertain, with projected potential increases or decreases in the volume of low
803   oxygen waters, depending on the model and the oxygen levels under consideration
804   (Bopp et al., 2013; Cocco et al., 2013).
805

5.3 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. As discussed before, regional eddy resolving modelling studies have been able to reproduce the OMZs and thus they have helped us to better 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). 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 and submesoscale 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 to poor representation of mesoscale and submesoscale features in global models, large uncertainties stem also from largely unknown biogeochemical and ecosystem responses to global physical changes.

6. Ecosystem responses

6.1 Benthic ecosystems

6.1.1 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. 11). 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).

841   Further, across the OMZ boundaries, clear "edge effects" have been observed; sharp
842   changes in community composition and faunal abundance linked to different oxygen
843   thresholds (e.g., Levin et al., 2009b). These have also been observed on other
844   hypoxia-impacted margins in the eastern Pacific and off SW Africa (e.g., Levin et al.,
845   1991), as well as in hypoxic basins such as the Baltic Sea, and at sites impacted by
846   excess organic matter input (e.g., Rosenberg, 2001). While there are some common
847   patterns, specific oxygen thresholds are difficult to constrain because of inter-margin
848   and inter-basin differences in faunal assemblages, which are also affected by local
849   differences in factors such as food availability and predator avoidance, as well as
850   inter-study differences in the availability and quality of bottom-water oxygen data.

851   **6.1.2 Benthic ecosystem function**
852   The strong but variable cross-OMZ gradients in bottom-water oxygen and benthic
853   communities translate to contrasts in benthic ecosystem function, which also varies
854   between margins. For example, the numbers, size and depth of faunal burrows, and
855   the extent of bioturbation and bio-irrigation, change across the OMZ boundaries
856   (e.g., Cowie et al., 2009a; Smith et al., 2000). In the extreme case, this leads to total
857   absence of bioturbation and bio-irrigation at the core of the OMZ off Pakistan, and
858   the resulting presence of annually laminated (varved) sediments, which are not
859   observed on the better-ventilated margins of the Arabian Sea or in the Bay of Bengal.
860   In the Arabian Sea, there are also clear oxygen-dependent differences in benthic
861   community organic matter processing, as have been revealed by tracer incubation
862   experiments. For example, a threshold oxygen concentration occurs, above which
863   macrofauna dominate short-term organic matter (OM) processing, and below which
864   meiofauna and bacteria dominate. This was illustrated on the Pakistan margin both
865   at sites that spanned the lower OMZ boundary and at a shelf-edge site that
866   underwent strong seasonal change in bottom-water oxygen levels, from fully
867   oxygenated (intermonsoon) to hypoxic (summer monsoon) (e.g., Andersson et al.,
868   2008; Pozzato et al., 2013; Woulds et al., 2009; Woulds et al., 2007).

869   Further, the "edge effect" seen in benthic community composition also has been
870   observed in faunal OM processing. At sites in the lower OMZ transition zone, the
871   polychaete *Linopherus sp.* showed clear morphological adaptation to low oxygen
872   levels, and overwhelmingly dominated both the benthic community and also the
873   uptake and processing of organic matter (Jeffreys et al., 2012). These results, and
874   those of other experiments (e.g., Hunter et al., 2012; White et al., 2019), illustrate
875   that faunal assemblage composition may represent an important factor determining
876   the pattern of seafloor processing, but also the composition, bioavailability and fate of

877 residual organic matter. It is certainly clear that faunal digestive processes are
878 recorded in the composition of organic matter deposited across the margins (e.g.,
879 Jeffreys et al., 2009; Smallwood et al., 1999). In summary, oxygen-dependent cross-
880 margin variability in benthic communities and ecosystem function (feeding,
881 bioturbation and bio-irrigation etc) may be important contributors to the role that
882 oxygen exposure plays in controlling organic carbon distribution and burial across
883 Arabian Sea margins, although other factors, most notably hydrodynamic processes,
884 are also important (e.g., Cowie, 2005; Cowie et al., 2009b; Koho et al., 2013; Kurian
885 et al., 2018).

886 **6.1.3 Sediment redox conditions and microbial processes**
887 Alongside the contrasts in faunal communities, bioturbation and irrigation, there are
888 cross-OMZ differences in sediment redox conditions and microbial processes. Again,
889 these are expressed to varying degree on the different margins of the Arabian Sea
890 (Cowie, 2005), and will be less apparent in the Bay of Bengal due to the less intense
891 oxygen depletion at the OMZ core. In the Arabian Sea, sulfate reduction has
892 generally been shown to be surprisingly limited in near-surface sediments (top ~50
893 cm) (e.g., Cowie, 2005; Law et al., 2009), and redox conditions overall to be only
894 moderately reducing (e.g., Crusius et al., 1996) relative to rates and conditions
895 observed on upwelling/OMZ margins in other basins. Nonetheless, Pakistan margin
896 sediments, and possibly those on other Arabian Sea margins, are home to significant
897 rates of denitrification and anammox (e.g., Schwartz et al., 2009; Sokoll et al., 2012)
898 and authigenic phosphorous (P) burial (e.g., Filippelli et al., 2017; Kraal et al., 2012).
899 These phenomena represent important sink terms in the N and P biogeochemical
900 cycles, and, along with sediment-water nutrient fluxes that vary in direction,
901 magnitude and N:P stoichiometry across the OMZ, serve as potential controls on
902 pelagic nutrient inventories.
903 Finally, there is evidence that Pakistan margin sediments (and possibly OMZ
904 sediments on other margins), sequester important amounts of "dark" (non-
905 photosynthetic) carbon arising from anammox and possibly other chemoautrophic
906 processes occurring in overlying waters or within the sediments (e.g., Cowie et al.,
907 1999; Cowie et al., 2009b; Lengger et al., in press). It is a term that is currently
908 underestimated or ignored in carbon budgets and biogeochemical models. On the
909 Pakistan margin, there are also chemosynthetic bacterial mats associated with
910 methane seeps (Himmler et al., 2018)

6.1.4 Implications

As mentioned above, the coastal hypoxia on the western Indian shelf can reach anoxic 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 Sea (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 – 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

948 between hypoxic events. It would also result in expanded areas of reducing
949 sediments and potential changes to carbon sequestration, N and P cycling and N_2O
950 emissions (Middelburg & Levin, 2009). Further, the magnitudes and the dramatic
951 intermonsoon/monsoon (oxic/hypoxic) changes in benthic processes and nutrient
952 fluxes seen at sites on the western Indian shelf (Pratihary et al., 2014), imply that
953 expanded or intensified hypoxia could, through benthic-pelagic coupling, have major
954 influences on nutrient inventories and processes occurring in shallow overlying
955 waters.

956

6.2 Pelagic ecosystems

957

958 There is a large body of evidence on the effects of hypoxia on macro-organisms.
959 This includes reduced diel migration depths, vertical habitat compression and
960 shoaling distributions of fishery species and their prey (Breitburg et al., 2018).
961 However, few reports exist on the effects of hypoxia on phytoplankton, the primary
962 producers of the marine ecosystem. This is because it is generally understood that
963 biological consequences of reduced oxygen concentrations are likely to be most
964 notable for the 200 – 300 m layer, as these waters impinge on the euphotic zone
965 (Stramma et al., 2010b). There have been several reports of coastal upwelling
966 bringing up nutrient-enriched and hypoxic waters onto continental shelves stimulating
967 production and increasing local biological oxygen demand (Stramma et al., 2010b).
968 In the Arabian Sea, the increasing expansion of hypoxia discussed in Section 2.4
969 both on the shelf and offshore is the predominant driver for a shift in the base of the
970 pelagic ecosystem from mainly autotrophy before 2000 (Garrison et al., 1998;
971 Garrison et al., 2000; Smith et al., 1998a), to greater dependence on mixotrophy
972 more recently (Gomes et al., 2014). A large-scale, ongoing study conducted by the
973 National Institute of Oceanography, India, from 2003 onward, in support of India's
974 ocean color program, first documented the appearance of extensive blooms of the
975 green mixotrophic dinoflagellate, *Noctiluca scintillans* (*Noctiluca*).

6.2.1 *Noctiluca* blooms

976

977 *Noctiluca* is large (~1 mm in diameter) dinoflagellate, capable of sustaining itself via
978 photosynthesis from its green free-swimming endosymbionts, *Pedinomonas*
979 *noctilucae* (Wang et al., 2016) and/or by ingestion of exogenous prey (Goes et al.,
980 2016; Gomes et al., 2014; Gomes et al., 2009; Prakash et al., 2008; Prakash et al.,
981 2017). Within a decade and a half, *Noctiluca,* has taken over the once diatom-
982 dominated food chain of the Arabian Sea and the Sea of Oman, forming large green
983 mats that can be observed from space with regular predictability (Fig. 12).

In their quest to find the ecological drivers of *Noctiluca*, Gomes et al. (2014) conducted on-deck dissolved oxygen amendment experiments, in the central and western Arabian Sea during the winter monsoons of 2009, 2010, and 2011 to provide the first conclusive evidence that the growth of green *Noctiluca* blooms was being facilitated by hypoxia. Results from this study showed that green *Noctiluca* is predisposed to hypoxic waters and is able to fix CO_2 more efficiently under hypoxic conditions than at higher concentrations of dissolved oxygen. In contrast, diatoms and other phytoplankton showed a > 50% decrease in CO_2 fixation rates under lower oxygen concentrations. While it appears that green *Noctiluca* thrives in hypoxic waters, it is unclear whether *Noctiluca* is capable of modulating its intracellular environment in order to maximize photosynthetic rates by its endosymbionts. However, the regular occurrence of *Noctiluca* seems to be in line with the decreasing oxygen concentrations in the Arabian Sea as discussed in the earlier sections.

Continuous long-term sampling at a coastal station (Bay of Bhandar Khayran), from 2001, and at another location offshore from 2005, both in the Sea of Oman, supplemented by field observations, provide a mesocosm-like situation to study the ecophysiological characteristics that underpin *Noctiluca*'s recent success. The glider-based study of Piontkovski et al. (2017) and an earlier observational study (Goes & Gomes, 2016) showed that prior to appearing as surface blooms in late winter, *Noctiluca* are seen at deeper depths close to the oxycline, often as large, actively photosynthesizing subsurface blooms advantaged by the intrusion of hypoxic waters into the euphotic column and the higher concentrations of nutrients beneficial for endosymbiont photosynthesis. In this region, *Noctiluca* blooms (Al-Azri et al., 2015; Al-Hashmi et al., 2015) are found in association with a large cyclonic eddy that facilitates the up-shoaling of low-oxygen, high-nutrient waters to the surface (Gomes et al., 2009; Harrison et al., 2017). As the water column warms and stabilizes, a requirement for dinoflagellates to proliferate, *Noctiluca* blooms, as mixotrophs with phagotrophic abilities, proliferate, now advantaged by the plentiful food of phytoplankton, associated bacteria and detritus. Altimetry data show furthermore that this semi-permanent cyclonic and mesoscale eddy is responsible for sustaining this bloom for a prolonged period along the coasts of Oman and Iran even until February (Gomes et al., 2009). Both cyclonic and anticyclonic eddies disperse *Noctiluca* eastwards into the central and eastern Arabian Sea, ultimately engulfing the entire northern Arabian Sea (Gomes et al., 2009).

A more recent study (Lotliker et al., 2018) refutes the connection between *Noctiluca's* blooms and the spread of hypoxia. However, their conclusions were not backed by any experimental data and their O_2 data were from Bio-ARGO floats that were

located south of where *Noctiluca* blooms occur. Sensor calibration was also a contentious issue, and Lotliker et al. (2018) provided only 6 calibration points for a dataset that spanned from Feb 2013 to April 2016. However, we are still uncertain if these large blooms will further intensify the Arabian Sea OMZ. Nonetheless, we are aware that *Noctiluca* is not a preferred food for most zooplankton, but is voraciously grazed upon by gelatinous tunicates such as salps and tunicates. During our field campaigns, we have seen large swarms of salps, known to be efficient filter feeders, devouring *Noctiluca* (Gomes et al., 2014) and depositing large pellets. Salp pellets are known to be fast sinking, (up to 2700 m day−1), carbon-rich (up to 37% DW), contributing disproportionately to carbon flux compared with other zooplankton (Henschke et al., 2016; Martin et al., 2017).

6.2.2 Zooplankton migration

Vertical oxygen gradients of the OMZ set the limits to the horizontal and vertical distribution of zooplankton, affecting their distribution, diel vertical migration, and ecological functions strongly (Saltzman et al., 1997; Wishner et al., 2008). Recent modeling studies (Aumont et al., 2018) estimate that about one third of the epipelagic biomass performs diurnal vertical migrations.

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). 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 of lactic dehydrogenase (LDH), an enzyme associated with anaerobic metabolism (Escribano, 2006; Gonzalez & Quiñones, 2002).

In the Arabian Sea, almost 85% of the epipelagic mesozooplankton biomass is found within the upper aerobic part of the seasonal thermocline or approximately in the upper 100 m. Below this region, in the anaerobic part of the seasonal thermocline, zooplankton concentrations decline sharply (Banse, 1994; Böttger-Schnack, 1996; Smith et al., 2005; Wishner et al., 1998). The most comprehensive study of this region, has been JGOFS (Smith et al., 1998b; Smith & Madhupratap, 2005), which concluded the following *vis a vis* zooplankton distributions and the OMZ: 1) exclusion from the suboxic core of the OMZ of most zooplankton biomass 2) the occurrence of extremely high abundances of a few species of diel vertical migrators at depth during the daytime, well within the suboxic zone 3) organism-specific (and probably species-

specific) distribution boundaries at the upper and lower edges of the OMZ 4) very high biomass of diel vertical migrators that moved between the surface waters at night and the suboxic waters during the day with many of these animals spending the day at depths where the oxygen was less than 4.5 μM and 5) aggregation of mesozooplankton communities to surface layers, in locations where the OMZ was forced upwards due to physical processes but where they are susceptible to predators.

A comparison between a eutrophic, more oxygenated onshore station and an offshore station with a strong OMZ elucidated the influence of depth and oxygen concentrations, as well as other factors on the copepod distribution in the Arabian Sea (Wishner et al., 2008). The extent and intensity of the oxycline at the lower boundary of the OMZ, and its spatial and temporal variability over the year of sampling, was an important factor affecting distributional patterns. Calanoid copepod species showed vertical zonation through the lower OMZ, but no apparent diel vertical migration for either calanoid or non-calanoid copepods was observed at these midwater depths. Subzones of the OMZ, termed the OMZ Core, the lower oxycline, and the sub-oxycline, had different copepod communities and ecological interactions. The calanoid copepod community was most diverse in the most oxygenated environments (oxygen > 6.25 μM), but the rank order of abundance of species was similar in the lower oxycline and sub-oxycline. Some species were absent or much scarcer in the OMZ core. It thus appears that the vertical zonation of copepod species through the lower OMZ oxycline is probably a complex interplay between physiological limitation by low oxygen, potential predator control, and potential food resources.

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

While a considerable body of information is available on the OMZ as a determinant of zooplankton distribution, less is known on the extent of the effects of diel migration on oxygen depletion in OMZs of the world. Using measurements from shipboard acoustic Doppler current profilers (ADCPs) and a global biogeochemical model, Bianchi et al. (2013) found that by clustering in the upper margins of OMZs, vertical migrators accentuate organic matter breakdown in these waters, exacerbating the

1094 oxygen deficit. Aumont et al. (2018) used a fully coupled model to simulate the net
1095 impact of diurnal vertical migration on dissolved oxygen of the entire pelagic
1096 ecosystem on a global scale. Respiration and egestion by migratory organisms
1097 induce a modest decrease in oxygen between 150 and 500 m, which reaches about
1098 5 µM averaged globally at 500 m, although less so in the Arabian Sea and the Bay of
1099 Bengal. Three distinct vertical layers could be distinguished over the global ocean:
1100 1) Vertical migration generates a positive dissolved oxygen anomaly in the
1101 subsurface above 200 m, that can exceed 10 µM which is explained by less intense
1102 respiration in the seasonal thermocline 2) Further below, down to about 1,000 m diel
1103 vertical migration produces a depletion in oxygen from respiration by migrators with
1104 greatest depletion at middle and high latitudes 3) Finally, in the bathypelagic domain
1105 (below 1,000 m), oxygen levels are increased by almost 2 µM as a result of a slightly
1106 lower oxygen consumption.

1107 **6.2.3. Implications**

1108 We are still uncertain if the recent emergence and persistence of *Noctiluca* blooms
1109 will further intensify the Arabian Sea's OMZ. Satellite-derived Chlorophyll-*a* trends
1110 (1980-2019) reveal an almost three-fold increase in phytoplankton biomass, with
1111 increases particularly in the northwestern and central Arabian Sea (Goes et al.,
1112 2020). With respect to repercussions for the food chain, we are aware that *Noctiluca*
1113 is not a preferred food for most zooplankton, but is voraciously grazed upon by
1114 gelatinous tunicates such as salps and tunicates. High gelatinous zooplankton
1115 biomass is often observed in regions of persistent low oxygen concentrations (Lucas
1116 et al., 2014) suggesting that the recent appearance of extensive blooms of *Noctiluca*
1117 reflect the intensification of the Arabian Sea OMZ. The earlier, comprehensive
1118 JGOFS studies of the 1990s, which investigated the vertical migration and
1119 distributions patterns Arabian Sea's OMZ, have not been repeated even on a
1120 moderate scale as acute piracy and political instability have hindered campaigns to
1121 the region. Thus, while modeling (Lachkar et al., 2019; Lachkar et al., 2018) and data
1122 compilation studies (Banse et al., 2014; Rixen et al., 2014) suggest the expansion of
1123 the OMZ in the Arabian Sea, as discussed earlier, little is known of its effect on
1124 zooplankton distribution and vertical migration and this also holds true for the Bay of
1125 Bengal OMZ.

1126 **7. Summary**

1127 The Arabian Sea and the Bay of Bengal are home to ~59% of the Earth's marine
1128 sediments exposed to severe oxygen depletion and approximately 21% of the total

1129 volume of oxygen-depleted waters. The Arabian Sea OMZ is larger, more intense
1130 and reveals functional anoxia in its upper part, whereas the smaller and less intense
1131 Bay of Bengal OMZ only seems to be on the verge of becoming functionally anoxic.
1132 Since oxygen concentrations within this range can presently only be measured by
1133 STOX sensors, and are below detecting limits of standard methods, our
1134 understanding of the response of the nitrogen cycle to such low oxygen
1135 concentrations is based on only a few measurements and suffers from the lack of
1136 data.

1137 Although there are a few reports on the occurrence of anoxia prior to the first large
1138 international Indian Ocean Expedition (IIOE), anoxic events have so far not been
1139 reported from the open northern Indian Ocean (i.e. beyond coastal waters) during the
1140 last 60 years. Maintenance of functional anoxia in the Arabian Sea OMZ is highly
1141 extraordinary considering the impact of the monsoon-driven seasonality on the
1142 surface ocean circulation and the productivity in the Arabian Sea. Stable balances
1143 between physical oxygen supply and biological oxygen consumption including
1144 feedback mechanisms caused by the negative influence of decreasing oxygen
1145 concentrations on the biological oxygen consumption, seem to have prevented the
1146 occurrence of persistent anoxic conditions in the Arabian Sea OMZ and functional
1147 anoxia in the Bay of Bengal OMZ. A reduced biological oxygen consumption due to a
1148 lower productivity and a stronger ballast effect is in line with a less intense Bay of
1149 Bengal OMZ. The lower oxygen consumption in the Bay of Bengal is largely driven
1150 by river discharges, which supply huge amounts of ballast minerals and lower the
1151 nutrient supply from subsurface waters into the sunlit surface ocean by enhancing
1152 the stratification in the surface ocean. However, there is still very little known about
1153 the interannual variability of the Indian Ocean OMZs, as there are limited long-term
1154 observational data and the influence of the remote forcing processes that drive this
1155 variability (e.g., IOD and ENSO) is not fully understood.

1156 Results obtained from the global atmosphere-ocean Kiel Climate Model and eddy
1157 resolving regional models indicate that a decreasing inflow of oxygen-enriched water
1158 masses from the south (ICW) intensified the Arabian Sea OMZ during the last 6000
1159 years, whereas a decreasing oxygen concentration within inflowing Persian Gulf
1160 Water intensifies the OMZ in response to global warming. These trends significantly
1161 affect benthic and pelagic ecosystems. The regular occurrence of *Noctiluca* is an
1162 example of a new phenomenon that is assumed to herald a regime shift within the
1163 pelagic ecosystem of the Arabian Sea in response to declining concentrations of
1164 dissolved oxygen. Comprehensive studies investigating possible repercussions on
1165 the OMZ through e.g. impacts on the export production and vertical migration and

distributions of zooplankton are missing. Accordingly, these recent changes augment the problems that arise when trying to represent the Indian Ocean OMZ in models, and thus in projecting the impact of the changing monsoon system on productivity and OMZ development under global change scenarios. This holds true for the CMIP5 models and is hardly improved in the new CMIP6 models.

8 Author contribution

The paper was written jointly by all co-authors. Tim Rixen coordinated the writing processes and co-authors focused on specific sections as listed in the following: Sections 1 – 3 (Tim Rixen and Zouhair Lachkar), section 4 (Birgit Gaye and Joachim Segschneider), section 5 (Henrike Schmidt and Raleigh R. Hood), section 6.2 (Greg Cowie) and section 6.2 (Joaquim Goes, Helga do Rosário Gomes and Arvind Singh).

9 Competing interests

The authors declare that they have no conflict of interest.

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Figure Captions:

Figure 1: Simplified schematic view of the nitrogen cycle

Figure 2: Schematic illustration showing the occurrence of microbial processes at varying oxygen levels, the subdivision of hypoxia into microbial hypoxia and functional anoxia as well as in red, detection limits of methods used to measure concentration of dissolved oxygen in sea water. Broken lines indicate processes, which occur but do not control the fate of nitrite (reduction to N_2 versus oxidation to nitrate).

Figure 3: (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 the 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 4: (a, b) Monthly mean sea surface temperature in the Indian Ocean (Smith et al., 2008) and the surface ocean circulation simplified and redrawn from Schott and McCreary (2001). The arrows indicate the South Equatorial Current (SEC), South Monsoon Current (SMC), Sri Lanka Dome (SD), East Indian Coastal Current (EICC), South Java Current (SJC), Indonesian Through Flow (ITF), Somali Current (SC), Great Whirl (GW), Ras al Had Jet (RHJ), West Indian Coastal Current (WICC), North Monsoon Current (NMC). The maps were produced with Generic Mapping Tool.

Figure 5: (a) The mean seasonal areal extension and maximum thickness of the Arabian Sea OMZ. (b) Seasonal mean satellite-derived primary production which were obtained from ocean primary production website in August 2020 (http://www.science.oregonstate.edu/ocean.productivity/) and the seasonal mean oxygen concentration within the Arabian Sea OMZ. The satellite-data covered the period between 2002 and 2019 and were averaged seasonally for the Arabian Sea north of 10°. The OMZ data are obtained from Table 5 in Acharya and Panigrahi (2016).

Figure 6: (a) The seasonal mean satellite-derived primary production versus the seasonal mean oxygen concentration within the Arabian Sea OMZ and (b) the seasonal mean oxygen concentration versus the maximum OMZ thickness.

Figure 7: Vertical profiles of nitrite, nitrate, and dissolved oxygen (a) as well as $\delta^{15}N$ of nitrate (b) measured during the RV Meteor cruise M74/1b in 2007. The figure was obtained from Rixen et al. (2014).

Figure 8: Fluxes of protected and free particulate organic carbon versus water depth (black line). The fluxes were 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 shows the long-term mean organic carbon fluxes measured by sediment traps in the central Arabian Sea. The blue and broken black lines indicate concentrations of dissolved oxygen and nitrite measured during the cruise M74 in 2007 in the central Arabian Sea (Station 450). Rixen et al. (2014) provide further information about the sediment trap study and the RV Meteor cruise M74. The broken horizontal lines mark the depth of the OMZ, the surface mixed layer, and the seasonal thermocline. The latter is subdivided into an aerobic upper and a lower anaerobic part. SNM means 'Secondary Nitrite Maximum'.

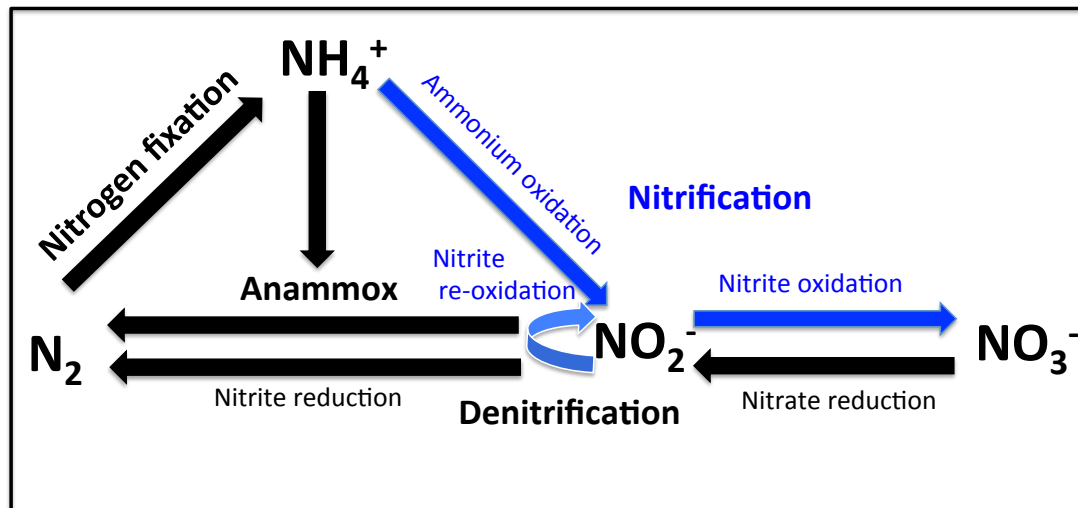
Figure 9: (a) Locations of high resolution cores (circles) and areas of model simulations (boxes). (b) Increasing $\delta^{15}N$ values in high resolution cores from the Arabian Sea (note inverted scale) show increasing denitrification since about 6000 – 8000 years BP; data from the northern (yellow; light brown), eastern (red), western (blue) and southwestern (black) Arabian Sea. Sediment cores: SO90-63KA (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 (c) 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 10: 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.

Figure 11: A summary of water-column conditions, sediment properties, benthic communities and processes influencing carbon 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).

Figure 12: (a) NOAA Suomi-VIIRS derived Chl *a* concentrations 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 1

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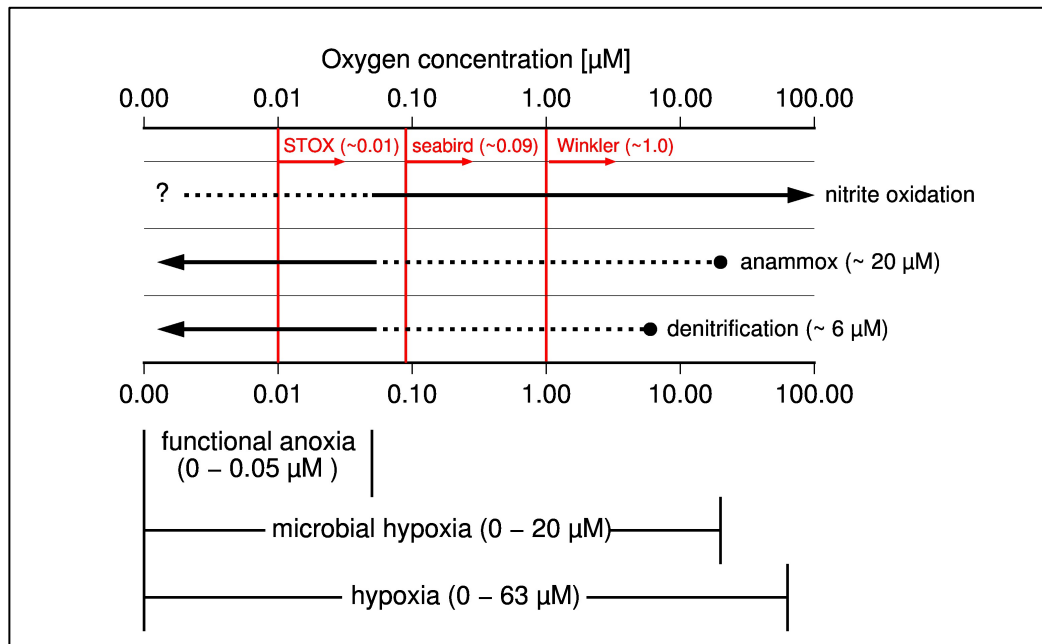
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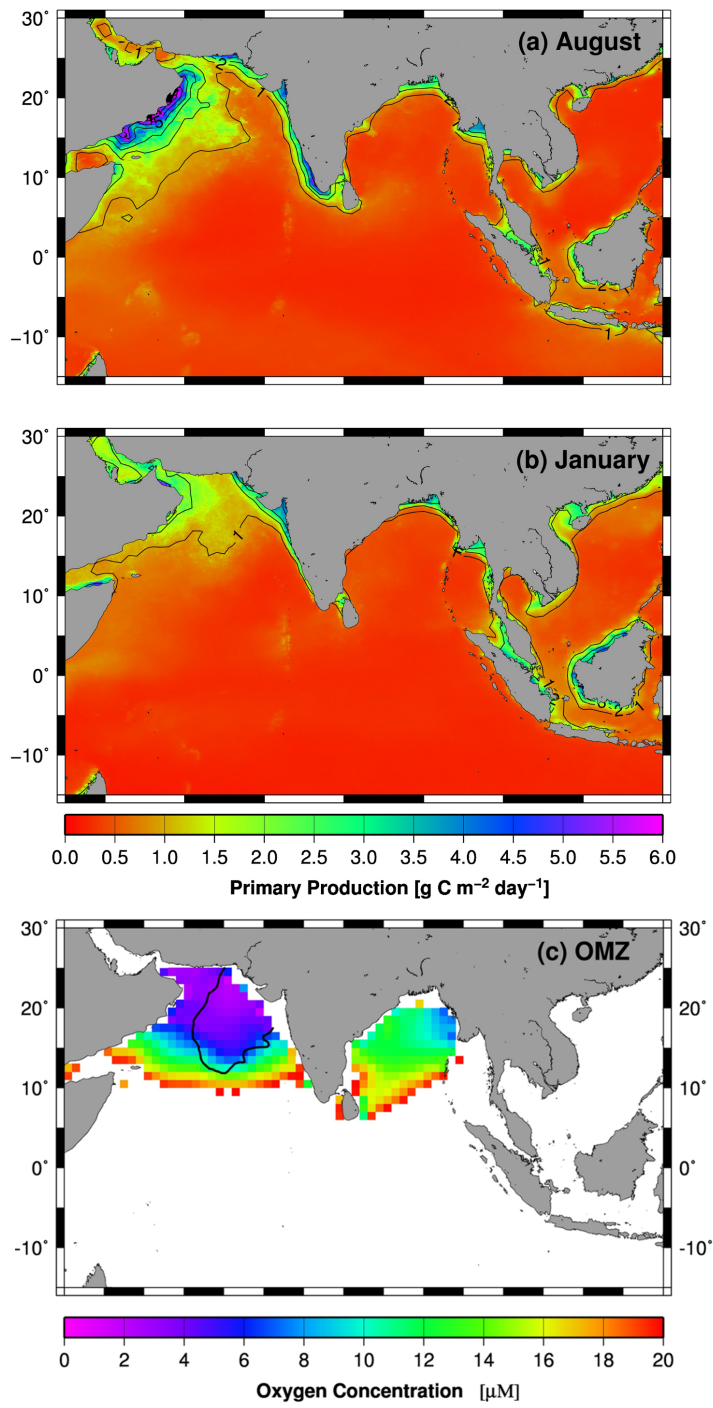
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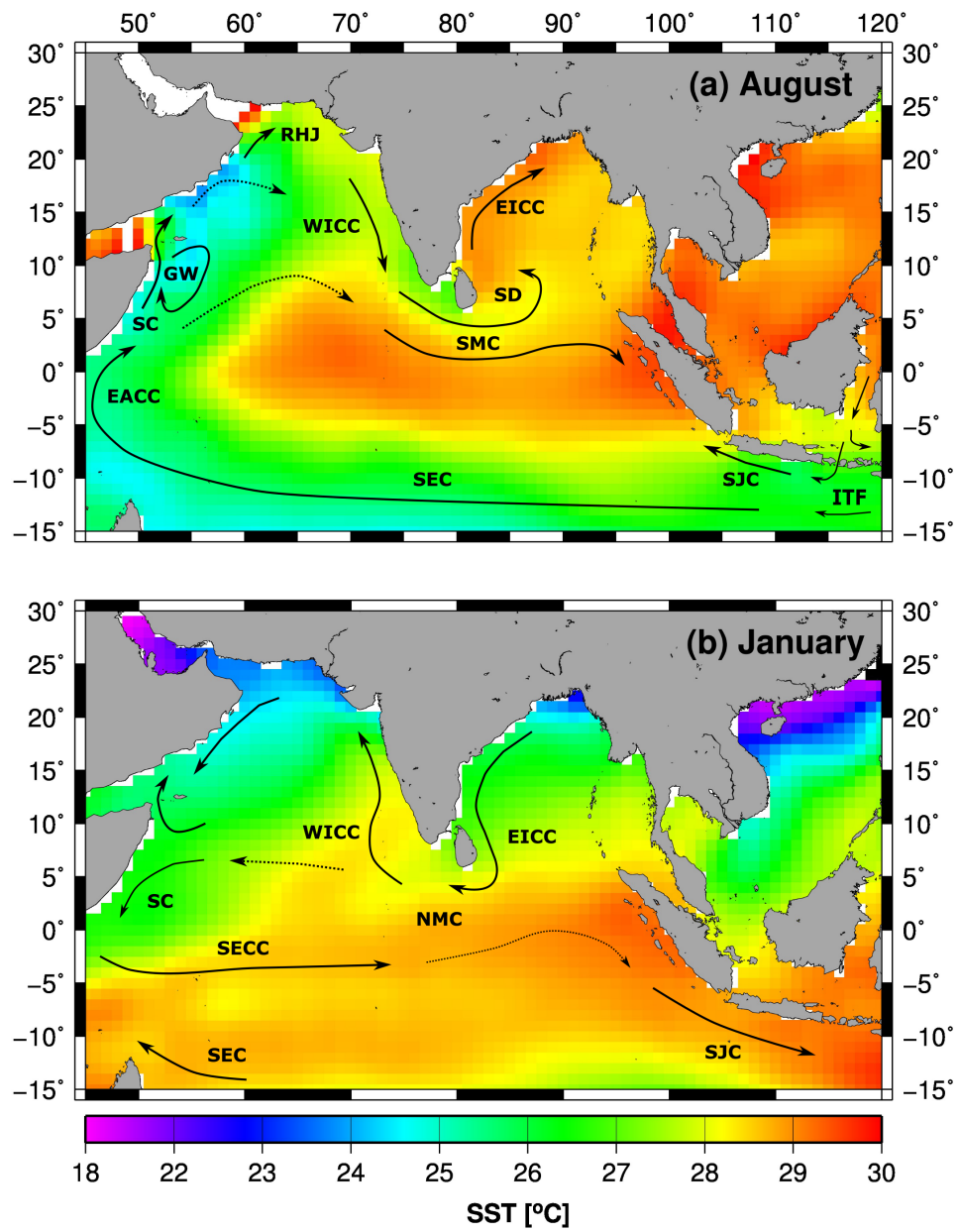
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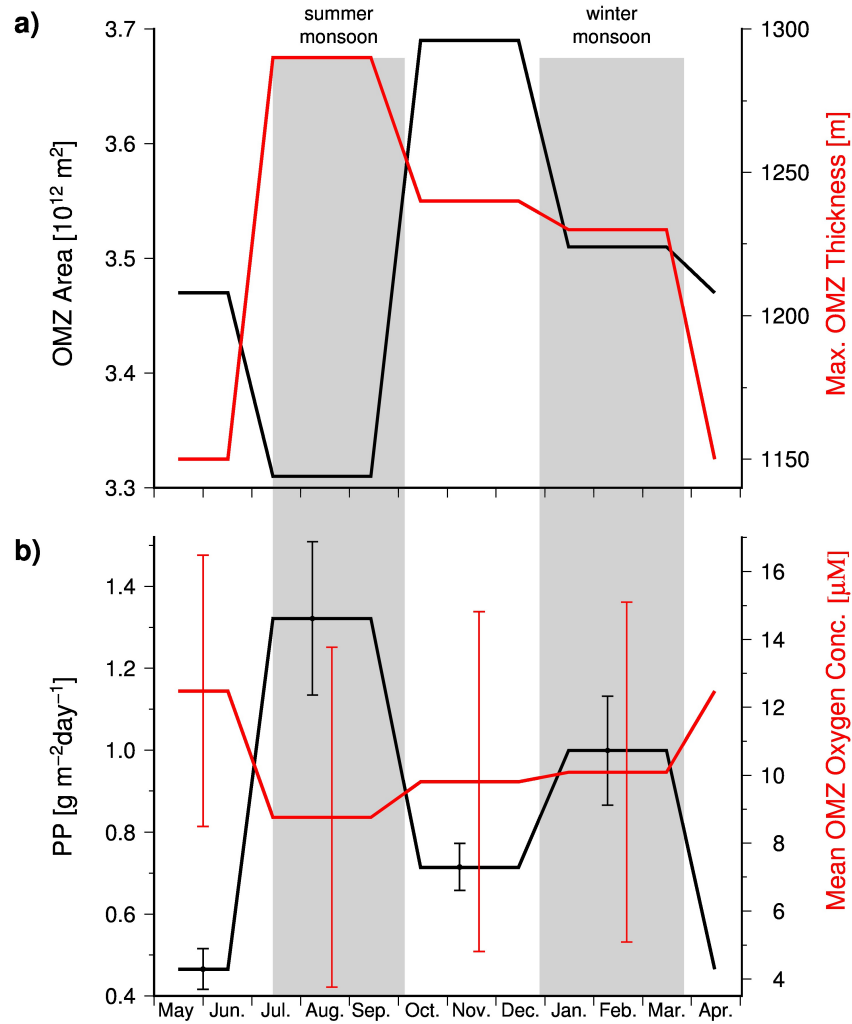
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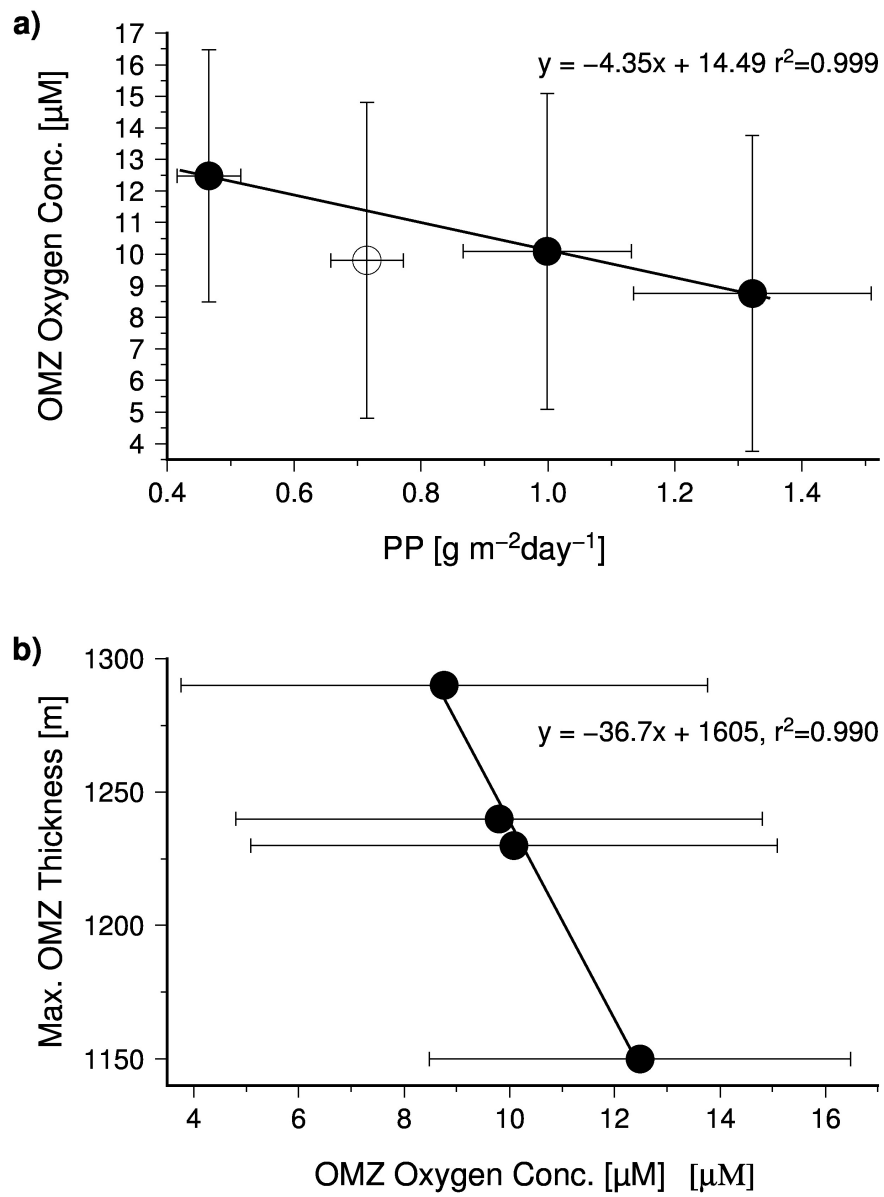
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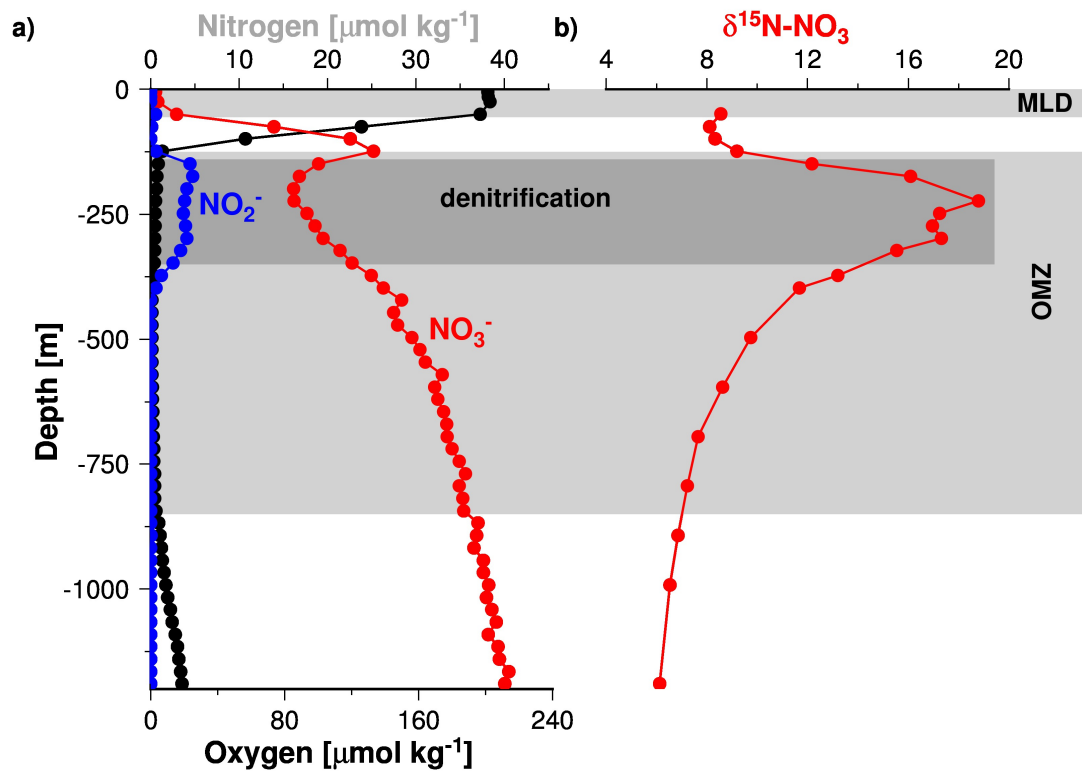
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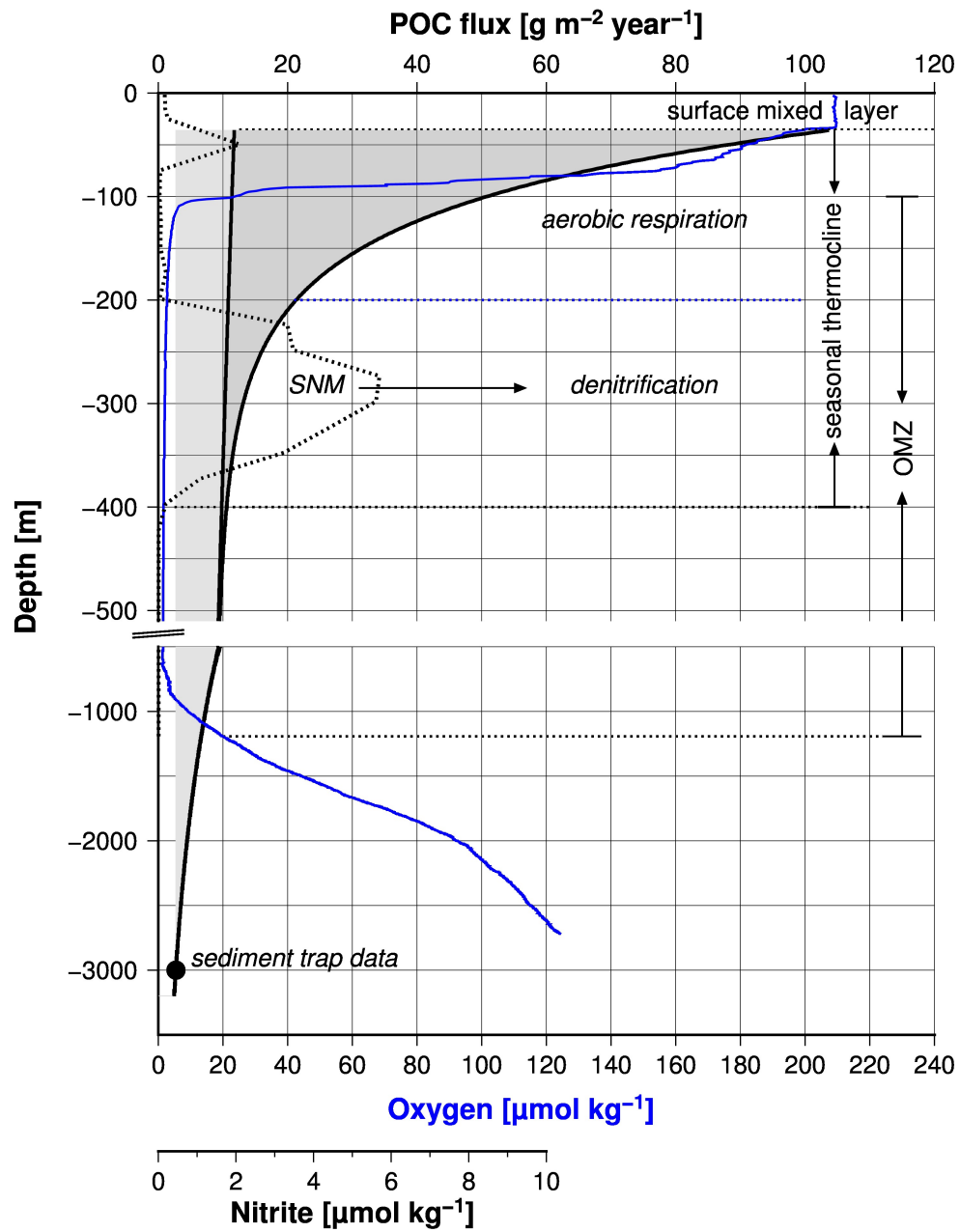
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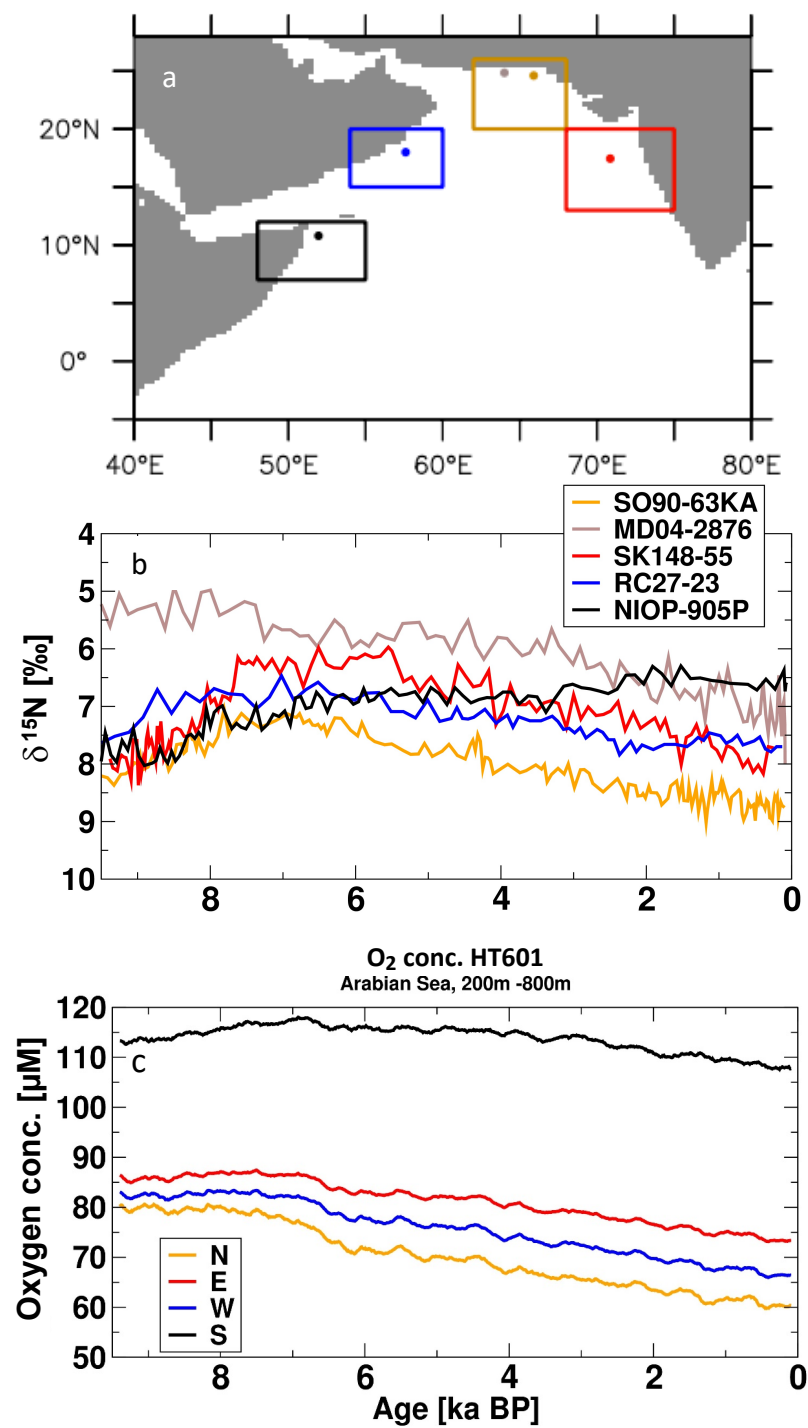
Figure 10

Figure 11

Figure 12