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 and alter the marine nitrogen cycle, which is strongly bound to the carbon

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

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

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

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

9 (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. This implies stable balances between the physical oxygen supply and the

21 biological oxygen consumption, which includes negative feedback mechanisms

22 reducing the biological oxygen consumption at decreasing oxygen concentrations. A

23 lower biological oxygen consumption is also assumed to be responsible for a less

24 intense OMZ in the Bay of Bengal. According to numerical model results, a

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

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

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

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

29 sedimentary record, and that latter concurs with observations of decreasing oxygen

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

31 Arabian Sea. In the Arabian Sea this seems to have initiated a regime shift within the

32 pelagic ecosystem structure, and the trend also affects benthic ecosystems.

33 Consequences for biogeochemical cycles are unknown, which, in addition to the poor

34 representation of mesoscale features, reduces the reliability of predictions of the

35 future OMZ development in the northern Indian Ocean.

1. Introduction

The rise of atmospheric oxygen 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).

The transition from anaerobic to aerobic systems occurs in steps, whereas in the absence of elementary oxygen (anoxia) methane is oxidized to CO_2 by the reduction of sulfate to hydrogen sulfide. Such fully 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, at low levels of dissolved oxygen, aerobic and anaerobic processes occur simultaneously and compete against each other. 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),

72 whereas anammox bacteria utilize nitrite to oxidize ammonium ($NO_2^- + NH_4^+ \rightarrow N_2$).

73 Thus, nitrite plays an import role in the competition between these anaerobic and

74 aerobic processes because, independent of its formation via nitrification and

75 denitrification, it can either be oxidized to nitrate or reduced to N_2. Concentrations of

76 dissolved oxygen strongly influence the fate of nitrite and thereby exert a control on

77 the availability of fixed nitrogen in the ocean (Bristow et al., 2016; Gaye et al., 2013).

78 According to experiments and *in situ* observations, anammox sets in when oxygen

79 concentrations drop below ~20 µM, while denitrification occurs at oxygen

80 concentrations of approximately < 6 µM (Fig. 2, Bristow et al., 2016; Dalsgaard et al.,

81 2014; Kalvelage et al., 2011). Consequently, anammox competes with nitrification for

82 nitrite at oxygen level between 6 and 10 µM, and additionally with denitrification at

83 oxygen level < 6 µM. Decreasing oxygen concentrations favor anammox and

84 denitrification while, in addition to the influence of oxygen, the quality of the supplied

85 organic matter appears to also control the relative importance of denitrification vs.

86 anammox for the reduction of nitrite to N_2 (Babbin et al., 2014; Bristow et al., 2016;

87 Ward et al., 2009). However, since denitrification and anammox ultimately produce

88 N_2 at the expense of fixed nitrogen, the term denitrification is used as a synonym for

89 both processes in the following discussion if anammox is not specifically mentioned.

90 Hypoxia, which means 'low oxygen concentrations', describes oxygen concentrations

91 below which higher organisms start to suffer from the lack of oxygen (Ekau et al.,

92 2010; Vaquer-Sunyer et al., 2008). Accordingly, an oxygen concentration of 60 – 63

93 µM is commonly applied as upper limit of hypoxia in fisheries and ecology. Since

94 such high threshold values do not reflect oxygen-dependent changes in the nitrogen

95 cycle, it is suggested to subdivide hypoxia into microbial hypoxia and functional

96 anoxia (Fig. 2). Functional anoxia was defined already in other works (Canfield et al.,

97 2019; Thamdrup et al., 2012) and covers oxygen levels below which denitrification

98 dominates the nitrogen cycle. Microbial hypoxia is suggested here as the range at

99 which decreasing oxygen levels progressively offset the oxygen-inhibition of

100 denitrification. Since this starts with the occurrence of anammox, we consider 20 µM

101 as the upper threshold of microbial hypoxia whereas anoxia (zero oxygen) terminates

102 hypoxia and therewith also functional anoxia and microbial hypoxia. Because oxygen

103 detection limits of classical Winkler titration (~1 µM), seabird sensors (~0.09 µM) and

104 the newly developed switchable trace oxygen sensors (STOX, ~0.01 µM) are too

105 high to prove anoxia (Thamdrup et al., 2012; Ulloa et al., 2012) the appearance of

106 hydrogen sulfide is generally considered as an indicator of anoxia.

107 Since hypoxic and anoxic conditions repress and prevent, respectively, the growth of

108 all life forms that depend on oxygen, their occurrence is often associated with mass

109　mortality of fish and invertebrates (e.g. Weeks et al., 2002). Thus, the spatial
110　expansion of hypoxia, which seems to be an increasingly common feature in coastal
111　waters, is called the "spreading of dead zones" (Altieri et al., 2017; Diaz et al., 2008).
112　This term ignores the life of anaerobic microbes, which dominated the world's
113　biosphere long before oxygen-breathing organisms evolved, but expresses the threat
114　of oxygen-depletion to many commercially important marine species. Eutrophication
115　and global warming mainly cause the spread of dead zones whereas eutrophication
116　increases oxygen consumption by enhancing the production of organic matter, while
117　global warming decreases the oxygen supply due to a reduced solubility of oxygen in
118　warmer waters. Since decreasing concentrations of dissolved oxygen have also been
119　widely observed in the open ocean (i.e. beyond coastal systems) during the last 50
120　years, deoxygenation of the ocean is considered as one of the main threats to
121　pelagic ecosystems (Breitburg et al., 2018; Keeling et al., 2009; Schmidtko et al.,
122　2017; Stramma et al., 2010a; Stramma et al., 2008; Stramma et al., 2010b).
123　Based on data obtained from the World Ocean Atlas, the total volume of waters
124　characterized by oxygen concentrations < 20 µM in the global ocean is
125　approximately 15 x 10^{15} m^3, of which 21% (3.13 x 10^{15} m^3) is located in the northern
126　Indian Ocean (Fig. 3c, Acharya et al., 2016; Garcia et al., 2010). The largest
127　proportion of this oxygen-poor water body is in the Arabian Sea (2.5 x 10^{15} m^3) and
128　only a small fraction in the Bay of Bengal (0.6 10^{15} m^3). In comparison to the Bay of
129　Bengal OMZ, with a mean concentration of dissolved oxygen of 14.51 µM, the
130　Arabian Sea OMZ is more intense, as indicated by mean concentration of dissolved
131　oxygen of 10.45 µM (Acharya & Panigrahi, 2016). Notably, in regions where these
132　OMZs impinge on continental margins, sediments and benthic communities are
133　exposed to semi-permanent bottom-water hypoxia. The Arabian Sea and the Bay of
134　Bengal together are currently home to ~59% of the Earth's marine sediments
135　exposed to hypoxia (Helly et al., 2004).
136　Denitrification, within sediments (benthic denitrification) and under hypoxic conditions
137　in the water column, is by far the largest sink of nitrate in the ocean (Gruber, 2004).
138　However, estimates of benthic and water column denitrification rates are still fraught
139　with large uncertainties on global as well as on regional scales. Global scale
140　estimates of benthic and water-column denitrification range between 65 and 300 Tg
141　N year^{-1} and 39 and 270 Tg N year^{-1}, respectively (Eugster et al., 2012; Gruber,
142　2004; Somes et al., 2013). Although denitrification in the Arabian Sea has been
143　much more intensively studied than in the Bay of Bengal, estimates of benthic (1 to
144　6.8 Tg N year^{-1}) and water column (1 to 33 Tg N year^{-1}) denitrification in the Arabian
145　still reveal a wide range (Bange et al., 2000; Bristow et al., 2017; Deuser et al., 1978;

146 Gaye et al., 2013; Howell et al., 1997; Naqvi et al., 1982; Somasundar et al., 1990).

147 However, these estimates imply that on average the Arabian Sea contributes

148 approximately 2 % and 11 % to the global mean benthic and water column

149 denitrification, respectively, although published data indicate that the estimated

150 benthic denitrification rates might be too low. According to these more recent data,

151 the benthic denitrification at the Pakistan continental margin amounts to up to 10.5

152 Tg N year^{-1} (Schwartz et al., 2009; Somes et al., 2013), which exceeds the former

153 budget (6.8 Tg N year^{-1}) of the entire Arabian Sea sediments (Bange et al., 2000). In

154 line with a severe depletion of nitrate in bottom waters on the Indian shelf (Naqvi et

155 al., 2010) this implies that benthic denitrification rates contribute > 2% to the global

156 mean benthic denitrification rate. This further emphasizes the role of the northern

157 Indian Ocean OMZ for the marine nitrogen cycle, which was considered as one of

158 the least understood OMZs in the world's ocean (Schmidt et al., 2020; Segschneider

159 et al., 2018). The aim of this paper is to provide a short background on the

160 development of OMZs and recent trends in the OMZ of the Indian Ocean as well as

161 to discuss drivers, ecosystem responses and the future development of this OMZ.

162 **2. Background**

163 **2.1 Oxygen Minimum Zones (OMZ)**

164 The first large ocean-going oceanographic expeditions discovered OMZs in Pacific,

165 Atlantic, and Indian Ocean between the end of the 19th and the first third of the 20th

166 century (Sewell et al., 1948 and references therein). Their occurrence was explained

167 by a sluggish horizontal renewal of water within the OMZ and the consumption of

168 oxygen during the respiration of organic matter exported from the sunlit surface

169 ocean (Dietrich, 1936; Seiwell, 1937). Sverdrup (1938) presented the first model

170 showing that oxygen concentrations within the OMZ represent the balance between

171 biological oxygen consumption and oxygen supply. Primary production and fluxes of

172 oxygen across the air-sea interface are the sources of dissolved oxygen. Vertical

173 mixing and subduction of oxygen-enriched surface waters during the deep and mode

174 water formation at high latitudes are in turn the main processes ventilating the interior

175 of the ocean (McCartney, 1977; Sverdrup, 1938). Accordingly, Broecker and Peng

176 (1982) introduced a model in which upwelling of oxygen-enriched deep water and

177 vertical mixing serve to ventilate the OMZ from the bottom and the top, respectively,

178 whereas the respiration of exported organic matter decrease oxygen concentrations

179 in the OMZ (Fig. 4). The OMZ in general emerges at water-depths between ca. 100

180 and 1000 m because this is the depth range at which the majority of the exported

181 organic matter is respired (Suess, 1980). Due to the respiration of exported organic

182   matter, oxygen concentrations decrease during the spreading of water masses in the

183   ocean and pronounced OMZs occur in these so-called 'shadow zones', where aged

184   water masses accumulate (Karstensen et al., 2008).

185   Since oxygen concentrations result from the balance between oxygen consumption

186   and supply, which in turn also influence these processes, a dynamic evolved such

187   that an enhanced oxygen supply does not necessarily result in increased oxygen

188   concentrations. Although, in principle, an enhanced physical oxygen supply

189   increases oxygen concentrations, an enhanced oxygen supply caused by increased

190   oxygen consumption can be associated with lower oxygen concentrations. The

191   underlying mechanism can be illustrated with a simple conceptual steady-state box

192   model (Fig. 4). Within this model, the OMZ is a box with a constant volume and

193   oxygen concentrations at steady-state due to an oxygen consumption that equals the

194   oxygen supply. Vertical mixing links the oxygen concentration in the OMZ to those at

195   the sea surface and therewith to the flux of oxygen across the air-sea interface. The

196   air-sea flux of oxygen is proportional to the oxygen partial pressure difference

197   between the ocean and the atmosphere and increases in response to decreasing

198   oxygen concentrations in the ocean. Accordingly, increased oxygen consumption can

199   enhance the flux of oxygen from the atmosphere into the ocean by decreasing

200   oxygen concentrations in the OMZ. Thereby, an enhanced oxygen supply balances

201   an increased oxygen consumption and re-establishes a steady-state that was

202   disturbed by the increase of the oxygen consumption. Steady-state oxygen

203   concentrations resulting from such a perturbation are inversely proportional to the

204   oxygen consumption/supply. They rise or fall if oxygen consumption/supply decrease

205   or increase, respectively.

206   The main processes controlling the physical oxygen supply include temperature- and

207   salinity-related changes of the solubility of oxygen in water, which are in turn related

208   to factors such as variation in ocean circulation and water movements associated

209   with mesoscale eddies. For instance, changes in the ocean's circulation can increase

210   oxygen concentrations by enhancing the lateral inflow of oxygen-enriched water

211   masses into the OMZ. The increased oxygen supply is in turn balanced by an

212   enhanced outflow of oxygen along with water, which compensates the inflow.

213   Secondly the enhanced oxygen concentrations lower the supply of oxygen from the

214   atmosphere by lowering the air-sea flux of oxygen as discussed before. Thereby, a

215   new steady state is established, but at a higher oxygen level. The impacts of

216   mesoscale eddies are more difficult to describe as they develop from baroclinic and

217   barotrophic instabilities related to the shear of horizontal currents, and create a

218   patchiness of environmental conditions with complex and non-linear impacts on the

219   OMZ and the marine carbon cycle (McWilliams, J.C., 2008, McGillicuddy Jr, D.J.,
220   2016, Fassbender et al., 2018). In order to elucidate their role for the development of
221   OMZs, multidisciplinary approaches involving *in situ* observations, remote sensing,
222   and modeling are required (McGillicuddy, 2016). Results obtained from numerical
223   model studies in the Indian Ocean (Lachkar et al., 2019; Lachkar et al., 2016;
224   McCreary Jr et al., 2013; Resplandy et al., 2012) will be introduced in a separate
225   section. Nevertheless, oxygen concentrations as observed in the OMZ of the Arabian
226   Sea and Bay of Bengal can be seen as steady-state concentration. This implies that
227   higher oxygen concentrations in the Bay of Bengal OMZ relative to that of the
228   Arabian Sea reflect a lower oxygen consumption or a higher physical oxygen supply.
229   In order to test these two options, we will first of all provide a general overview about
230   processes controlling oxygen consumption and the physical oxygen supply in the
231   Arabian Sea and Bay of Bengal.
232

233   2.2 OMZ and upwelling

234   In the Atlantic and Pacific Oceans, hypoxic OMZs are associated with major eastern
235   boundary current upwelling systems. They are among the most productive regions in
236   the ocean and account for circa 20% of the global fish catch (Carr, 2001; Pauly et al.,
237   1995). The high productivity emphasizes the role of oxygen consumption for the
238   development of OMZ. In the Indian Ocean, the geographic setting prevents the
239   development of a strong eastern boundary current upwelling system but a major
240   monsoon-driven seasonal upwelling system emerges in the western Arabian Sea off
241   the Arabian Peninsula (Fig. 3a). Initially described by Schott (1935), this upwelling
242   system was subject to intense studies including the International Indian Ocean
243   Expedition (IIOE) between 1959 and 1965 and the Joint Global Ocean Flux Study
244   (JGOFS) in the Arabian Sea with its field phase between 1994 and 1997 (e.g. Bauer
245   et al., 1991; Brock et al., 1991; Bruce, 1974; Currie et al., 1973; Sastry et al., 1972;
246   Wyrtki, 1973).
247   High monsoonal upwelling-driven productivity sustains a high export of organic
248   matter into the deep sea (Haake et al., 1993; Rixen et al., 1996) but the impact of
249   upwelling is not restricted to coastal areas because upwelling–driven blooms advect
250   offshore and increase the organic carbon export in the central Arabian Sea (Rixen et
251   al., 2006a). Nevertheless, against expectations, the OMZ is most intense in the
252   eastern Arabian Sea and not in western Arabian Sea where the upwelling-driven
253   productivity is highest (Fig. 4c, Antoine et al., 1996; Naqvi, 1991). The seasonal
254   monsoon-driven reversal of the surface circulation in combination (Fig. 5) with the a
255   strong inflow of oxygen-enriched Indian Ocean Central Water (ICW) into the western

Arabian Sea is assumed to cause this eastwards displacement of the OMZ in the Arabian Sea (Rixen et al., 2005; Sen Gupta et al., 1984; Swallow, 1984). The ICW originates by convective mixing as Subantarctic Mode Water (SAMW) in the southern Indian Ocean (McCartney, 1977; Sverdrup et al., 1942) and enters the western Arabian Sea along with Timor Sea Water and the Subtropical Subsurface Water via the Somali Current (Schott et al., 2001; Stramma et al., 1996; You, 1997). The inflow of the ICW is part of the meridional overturning circulation of the upper Indian Ocean, which includes a cross-equatorial cell, driven by downwelling in the south and upwelling in the north (Fig. 6, Rahaman et al., 2020).

In addition to the strong upwelling off the Arabian Peninsula, a weaker summer monsoon-driven upwelling develops along the Indian southwest coast (Fig. 3a, Schott, 1935; Sharma, 1978; Shetye et al., 1990). Here an undercurrent emerges, which compensates the poleward flowing West Indian Coastal Current (Fig 5a) and carries the ICW northwards into the eastern Arabian Sea (Schmidt et al., 2020; Shenoy et al., 2020; Shetye et al., 1990). Despite the inflow of ICW, the OMZ expands southwards during the summer monsoon, and retreats northwards during the winter monsoon in the eastern Arabian Sea (Shenoy et al., 2020). In contrast to these movements, the OMZ retreats eastwards in summer and expands westwards in winter in the western Arabian Sea (Rixen et al., 2014). This opposing behavior creates a seesaw billowing of the OMZ as a consequence of the seasonal reversal of the surface ocean circulation - anticlockwise during the winter monsoon and clockwise during summer monsoon.

Influences of the seasonally reversing surface ocean circulation on the volume and intensity of the OMZ were studied by Acharya and Panigrahi (2016). These authors analyzed the Word Ocean Atlas 2013 (WOA13) and data compiled by the Global Ocean Data Analysis Project. Thereby, they took methodical biases into account, corrected the WOA13 data, and applied the 20-μM threshold to define the OMZ. Based on the corrected data set, these authors determined the areal extension and depth of the OMZ and calculated the mean oxygen concentration within the OMZ. According to this data, the OMZ reveals its lowest areal extension in summer (Fig. 7a) due to the inflow of ICW, which favors the eastward retreat of the OMZ in the western Arabian Sea and attenuates the influence of the clockwise circulation and the associated southwards expansion of the OMZ in the eastern Arabian Sea. Since the shrinking spatial extension of the OMZ is associated with a deepening, the OMZ reveals its largest volume in summer, which in turn is accompanied by the lowest concentration of oxygen within the OMZ (Fig. 7b). The deepening of the OMZ is favored by the negative wind stress curl and the associated downwelling in the

293   central Arabian Sea, and is coincident with the confluence of ICW that enters the
294   Arabian Sea in west and east (Brock et al., 1991; Rao et al., 1989).
295   The low oxygen concentration reflects in turn impacts of the enhanced upwelling-
296   driven productivity and the associated increased oxygen consumption in the OMZ,
297   which apparently exceeds the increased physical oxygen supply via the inflow of
298   ICW. According to the conceptual box model, such a situation represents a steady-
299   state characterized by high oxygen consumption and air-sea oxygen supply that
300   establishes in response to the monsoon-driven increase of the biological production.
301   Thereby the enhanced supply of oxygen via the inflow of ICW acts as an additional
302   oxygen sources, which lowers the impact of the high oxygen consumption on the air-
303   sea oxygen supply. In order to test whether the monsoon establishes steady states
304   and controls therewith the intensity of the OMZ via its impact on the biological
305   production, satellite-derived primary production values were obtained from ocean
306   primary production website (http://www.science.oregonstate.edu/ocean.productivity/).
307   The data covered the period between 2002 and 2019 and were averaged seasonally
308   for the Arabian Sea north of 10°. In general, the obtained mean primary production
309   rates were inversely linked to the OMZ oxygen concentrations (Fig. 7b, 8a), which
310   supports the assumption that monsoon-driven changes in the biological carbon
311   production and export exert a strong control on the intensity of the OMZ on a
312   seasonal time scale. However, the fall appears to be an exception. During this
313   season the OMZ oxygen concentration was lower as expected from the primary
314   production rate (Fig. 8a) indicating a physical oxygen supply, which was too low to
315   establish a steady-state. One explanation could be the strongly reduced inflow of
316   ICW in combination with a low air-sea oxygen supply in response to the warming and
317   the resulting enhanced stratification of surface waters after the upwelling season in
318   fall.
319   Similar to the Arabian Sea, upwelling-favorable winds also occur in the Bay of Bengal
320   during the summer monsoon (Hood et al., 2017; Shetye et al., 1988). However, high
321   freshwater fluxes, from both river runoff and precipitation, form a buoyant low-salinity
322   surface layer that isolates nutrient-enriched subsurface water and increases
323   stratification (Kumar et al., 1996). This weakens upwelling and vertical mixing, and
324   thus nutrient supply into the sunlit surface ocean (Rixen et al., 2006b). Hence,
325   productivity in the Bay of Bengal is lower than in the Arabian Sea and reveals only a
326   weakly pronounced seasonality (Fig. 3a,b). Nevertheless, sediment trap studies have
327   shown that, despite a lower productivity, organic carbon fluxes into the deep Bay of
328   Bengal are almost as high as those in the central and eastern Arabian Sea, due to a
329   ballast effect associated with high loadings of lithogenic mineral material (Rao et al.,

1994; Rixen et al., 2019b). Ballast minerals, supplied from land via rivers or as dust, protect organic matter against bacterial attacks by adsorbing organic molecules to atomic lattices (Armstrong et al., 2002) and accelerate the sinking speed of particles (Haake et al., 1990; Hamm, 2002; Ramaswamy et al., 1991). Enhanced sinking speeds reduce respiration in shallower waters and thereby increase the flux of organic matter to deeper waters (Banse, 1990; Ittekkot, 1993). A stronger ballast effect, in addition to the lower primary production, was assumed to lower the oxygen consumption in the Bay of Bengal in comparison to that in Arabian Sea OMZ (Al Azhar et al., 2017; Rao et al., 1994). On the other hand, in contrast to the Arabian Sea, a buoyant low-salinity layer reduces the oxygen supply via vertical mixing. Furthermore, instead of oxygen-enriched ICW, oxygen-poor Arabian Sea Water flows into the Bay of Bengal OMZ, as indicated 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). Hence, higher oxygen concentrations in the Bay of Bengal relative to the Arabian Sea can be seen as a consequence of the lower oxygen consumption, which is balanced by a lower oxygen supply.

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

In contrast to the monsoon, which seems to influence the intensity of the OMZ mainly by its impact on the productivity and resulting biological oxygen consumption, global warming is assumed to intensify OMZs through its influence on the solubility of oxygen in water and the resulting physical oxygen supply. However, there are indications that at least the Arabian Sea OMZ was more intense in the past, prior to the Indian Ocean Expedition (IIOE, 1959 - 1965), than thereafter. For instance, Carruthers et al (1959) described mass mortality of fish along the Arabian and Indian coast as well as in the central Arabian Sea at around 62.5°E and 9 °N. The development of harmful algae blooms were discussed but oxygen depletion was preferred as the more likely mechanism explaining these mass mortalities (Carruthers et al., 1959). This view was supported by a report on the occurrence of hydrogen sulfide from the north-eastern Arabian Sea and off Oman at Ras-al-Hadd (Ivanenkov et al., 1961). These were the only reports on the occurrence of hydrogen sulfide in Arabian Sea (Naqvi et al., 2000; Swallow, 1984) except for Naqvi et al. (2000) who discovered an anoxic event that developed along the western Indian coast off Mumbai in the late summer of 1999. Such strong events do not evolve every year (Gupta et al., 2016; Sudheesh et al., 2016), but their appearance shows that the spreading of 'dead zones' in coastal regions does not spare the Indian shelf (Altieri et al., 2017; Diaz & Rosenberg, 2008; Diaz et al., 2019).

366 In contrast to these shelf processes, global syntheses of OMZs (beyond continental
367 shelves) reveal only a weak decrease of dissolved oxygen concentrations in the
368 OMZs of the Arabian Sea and the Bay of Bengal in comparison to OMZs of the South
369 Atlantic Ocean and the Pacific Ocean (Ito et al., 2017; Naqvi, 2019; Schmidtko et al.,
370 2017; Stramma et al., 2008). The detailed analysis of all oxygen data available from
371 the central Arabian Sea by Banse et al. (2014) ascribes this to opposing regional
372 trends within the Arabian Sea. The authors analyzed oxygen data, which were
373 measured between 1959 and 2004 in the Arabian Sea and in the depth range
374 between 100 and 500 m. Biases caused by different analytical procedures were
375 taken into account and oxygen data were compiled for sub-regions within the Arabian
376 Sea. The results showed that oxygen concentrations increased in the southern part
377 of the Arabian Sea and declined in the central Arabian Sea. Follow-up studies also
378 reported decreasing oxygen concentrations in the western and northern Arabian Sea
379 (Piontkovski et al., 2015; Queste et al., 2018). In the northern Arabian Sea, dissolved
380 oxygen concentrations in the surface mixed layer largely reflect the trend seen in the
381 OMZ, as indicated by a compilation of dissolved oxygen data covering the period
382 from the 1960s to 2010 (Gomes et al., 2014).

383 Since STOX data for the Arabian Sea were unavailable prior to 2007, the data
384 compiled by Banse et al. (2014) do not resolve any changes in the oxygen
385 concentrations below 0.09 µM (Fig. 2). Such low oxygen concentrations have
386 recently been measured in the Arabian Sea and in the Bay of Bengal as well as in
387 OMZ of the eastern Pacific Ocean (Bristow et al., 2017; Jensen et al., 2011;
388 Thamdrup et al., 2012). In the latter study, it was shown that nitrite accumulates in
389 the water column at oxygen concentrations of < 0.05 µM. In the Arabian Sea OMZ,
390 the accumulation of nitrite was first described during the John Murray expedition of
391 1933 - 34 (Gilson, 1937). It is called the secondary nitrite maximum (SNM) and
392 assumed to indicate active denitrification (Naqvi, 1991). The role of the SNM as
393 indicator of active denitrification is further supported by profiles of stable isotope
394 ratios of nitrogen in nitrate ($\delta^{15}N_{NO3}$) and nitrate (NO_3^-) concentration profiles (Fig. 9,
395 Gaye et al., 2013; Rixen et al., 2014). Since denitrification increases $\delta^{15}N_{NO3}$ in the
396 water column due to the preferential uptake of the lighter $^{14}NO_3^-$ (Cline et al., 1975;
397 Mariotti et al., 1981), low nitrate concentrations correspond to high $\delta^{15}N_{NO3}$ within the
398 SNM. Assuming a similar response of the nitrogen cycle to low oxygen concentration
399 in the Arabian Sea as in the eastern Pacific Ocean suggests that the Arabian Sea
400 SNM is characterized by oxygen concentrations of about ~0.05 µM, and in turn that
401 denitrification dominates the nitrogen cycle at such low oxygen concentrations.
402 Nevertheless, an isotope tracer study indicated that the re-oxidation of nitrite to

nitrate reduced the formation of N_2 by 50 to 60% (Gaye et al., 2013), which implies an active competition between aerobic and anaerobic processes even at such low oxygen concentrations. However, since anaerobic denitrification dominates the competition, as indicated by the accumulation of nitrite, the depletion of nitrate and the $\delta^{15}N_{NO3}$ maxima, an oxygen concentration of ~0.05 µM is seen as a threshold below which functional anoxia occurs (Fig. 2).

Naqvi (1991) was the first to use the SNM to map the spatial extent of functional anoxia in the Arabian Sea. His analysis was based on data obtained during the International Indian Ocean Expeditions between 1959 and 1965 and cruises thereafter but did not include data from Ivanenkov and Rozanov (1961) and JGOFS. The data of Ivanenkov and Rozanov (1961) indicate a more intense OMZ, including the occurrence of hydrogen sulfide as mentioned earlier and a larger extent of the SNM than calculated by Naqvi (1991), although there are doubts regarding the reliability of the older data (Sen Gupta & Naqvi, 1984). Comparison of JGOFS data, collected in 1994/95, with those compiled by Naqvi (1991), shows that the SNM has expanded south- and westwards (Rixen et al., 2014). This implies, in accordance with decreasing oxygen concentrations, an expansion of the OMZ in the Arabian Sea, which might have started in the early 1990s. However, the reliability of this trend has been questioned by Naqvi (2019). While it is acknowledged that the data are too sparse to have unquestionable confidence in this trend, it is difficult to assess the doubts raised by Naqvi (2019), as these are based on data derived from sediment cores that do not cover the most recent past.

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

439   and prevented persistent anoxia in the Arabian Sea and functional anoxia in the Bay
440   of Bengal OMZ.

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

442   **3.1 Interplay between the intensity of the OMZ and export production**

443   Maintenance of functional anoxia in the Arabian Sea OMZ with oxygen
444   concentrations ranging between > 0 and ~0.05 µM is highly extraordinary considering
445   that the monsoon-driven seasonality reverses the surface ocean currents and turns
446   the Arabian Sea from an oligotrophic oceanic desert into one of the most productive
447   regions in the world's ocean within weeks. This calls for feedback mechanisms
448   counteracting impacts of the monsoon on the intensity of the OMZ. Since there is
449   growing evidence that concentrations of dissolved oxygen influence the respiration of
450   organic matter in the water column (Aumont et al., 2015; Cavan et al., 2017;
451   Laufkötter et al., 2017; Thamdrup et al., 2012; Van Mooy et al., 2002), it has been
452   assumed that an oxygen–related feedback mechanism stabilizes the Arabian Sea
453   OMZ (Rixen et al., 2019a). This feedback mechanism is evident if one considers the
454   sunlit surface mixed layer and the seasonal thermocline, which serves as the habitat
455   of the pelagic ecosystems (Fig. 10).

456   The seasonal thermocline is the subsurface layer from which water is introduced into
457   the euphotic zone via physical processes such as upwelling and vertical mixing on a
458   seasonal timescale. Nutrients supplied by these mechanisms largely sustain the
459   productivity of pelagic ecosystems and the associated export production (Eppley et
460   al., 1979). Hence, the seasonal thermocline is the main nutrient reservoir of pelagic
461   ecosystems, and to fulfill this role the vast majority of the exported organic matter
462   must be respired within the seasonal thermocline. Accordingly, the seasonal
463   thermocline represents the main zone of respiration and, similar to soils on land,
464   accommodates the nutrient recycling machinery of the pelagic ecosystem. Nutrient
465   losses from the seasonal thermocline, via particle fluxes into the deep sea,
466   denitrification, and lateral advection, must be compensated by nutrient inputs in order
467   to maintain the productivity (Rixen et al., 2019a). Nitrogen fixation, river discharges,
468   and atmospheric deposition can be important nutrient sources, but in the Arabian
469   Sea lateral inflow of water masses from the south via the cross-equatorial cell are the
470   main source balancing nutrient losses from the seasonal thermocline (Bange et al.,
471   2000; Gaye et al., 2013). Accordingly, a significant negative impact of denitrification
472   on primary and export production and the associated oxygen consumption appear to
473   be unlikely on seasonal to centennial time scales in the Arabian Sea.

474   The SNM, which occurs at water depths between 200 and 400 m in the central
475   Arabian Sea and as deep as 500 m in the eastern Arabian Sea, divides the seasonal
476   thermocline into an aerobic part at water depths between ~40 and 200 m and an
477   anaerobic part down to the base of the SNM (Fig. 10). The depth of the seasonal
478   thermocline of approximately 300 – 400 m corresponds to the depth range of
479   vertically migrating zooplankton as observed during the large summer bloom in the
480   Arabian Sea (Smith, 2001), and roughly matches the water depth range from where
481   subsurface water is introduced via upwelling into the euphotic zone in the western
482   Arabian Sea (Brock et al., 1992; Rixen et al., 2000). Furthermore, nitrate
483   concentrations, which decrease within the SNM, remain above 10 µM (Fig. 9),
484   suggesting that supply of decomposable organic matter (rather than nitrate
485   availability) limits denitrification, as also suggested by other studies (Bristow et al.,
486   2016; Ward et al., 2009). A substrate limitation at a water depth of 400 to 500 m, and
487   the arrival of organic matter at sediment traps deployed in the deep sea at a water
488   depth of 3000 m, support the concept of export production that is divided between
489   free (reactive) and protected (low reactivity) organic matter (Armstrong et al., 2002).
490   This partition is based on the assumption that ballast-associated, protected organic
491   matter is preferentially exported to deeper waters as fast sinking particles, whereas
492   the slow sinking free organic matter is preferentially respired within the seasonal
493   thermocline.

494   Similar to the ballast-effect also decreasing oxygen concentrations could increase
495   the organic carbon flux into the deep sea. This is assumed to be caused by the
496   negative impact of low oxygen concentrations on the respiration rate (Aumont et al.,
497   2015; Laufkötter et al., 2017; Thamdrup et al., 2012; Van Mooy et al., 2002) and the
498   low zooplankton abundance in the OMZ (Cavan et al., 2017), which will further be
499   discussed in the following section. However, a reduced respiration due to decreasing
500   oxygen concentrations prevents further depletion of oxygen and the development of
501   anoxia in the SNM by lowering the oxygen consumption and increasing the export of
502   organic matter out of the seasonal thermocline. An increased export of carbon into
503   the deep sea could, in turn, favor a deepening of the OMZ by enhancing the oxygen
504   consumption at the base of the OMZ at water-depths between 1150 m and 1240 m.
505   This would imply that low OMZ oxygen concentrations are accompanied by a
506   deepening of the OMZ. Data compiled by Acharya and Panigrahi (2016) support this
507   view by showing the link between primary production and OMZ oxygen
508   concentrations as discussed before and furthermore a correlation between the
509   seasonal mean oxygen concentrations within the OMZ and the depth of the OMZ
510   (Fig. 8), even though the latter is also influenced by physical processes as also

511 discussed above. Accordingly, it seems that the influence of decreasing oxygen
512 concentrations on respiration within the SNM mitigates impacts of monsoon-driven
513 primary and export production on the intensity of the OMZ.
514

515 **3.12 Biological oxygen consumption**
516 The role of an oxygen-dependent, biologically driven feedback mechanism,
517 counteracting impacts of the monsoon on the intensity of the OMZ, depends on the
518 local oxygen consumption. If this is too low, remote processes instead of the local
519 monsoon-driven carbon export rates need to be considered as forces controlling the
520 intensity of the OMZ. The apparent oxygen utilization (AOU), in addition to mixing
521 analyses, provide information that helps to estimate the role of the local oxygen
522 consumption for maintaining the intensity of the OMZ in the Arabian Sea. The AOU
523 represents the oxygen deficit caused by biological oxygen consumption and is
524 calculated by subtracting the measured oxygen concentration from the temperature-
525 and salinity-dependent oxygen saturation concentration. This approach is based on
526 the assumption that the water mass of interest was saturated with respect to oxygen
527 during its formation and, since then, the respiration of exported organic matter
528 consumed oxygen within the water mass. The OMZs in the northern Indian Ocean
529 are melting pots collecting the influence of a variety of water masses with different
530 origins and histories (e.g. Morcos et al., 2012; Schott & McCreary, 2001; You, 1997).
531 Mixing analyses indicate that in the Arabian Sea the inflow of oxygen-rich Indian
532 Ocean Deep Water affects the lower OMZ (water-depth > 500 m) as already
533 discussed before (Fig. 3, Acharya & Panigrahi, 2016; Hupe et al., 2000; Rixen &
534 Ittekkot, 2005). In addition to the formation of the Arabian Sea Water (ASW), the
535 intrusion of ICW and water masses from the Persian Gulf and Red Sea strongly
536 influenced the upper OMZ. A mixing analyses based on data measured during
537 JGOFS in 1994/95 reveals that oxygen-deficits inherited from ICW contribute
538 approximately 25% to the AOU determined in the Arabian Sea OMZ (Rixen &
539 Ittekkot, 2005). Accordingly, the respiration of organic matter produced in the Arabian
540 Sea largely causes the low oxygen consumption in the Arabian Sea OMZ, which
541 further supports the hypothesis that monsoon-driven productivity, including the
542 oxygen-dependent biologically driven feedback mechanism, controls and stabilizes
543 the OMZ in the Arabian Sea.
544 However, in the Arabian Sea, mean satellite-derived export production rates were too
545 low to sustain a high biological oxygen consumption considering a residence time of
546 water within the OMZ of 10 years (Rixen & Ittekkot, 2005). The mismatch reflects
547 uncertainties caused by the poorly constrained residence time of water within the

548   OMZ and export production rates. Even though residence times of water within the
549   Arabian Sea and Bay of Bengal OMZ of 10 and 12 years seems to be well accepted
550   (Bristow et al., 2017; Olson et al., 1993), there also are estimates ranging from 1 to
551   51 years for the Arabian Sea OMZ (Naqvi et al., 1993; Sen Gupta & Naqvi, 1984). In
552   the Arabian Sea, satellite-derived export production rates vary by a factor of 10
553   (Rixen et al., 2019b) and an even larger variability can be seen on the global scale.
554   Global export production rates derived from satellite-data, numerical models,
555   extrapolated from sediment trap data and based on estimates of the biological
556   oxygen demand vary approximately between 1.8 and 27.5 Pg C yr$^-$. In general
557   estimates based on the biological oxygen demand, in line with inverse modeling
558   studies, call for higher export production rates (Burd et al., 2010; del Giorgio et al.,
559   2002; Schlitzer, 2000; Schlitzer, 2002), whereas satellite and sediment trap data, as
560   well as numerical model studies, suggest lower export production rates (Emerson,
561   2014). However, a longer residence time, in addition to a higher carbon export could
562   explain the AOU determined in the Arabian Sea (Rixen & Ittekkot, 2005).
563
564   **3.3 Implications**
565   Understanding of the processes controlling oxygen consumption within OMZs, such
566   as export production and the residence time of water, is still fraught with large
567   uncertainties. Nevertheless, it seems that there are oxygen-dependent, biologically
568   driven feedback mechanisms countering impacts of the monsoon on the intensity
569   of the OMZ. This could explain the absence of persistent anoxia and functional
570   anoxia in the Arabian Sea and Bay of Bengal OMZs. However, the recent expansion
571   of the OMZ in the Arabian Sea, and the first indication of denitrification in the Bay of
572   Bengal OMZ, indicate that there are other processes overriding effects of these
573   feedback mechanisms.

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

575   Previous studies have also shown that, in addition to upwelling and vertical mixing,
576   eddies influence biological production as well as OMZ, through upward and
577   downwards movements of water (Boyd et al., 2019; Chelton et al., 2011; Gruber et
578   al., 2011; Omand et al., 2015; Oschlies et al., 1998; Resplandy et al., 2019).
579   Furthermore, eddies also affect the transport of biological tracers, through eddy
580   stirring that enhances patchiness in the ocean, and through eddy trapping that can
581   maintain properties of the trapped fluid over relatively long time periods (Chelton et
582   al., 2011; d'Ovidio et al., 2013; Mahadevan, 2016). In particular, stirring of oxygen by
583   eddies along isopycnal surfaces has been suggested to modulate the intensity and

distribution of low-oxygen waters in the ocean (Fig. 5, Gnanadesikan et al., 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 circulation, thus contributing to the ventilation of the OMZ located there (Bettencourt et al., 2015; Brandt et al., 2015; Gnanadesikan et al., 2013). In this context, long-term changes in oxygen 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 in the tropical north Atlantic has contributed to a reduction in the ventilation of the OMZ located there. Eddy trapping in turn maintains properties of the trapped fluid over relatively long time periods which favors the development of localized low-oxygen environments 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).

4.1. Effects of eddies on the Arabian Sea OMZ

In the Arabian Sea, numerical model studies have shown that eddies play an important role in the transport of nutrients and oxygen (Lachkar et al., 2016; McCreary Jr et al., 2013; Resplandy et al., 2012; Resplandy et al., 2011). For instance, Resplandy et al., (2011) emphasized the role of mesoscale eddies in spreading nutrients vertically and horizontally in the Arabian Sea (Fig. 11). Furthermore, mesoscale eddies and filaments were shown to dominate, on an annual timescale, the vertical supply of oxygen to the OMZ in the Arabian Sea (Resplandy et al., 2012). This study also showed that eddy-driven horizontal advection substantially contributes to the lateral transport of ventilated waters into the central and northern Arabian Sea. In a process study aiming to explore the dynamics of the Indian Ocean OMZs, McCreary et al (2013) also highlighted the important role of vertical eddy mixing in the ventilation of the western Arabian Sea in addition to the inflow of ICW. Their work further stresses the importance of this mechanism in the eastward shift of the upper OMZ relative to the region of highest productivity located along the western part of the Arabian Sea, as mentioned before.

Using a suite of regional model simulations with increasing horizontal resolution, Lachkar et al (2016) found that isopycnal eddy transport of oxygen to the Arabian Sea OMZ strongly limits the extent of its suboxic core. Within the model, an enhanced vertical mixing enhances the oxygen supply into the upper OMZ and the upward transport of nitrate into sunlit surface ocean. The latter enhanced the

biological production and the resulting export of organic matter, which in turn increased the oxygen consumption at depth. The consequence is an expansion of the volume of the OMZ. Finally, eddies have also been shown to control the transport and the spreading of the Persian Gulf Water (PGW) into the Gulf of Oman (Queste et al., 2018; Vic et al., 2015). These dense waters, relatively rich in O_2, subduct in the northern Arabian Sea and strongly contribute to the ventilation of the upper OMZ there (Lachkar et al., 2019; Schmidt et al., 2020). The projected future warming of the Persian Gulf can cause a reduction in the sinking of PGW in the Gulf of Oman, and hence a drop in oxygen at depths between 200 and 300 m in the northern Arabian Sea.

4.2. Eddies and the ventilation of the Bay of Bengal

In the Bay of Bengal, previous studies have highlighted the role of eddy pumping of nutrients in enhancing biological productivity during all seasons (Kumar et al., 2007; Prasanna Kumar et al., 2004; Singh et al., 2015). Eddies have also been shown to affect the ventilation of the Bay of Bengal and subsequently the intensity of its OMZ. For instance, Sarma et al (2018a) showed that while cyclonic eddies inject nutrients into the euphotic zone, thus enhancing productivity and oxygen consumption at depth, anticyclonic eddies supply oxygen to the subsurface layer and hence weaken the OMZ. Sarma and Baskhar (2018b) focused on anticyclonic eddies sampled by bio-Argo floats between 2012 and 2016 in the Bay of Bengal. These anticyclonic eddies seem to be formed in the eastern side of the basin and propagate westward. They ventilate the layer between 150 and 300 m and weaken the OMZ. The frequent episodic injection of oxygen, likely by mesoscale eddies, could be mechanism that enhances the oxygen supply by lowering impacts of the strong stratification on vertical mixing. However, in the Bay of Bengal, strong interannual variations in the intensity of the eddy activity have been reported (Chen et al., 2012). These are expected to cause strong variations in the subsurface ventilation that may eventually lead to an intensification of the OMZ (Johnson et al., 2019).

4.3 Implications

So far, numerical model studies have shown that the variability of eddy activity in space and time can modulate the intensity of OMZs between different regions and across time, thus contributing to the observed variability of dissolved oxygen. The fact that eddies affect both the supply of oxygen (through ventilation) and its consumption (through biological productivity) in a non-trivial manner can explain the

657 fundamental difficulty to adequately parameterize the effects of eddies on dissolved
658 oxygen in coarse resolution models. An additional potential source of error in the
659 currently used parameterizations is their underlying assumption that the eddy-driven
660 isopycnal tracer mixing (i.e., diffusive part of eddy mixing) and the adiabatic
661 isopycnal flattening (i.e., advective effect of eddies) occur at similar rates (Griffies,
662 1998). Yet, recent studies (e.g. Gnanadesikan et al., 2013) suggest that the two can
663 be substantially different. In the Arabian Sea, Lachkar et al (2016) showed that the
664 eddy driven transport of oxygen is mostly driven by enhanced mixing along the
665 isopycnal surfaces, with very little change in the slope of the isopycnals. The
666 postulated decrease in the physical oxygen supply caused by the inflow of warmer
667 and hence more oxygen-depleted PGW agreed with the observed decreasing
668 oxygen concentrations and expansion of the SNM in the Arabian Sea. In the Bay of
669 Bengal, a response to global warming is more difficult to establish due to strong
670 interannual variations in the intensity of the eddy activity.

671 **5. Holocene records**

672 **5.1. Sediment δ^{15}N records of OMZ strength**

673 On millennial and even longer timescales, sedimentary records have been used to
674 trace changes in the OMZ intensities. The δ^{15}N values of particulate nitrogen in
675 sediments are often used as tracers of OMZ intensify because they reflect major
676 shifts in the pool of fixed nitrogen due denitrification, as discussed before (Altabet et
677 al., 1995; Altabet et al., 1999; Brandes et al., 1998; Ganeshram et al., 1995). Locally,
678 eolian and riverine nitrogen supply affect δ^{15}N values (Kendall et al., 2007; Voss et
679 al., 2006), but in the Indian Ocean sedimentary δ^{15}N reflects the balance between
680 denitrification vs. nitrogen fixation. Deep water nitrate has an average δ^{15}N value of
681 ~5‰ (Sigman et al., 2005) but, due to denitrification, the δ^{15}N of nitrate in Arabian
682 Sea increase to values > 17 ‰ (Fig. 9). Convective mixing, eddy pumping, and
683 especially upwelling, move nitrate-deficient water masses from the OMZ to the
684 surface, so that nitrate with high δ^{15}N values is transported into the euphotic zone.
685 After assimilation into biomass by phytoplankton, ^{15}N-enriched particulate matter
686 sinks through the water column to the seafloor where the signal of denitrification, and
687 hence OMZ intensity, is preserved in sediments (Altabet et al., 1995; Gaye-Haake et
688 al., 2005; Naqvi et al., 1998; Suthhof et al., 2001). Early diagenesis may raise
689 sedimentary δ^{15}N values by 2 - 5 ‰, and the diagenetic effect increases with water
690 depth (Altabet, 2006; Tesdal et al., 2013). Nevertheless, the relative changes of δ^{15}N
691 in deep-sea sediments record variations in the OMZ intensity while records from the

692   continental slopes are subjected to negligible diagenetic enrichments so that they
693   retain the signal of the nitrogen source (Altabet et al., 1999; Gaye et al., 2018).

5.2. OMZ Fluctuations during the Holocene

695   A sediment core from the northern Bay of Bengal (Contreras-Rosales et al., 2016)
696   indicates that the highest δ^{15}N values (and thus the lowest OMZ oxygen
697   concentrations) recorded in the core prevailed during the Holocene and the last
698   glacial maximum, with a δ^{15}N range between 4.4 and 5.0 ‰ (i.e., in the range of the
699   average value of deep ocean waters, see above). Therefore, denitrification in the
700   past 21,000 years can be ruled out in the Bay of Bengal from a paleoceanographic
701   perspective (Contreras-Rosales et al., 2016). The δ^{15}N values at the core top (4.6 ‰)
702   were similar to values in sediment trap materials (3.7 - 4.5 ‰), and were explained
703   by a mixture of nutrients or suspended matter from the Ganges-Brahmaputra-
704   Meghan river system with nitrate from subsurface water (Contreras-Rosales et al.,
705   2016; Gaye-Haake et al., 2005; Unger et al., 2006). Enhanced δ^{15}N values in the
706   early Holocene to 6000 years BP (BP = before present, where present means 1950)
707   coincide with a stronger monsoon and were attributed to enhanced supply of nitrate
708   from the subsurface, which has elevated δ^{15}N compared to the depleted values of the
709   riverine end-member (Sarkar et al., 2009). However, to our knowledge there is only
710   one published sediment record from the Bay of Bengal spanning the entire Holocene
711   (Contreras-Rosales et al., 2016) so that we know nothing about the spatial variability
712   within the basin.

713   In contrast to the Bay of Bengal, denitrification in the Arabian Sea has prevailed
714   during the warm interstadials of the Pleistocene and during the entire Holocene, as
715   can be discerned from sedimentary δ^{15}N values > 6 ‰, with maxima of > 11 ‰
716   (Agnihotri et al., 2003; Higginson et al., 2004; Kessarkar et al., 2018; Möbius et al.,
717   2011; Pichevin et al., 2007). Productivity increased with the onset of the Holocene as
718   the summer monsoon strengthened and monsoonal upwelling off Somalia and Oman
719   commenced and became a permanent feature of the Holocene Arabian Sea (Böning
720   et al., 2009; Gaye et al., 2018). A rise of δ^{15}N by at least 2 ‰ shows that an onset of
721   upwelling immediately strengthened the OMZ and led to denitrification across the
722   entire basin in the beginning of the Holocene (Böll et al., 2015; Gaye et al., 2018).

723   Furthermore, southward retreat of Antarctic Sea Ice is assumed to have reduced
724   ventilation of the Arabian Sea OMZ through its influences on the formation of the
725   oxygen-enriched ICW and associated meridional overturning circulation of the upper
726   Indian Ocean (Fig. 6 Böning & Bard, 2009; Naidu et al., 2010). A decline in δ^{15}N by
727   about 1 ‰ is found in the early Holocene until 6000 years BP in high-resolution

728 sediment cores from the western, northern and eastern Arabian Sea, and indicates
729 that the OMZ weakened and became less persistent during this period (Fig. 6a).
730 More vigorous upwelling, discernible from benthic foraminifera, may have led to a
731 better ventilation of the basin by ICW from the south during this period, by reducing
732 the residence time of OMZ waters (Das et al., 2017).

733 After 6000 years BP, increasing δ^{15}N values indicate a strengthening of the OMZ
734 across the entire basin (Fig 12 b). It is assumed that a weaker ventilation is
735 responsible for decreasing oxygen concentrations and it could be due to reduced
736 inflow of ICW, as it was blocked by the enhanced inflow of PGW and RSW since the
737 sea level high stand at 6000 years BP (Pichevin et al., 2007). Furthermore, a
738 southward shift of the West Indian Coastal Current and the associate poleward
739 undercurrent lowered the inflow of ICW and the thereby the ventilation of the OMZ in
740 the eastern Arabian Sea (Mahesh et al., 2014). The reduced inflow of ICW generally
741 might have not only reduced ventilation but also prolonged the residence time of
742 water within the OMZ (Böning & Bard, 2009; Pichevin et al., 2007).

743

744 5.3 Holocene model simulations

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

749 In a first step, KCM was forced with transient orbital parameters and greenhouse gas
750 concentrations from 9500 years BP to present. In a second step, the PISCES model
751 was forced with the ocean physical fields from the above KCM experiment in so-
752 called off-line mode. This model set-up comprised a ventilation age tracer of the
753 water masses (see Segschneider et al. (2018) for a more detailed description of the
754 model components and experiment set-up). While the oceanic 2° x 2° grid in this set-
755 up was refined to a meridional resolution of 0.5^o near the equator to allow a better
756 representation of equatorial waves, the long integrations (9500 model years) required
757 a coarse model resolution that is far from eddy resolving. The ballast scheme for the
758 export of POC also neglected the lithogenic ballast effect, which is important in the
759 Arabian Sea and Bay of Bengal a discussed before.

760 From these model experiments, temperature and oxygen fields have been analyzed
761 and compared to sedimentary records mainly in the Arabian Sea. Here the model
762 results were subdivided into areas corresponding to the binned sediment core
763 regions specified in Gaye et al (2018) (Fig. 12 a; North: 62^oE-68^oE, 20^oN-25^oN; East:

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).
The simulated oxygen concentrations in the Arabian Sea are generally somewhat too high at the surface due to a cold bias of the KCM, but the observed near-surface gradients of oxygen concentrations are very well matched. However, in the deeper layers the model overestimates oxygen concentrations (not shown, see supplementary figure A.1c in (Segschneider et al. (2018)). As a result, oxygen concentrations in the model Arabian Sea are nowhere low enough for denitrification to occur (denitrification sets in at 6 µM in the PISCES model, with a transition phase to full denitrification at lower oxygen concentrations). Moreover, no nitrogen isotopes are simulated in the current model version. Comparison to the δ^{15}N data from the sediment cores is, therefore, restricted to a qualitative assessment.

The simulated oxygen concentrations (averaged between 200 m and 800 m depth) show the lowest concentrations in the northern Arabian Sea (initially around 80 µM in the early Holocene, yellow curve in Fig. 12c). The concentrations are 10 µM higher in the western Arabian Sea (blue line), and a further 5 µM higher in the eastern Arabian Sea (red line), while they are much higher in the southern Arabian Sea (starting at 155 µM, grey line). Oxygen concentrations are fairly constant over the first 2.5 thousand years, and then gradually decrease until the late Holocene. This decrease is strongest in the northern Arabian Sea (-20 µM) and quite similar in the western and eastern Arabian Sea (-10 µM). This is in qualitative agreement with the Holocene trends of δ^{15}N data (Fig. 12b) that show highest δ^{15}N values (indicating strong denitrification and thus low oxygen) for the shallow northern core, and lower δ^{15}N for the western and eastern cores.

Simulated export production and water mass age in the Arabian Sea have been discussed for an earlier model experiment with the same model set-up (but accelerated forcing) by Gaye et al. (2018), and in more detail for the global OMZs including the Indian Ocean for the model experiment analyzed here by Segschneider et al. 2018. While simulated export production in the Arabian Sea is fairly constant throughout the Holocene (Fig. 7 in Gaye et al. 2018), ventilation age is increasing throughout the Holocene concurrent with decreasing oxygen concentrations (Fig. 15 in Segschneider et al., 2018). This implies that changes in the ocean circulation and the associated inflow of oxygen-enriched ICW largely influenced the OMZ during the Holocene after the onset of upwelling at the beginning of Holocene.

5.4 Implications

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

6. Model predictions

6.1 Global models

For future climate predictions we rely on earth system models (ESM). Although these models reproduce large-scale features and global trends, they suffer from considerable mismatches between measured and model oxygen concentrations in the ocean (Bopp et al., 2013; Cabré et al., 2015; Oschlies et al., 2018; Oschlies et al., 2008). In comparison to observational data, they underestimate oxygen losses significantly (e.g. Oschlies et al., 2018 and references therein), and simulated volumes of OMZs differ considerably. Unresolved physical oxygen supply mechanisms, poorly constrained biological oxygen consumption rates, and their hardly known responses to global change, cause these uncertainties (e.g., Oschlies et al., 2018; Segschneider et al., 2013). Furthermore, feedbacks caused by the strong coupling of the marine oxygen and nitrogen cycles complicate long-term predictions (Fu et al., 2018; Oschlies et al., 2019).

Especially in the Indian Ocean, global coupled biogeochemical ESMs struggle to represent the OMZs (Fig. 13, Oschlies et al., 2008). In most ESMs the east – west contrast between the Arabian Sea and Bay of Bengal is opposite to what observations show, with most global models producing lower oxygen concentrations

834   in the Bay of Bengal than in the Arabian Sea. Furthermore, half of the models cannot

835   predict hypoxic conditions in the Arabian Sea at all. A comparison of the thickness of

836   the hypoxic layer in the northern Indian Ocean shows a disagreement among all

837   models (Fig. 13). The maximum simulated volume (8.2×10^{15} m^3, CESM1-BGC) is

838   more than twice the hypoxic volume found from observations (3.1×10^{15} m^3,

839   WOA13). Moreover, this volume extends too far horizontally and does not cover the

840   thickness of the observed OMZ in the Arabian Sea (Fig.13).

841   To some degree, this problem may be attributed to the fact that ESMs are not tuned

842   for the northern Indian Ocean. In addition, global models generally have coarser

843   resolution to reduce computational costs, and thus are far from eddy resolving, as for

844   the KCM (results discussed in the previous section). Eddy transport is parameterized

845   in the ESMs, but these still fail to represent the OMZs in the northern Indian Ocean.

846   Even though the next generation of ESMs already targeted this problem, by providing

847   high-resolution options including mesoscale processes in models used in the 6th

848   coupled model intercomparison experiment (CMIP6), there are only moderate

849   improvements in subsurface oxygen representation (Kwiatkowski et al., 2020). The

850   CMIP6 models still tend to overestimate oxygen concentrations in the Arabian Sea

851   (Séférian et al., 2020).

852

853   **6.2 Future prediction**

854   The poor representation of the OMZs in the northern Indian ocean in ESMs reduces

855   the reliability of future predictions of potential changes in the OMZs related to natural

856   and anthropogenic forcing, and thus their ecological impacts and possible feedbacks

857   to climate change. Global models suggest a general decline of oxygen for the entire

858   ocean, but there is no clear trend visible in the Indian Ocean (Oschlies et al., 2017).

859   However, an older set of ESMs analyzed in Cocco et al. (2013) suggest a future

860   decrease in oxygen in the subtropical Indian Ocean in the upper mixed layer, and a

861   small increase in the western tropical Indian Ocean. This increasing oxygen

862   concentration is also seen in response to climate change in the RCP8.5 and RCP2.6

863   scenarios of the 5th coupled model intercomparison project (CMIP5, Bopp et al.,

864   2013). Specifically, Bopp et al. (2013) showed that a decrease in productivity is

865   consistently simulated across all CMIP5 models and scenarios in the tropical Indian

866   Ocean and that, by 2100, all models project an increase in the volume of waters

867   below an oxygen concentration of 80 µM, relative to 1990–1999. This response is

868   more consistent than that of the previous generation of ESMs, i.e., changes varying

869   from −26 to +16% over 1870 to 2099 under the SRES-A2 scenario (Cocco et al.,

870   2013).

871 However, for lower oxygen levels, there is less agreement among the CMIP5 models
872 and also compared to observations regarding the volume of the OMZ (Bopp et al.,
873 2013). Specifically, for the volume of waters below 50 µM, four models project an
874 expansion of 2 to 16% (both GFDL-ESMs, HadGEM2-ES and CESM1-BGC),
875 whereas two other models project a slight contraction of 2% (NorESM1-ME and MPI-
876 ESMMR). For the volume of waters below an oxygen concentration of 5 µM, only one
877 model (IPSL-CM5A-MR) is close to the volume estimated from observations, and
878 projects a large expansion of this volume (+30% in the 2090s). These results for low
879 oxygen waters (oxygen concentrations of 5 - 50 µM) agree with those of Cocco et al.
880 (2013), with large model–data and model–model discrepancies, and simulated
881 responses varying in sign for the evolution of these volumes under climate change
882 (Bopp et al., 2013).

883 Globally, the models agree on a negative oxygen trend driven by declining solubility
884 through global warming (Resplandy, 2018; Schmidtko et al., 2017) and reduced
885 ventilation by changes in oxygen transport by circulation (Bopp et al., 2017), and take
886 into consideration negative feedback caused by reduced tropical export production
887 due to increased stratification of the upper water columns (Fu et al., 2018; Palter et
888 al., 2018). Uncertainties and disagreements among the models arise from subtle
889 differences in timing and magnitude of these opposing trends (Bopp et al., 2017).
890 Waters with low oxygen saturation are particularly sensitive to impacts of climate
891 warming (Fu et al., 2018) as well as vertical diffusivity that is parameterized by the
892 mixing coefficient in the models (Duteil et al., 2012) and also mesoscale eddy
893 transport and the lateral mixing coefficient (Bahl et al., 2019; Lachkar et al., 2016).
894 Globally, reduced mixing across the mixed layer explains 75% of the reduced
895 subduction, but regionally more important are changes in wind patterns that cause
896 modulations in Ekman pumping and subduction (Couespel et al., 2019). Thus, future
897 trends in the northern Indian Ocean OMZs derived from the ESMs are highly
898 uncertain, with predicted potential increases or decreases in the volume of low
899 oxygen waters, depending on the model and the oxygen levels under consideration
900 (Bopp et al., 2013; Cocco et al., 2013).

901

902 **6.3 Implications**

903 The OMZ in the Indian Ocean is the one we know least about but it may also be the
904 OMZ with the most complex dynamics in terms of forcing and variability. As
905 discussed before, regional eddy resolving modelling studies have been able to
906 reproduce the OMZs and thus they have helped us to understand the interplay
907 between physical and biogeochemical drivers (Lachkar et al., 2019; McCreary Jr et

908   al., 2013; Resplandy et al., 2012; Resplandy et al., 2011). Global models still struggle
909   to reproduce the Indian Ocean OMZ. One explanation for this is the coarse resolution
910   of these models, i.e., they cannot resolve the mesoscale and submesoscale
911   processes that ventilate the subsurface waters and they underestimate coastal
912   upwelling during the monsoon seasons and, therefore, also primary production and
913   biological oxygen demand. As a result, the oxygen trend in the tropical Indian Ocean
914   remains unclear. However, in addition to poor representation of mesoscale and
915   submesoscale features in global models, large uncertainties stem also from largely
916   unknown biogeochemical and ecosystem responses to global physical changes.

917   **7. Ecosystem responses**

918   **7.1 Pelagic ecosystems**

919   Dissolved oxygen concentrations in seawater are crucial for the successful
920   development of many pelagic organisms, particularly marine animals (both
921   vertebrates and invertebrates) whose metabolism, life cycle performance, growth
922   capacity, reproductive success and longevity are intimately linked to oxygen
923   availability. Even though an oxygen concentration of < 60 - 63 µM is widely accepted
924   as a threshold below which higher organisms start to suffer from the lack of oxygen
925   the tolerance to decreasing oxygen, critical concentrations vary enormously among
926   species and even within the same species (Ekau et al., 2010; Vaquer-Sunyer &
927   Duarte, 2008). Differences can be very large even at various growth stages of
928   animals (Miller et al., 2002). Many fish larvae present in the pelagic realm are
929   incapable of further growth and development at oxygen values < 134 µM, while
930   organisms such as euphausiids can survive to 4.5 µM. Thus, a change in the
931   average or the range of dissolved oxygen concentrations in the water column could
932   have significant impacts on the survival of certain species and consequently the
933   species composition in the ecosystem. As compared to marine vertebrates and
934   invertebrates, the impacts of hypoxia on phytoplankton physiology and growth are
935   less known.

936   **7.1.1 *Noctiluca* blooms**

937   There is a large body of evidence on the effects of hypoxia on macro-organisms.
938   This includes reduced diel migration depths, vertical habitat compression and
939   shoaling distributions of fishery species and their prey (Breitburg et al., 2018).
940   However, few reports exist on the effects of hypoxia on phytoplankton, the primary
941   producers of the marine ecosystem. This is because it is generally understood that
942   biological consequences of reduced oxygen concentrations are likely to be most

notable for the 200 – 300 m layer, as these waters impinge on the euphotic zone (Stramma et al., 2010b). There have been several reports of coastal upwelling bringing up nutrient-enriched and hypoxic waters onto continental shelves stimulating production and increasing local biological oxygen demand (Stramma et al., 2010b). Death and decay of phytoplankton blooms (often harmful algae), of exceptional biomass, can completely strip nearshore waters of oxygen. But in the Arabian Sea, which is seeing one of the most extreme and dramatic changes tied to anthropogenic planetary warming, there has been a shift in the base of the ecosystem from predominantly autotrophy before 2000 (Garrison et al., 1998; Garrison et al., 2000; Smith et al., 1998a), to greater dependence on mixotrophy more recently (Gomes et al., 2014). A large-scale, ongoing study conducted by the National Institute of Oceanography, India, from 2003 onward, in support of India's ocean color program, first documented the appearance of extensive blooms of green mixotrophic dinoflagellate, *Noctiluca scintillans* (*Noctiluca*). *Noctiluca* is large (~1 mm in diameter) and capable of sustaining itself via photosynthesis from its green free-swimming endosymbionts, *Pedinomonas noctilucae* (Wang et al., 2016) and/or by ingestion of exogenous prey (Goes et al., 2016; Gomes et al., 2014; Gomes et al., 2009; Prakash et al., 2008; Prakash et al., 2017). Within a decade and a half, *Noctiluca,* has taken over the once diatom-dominated food chain of the Arabian Sea and the Sea of Oman, forming large green mats that can be observed from space with regular predictability (Fig. 16).

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 before.

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, provided 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 required 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 as 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).

7.1.2 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

1016 ecological functions strongly (Saltzman et al., 1997; Wishner et al., 2008). Recent
1017 modeling studies (Aumont et al., 2018) estimate that about one third of the epipelagic
1018 biomass performs diurnal vertical migrations.
1019 In general, most zooplankton taxa show minimum abundances in the core of the
1020 OMZ, and higher abundances in well-oxygenated waters above or beneath the OMZ
1021 (Böttger-Schnack, 1996; Saltzman & Wishner, 1997; Wishner et al., 1995). Certain
1022 zooplankton, however, have developed vertical migration strategies that enable them
1023 to pass through or even live within the OMZ (Gonzalez et al., 2002; Herring et al.,
1024 1998; Longhurst, 1967). The ability to do so has been linked to the presence of lactic
1025 dehydrogenase (LDH), an enzyme associated with anaerobic metabolism
1026 (Escribano, 2006; Gonzalez & Quiñones, 2002).
1027 In the Arabian Sea, almost 85% of the epipelagic mesozooplankton biomass is found
1028 within the upper aerobic part of the seasonal thermocline or approximately in the
1029 upper 100 m. Below this region, in the anaerobic part of the seasonal thermocline,
1030 zooplankton concentrations decline sharply (Banse, 1994; Böttger-Schnack, 1996;
1031 Smith et al., 2005; Wishner et al., 1998). The most comprehensive study of this
1032 region, the US JGOFS (Smith et al., 1998b; Smith & Madhupratap, 2005), concluded
1033 the following *vis a vis* zooplankton distributions and the OMZ: 1) exclusion from the
1034 suboxic core of the OMZ of most zooplankton biomass 2) paradoxically, the
1035 occurrence of extremely high abundances of a few species of diel vertical migrators
1036 at depth during the daytime, well within the suboxic zone 3) organism-specific (and
1037 probably species-specific) distribution boundaries at the upper and lower edges of
1038 the OMZ, probably associated with particular oxyclines 4) very high biomass of diel
1039 vertical migrators that moved between the surface waters at night and the suboxic
1040 waters during the day with many of these animals spending the day at depths where
1041 the oxygen was less than 4.5 µM and 5) aggregation of mesozooplankton
1042 communities to surface layers, in locations where the OMZ was forced upwards due
1043 to physical processes and where they are susceptible to predators.
1044 A comparison between a eutrophic, more oxygenated onshore station and an
1045 offshore station with a strong OMZ elucidated the influence of depth and oxygen
1046 concentration, as well as other factors on the copepod distribution in the Arabian Sea
1047 (Wishner et al., 2008). The extent and intensity of the oxycline at the lower boundary
1048 of the OMZ, and its spatial and temporal variability over the year of sampling, was an
1049 important factor affecting distributional patterns. Calanoid copepod species showed
1050 vertical zonation through the lower OMZ oxycline, but no apparent diel vertical
1051 migration for either calanoid or non-Calanoid copepods was observed at these
1052 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 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 oxygen deficit. Aumont et al. (2018) used a fully coupled model to simulate the net impact of diurnal vertical migration on dissolved oxygen of the entire pelagic ecosystem on a global scale. Respiration and egestion by migratory organisms induce a modest decrease in oxygen between 150 and 500 m, which reaches about 5 µM averaged globally at 500 m, although less so in the Arabian Sea and the Bay of Bengal. Three distinct vertical layers could be distinguished over the global ocean: 1) Vertical migration generates a positive dissolved oxygen anomaly in the subsurface above 200 m, that can exceed 10 µM which is explained by less intense respiration in the seasonal thermocline 2) Further below, down to about 1,000 diel vertical migration produces a depletion in oxygen from respiration by migrators with greatest depletion at middle and high latitudes 3) Finally, in the bathypelagic domain (below 1,000 m), oxygen levels are increased by almost 2 µM as a result of a slightly lower oxygen consumption.

7.1.3. Implications

We are still uncertain if the recent emergence and persistence of *Noctiluca* blooms will further intensify the Arabian Sea's OMZ. Satellite-derived Chlorophyll-*a* trends (1980-2019) reveal an almost three-fold increase in phytoplankton biomass, with increases particularly in the northwestern and central Arabian Sea (Goes et al., 2020). With respect to repercussions for the food chain, 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. High gelatinous zooplankton biomass is often observed in regions of persistent low oxygen concentrations (Lucas et al., 2014) suggesting that the recent appearance of extensive blooms of *Noctiluca* reflect the intensification of the Arabian Sea OMZ. The earlier, comprehensive JGOFS studies of the 1990s, which investigated the vertical migration and distributions patterns Arabian Sea's OMZ, have not been repeated even on a moderate scale as acute piracy and political instability have hindered campaigns to the region. Thus, while modeling (Lachkar et al., 2019; Lachkar et al., 2018) and data compilation studies (Banse et al., 2014; Rixen et al., 2014) suggest the expansion of the OMZ in the Arabian Sea, as discussed earlier, little is known of its effect on zooplankton distribution and vertical migration.

7.2 Benthic ecosystems

7.2.1 Benthic communities

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

1123 reduced numbers and diversity at the OMZ core (e.g., Ingole et al., 2010; Levin et al.,
1124 2000).

1125 Further, across the OMZ boundaries, clear "edge effects" have been observed; sharp
1126 changes in community composition and faunal abundance linked to different oxygen
1127 thresholds (e.g., Levin et al., 2009b). These have also been observed on other
1128 hypoxia-impacted margins in the eastern Pacific and off SW Africa (e.g., Levin et al.,
1129 1991), as well as in hypoxic basins such as the Baltic Sea, and at sites impacted by
1130 excess organic matter input (e.g., Rosenberg, 2001). While there are some common
1131 patterns, specific oxygen thresholds are difficult to constrain because of inter-margin
1132 and inter-basin differences in faunal assemblages, which are also affected by local
1133 differences in factors such as food availability and predator avoidance, as well as
1134 inter-study differences in the availability and quality of bottom-water oxygen data.

7.2.2 Benthic ecosystem function

1136 The strong but variable cross-OMZ gradients in bottom-water oxygen and benthic
1137 communities translate to contrasts in benthic ecosystem function, which also varies
1138 between margins. For example, the numbers, size and depth of faunal burrows, and
1139 the extent of bioturbation and bio-irrigation, change across the OMZ boundaries
1140 (e.g., Cowie et al., 2009a; Smith et al., 2000). In the extreme case, this leads to total
1141 absence of bioturbation and bio-irrigation at the core of the OMZ off Pakistan, and
1142 the resulting presence of annually laminated (varved) sediments, which are not
1143 observed on the better-ventilated margins of the Arabian Sea or in the Bay of Bengal.
1144 In the Arabian Sea, there are also clear oxygen-dependent differences in benthic
1145 community organic matter processing, as have been revealed by tracer incubation
1146 experiments. For example, a threshold oxygen concentration occurs, above which
1147 macrofauna dominate short-term organic matter (OM) processing, and below which
1148 meiofauna and bacteria dominate. This was illustrated on the Pakistan margin both
1149 at sites that spanned the lower OMZ boundary and at a shelf-edge site that
1150 underwent strong seasonal change in bottom-water oxygen levels, from fully
1151 oxygenated (intermonsoon) to hypoxic (summer monsoon) (e.g., Andersson et al.,
1152 2008; Pozzato et al., 2013; Woulds et al., 2009; Woulds et al., 2007).

1153 Further, the "edge effect" seen in benthic community composition also has been
1154 observed in faunal OM processing. At sites in the lower OMZ transition zone, the
1155 polychaete *Linopherus sp.* showed clear morphological adaptation to low oxygen
1156 levels, and overwhelmingly dominated both the benthic community and also the
1157 uptake and processing of organic matter (Jeffreys et al., 2012). These results, and
1158 those of other experiments (e.g., Hunter et al., 2012; White et al., 2019), illustrate

that faunal assemblage composition may represent an important factor determining the pattern of seafloor processing, but also the composition, bioavailability and fate of residual organic matter. It is certainly clear that faunal digestive processes are recorded in the composition of organic matter deposited across the margins (e.g., Jeffreys et al., 2009; Smallwood et al., 1999). In summary, oxygen-dependent cross-margin variability in benthic communities and ecosystem function (feeding, bioturbation and bio-irrigation etc) may be important contributors to the role that oxygen exposure plays in controlling organic carbon distribution and burial across Arabian Sea margins, although other factors, most notably hydrodynamic processes, are also important (e.g., Cowie, 2005; Cowie et al., 2009b; Koho et al., 2013; Kurian et al., 2018).

7.2.3 Sediment redox conditions and microbial processes

Alongside the contrasts in faunal communities, bioturbation and irrigation, there are cross-OMZ differences in sediment redox conditions and microbial processes. Again, these are expressed to varying degree on the different margins of the Arabian Sea (Cowie, 2005), and will be less apparent in the Bay of Bengal due to the less intense oxygen depletion at the OMZ core. In the Arabian Sea, sulfate reduction has generally been shown to be surprisingly limited in near-surface sediments (top ~50 cm) (e.g., Cowie, 2005; Law et al., 2009), and redox conditions overall to be only moderately reducing (e.g., Crusius et al., 1996) relative to rates and conditions observed on upwelling/OMZ margins in other basins. Nonetheless, Pakistan margin sediments, and possibly those on other Arabian Sea margins, are home to significant rates of denitrification and anammox (e.g., Schwartz et al., 2009; Sokoll et al., 2012) and authigenic phosphorous (P) burial (e.g., Filippelli et al., 2017; Kraal et al., 2012). These phenomena represent important sink terms in the N and P biogeochemical cycles, and, along with sediment-water nutrient fluxes that vary in direction, magnitude and N:P stoichiometry across the OMZ, serve as potential controls on pelagic nutrient inventories.

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

7.2.4 Implications

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

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

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

Intensification or increased duration of coastal hypoxia could lead to increasing occurrence of mass mortality or to reduced ability of faunal populations to recover

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

8. Conclusion

The Arabian Sea and the Bay of Bengal are home to ~59% of the Earth's marine sediments exposed to severe oxygen depletion and approximately 21% of the total volume of oxygen-depleted waters. However, the Arabian Sea OMZ is larger, more intense and reveals functional anoxia in its upper part, whereas the smaller and less intense Bay of Bengal OMZ seems to be on the verge of becoming functionally anoxic. Since oxygen concentrations within this range can presently only be measured by STOX sensors, and are below detecting limits of standards methods, our understanding of the response of the nitrogen cycle to such low oxygen concentrations is based on only a few measurements and suffers from the lack of data.

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

1268 data and the influence of the remote forcing processes that drive this variability (e.g.,
1269 IOD and ENSO) is not fully understood.

1270 Results obtained from the global atmosphere-ocean Kiel Climate Model and eddy
1271 resolving regional models indicate that a decreasing inflow of oxygen-enriched water
1272 masses from the south (ICW) intensified the Arabian Sea OMZ during the last 6000
1273 years, whereas a decreasing oxygen concentration within inflowing Persian Gulf
1274 Water intensifies the OMZ in response to global warming. These trends significantly
1275 affect benthic and pelagic ecosystems. The regular occurrence of *Noctiluca* is an
1276 example of a new phenomenon that is assumed to herald a regime shift within the
1277 pelagic ecosystem of the Arabian Sea in response to declining concentrations of
1278 dissolved oxygen. Comprehensive studies investigating possible repercussions on
1279 the OMZ through e.g. impacts on the export production and vertical migration and
1280 distributions of zooplankton are missing. Accordingly, these recent changes augment
1281 the problems that arise when trying to represent the Indian Ocean OMZ in models,
1282 and thus in predicting the impact of the changing monsoon system on productivity
1283 and OMZ development under global change scenarios. This holds true for the CMIP5
1284 models and is hardly improved in the new CMIP6 models.

1285 **9 Author contribution**

1286 The paper was written jointly by all co-authors whereas Tim Rixen coordinated the
1287 writing processes and co-authors focused on specific sections as listed in the
1288 following: Sections 1 – 3 (Tim Rixen), section 4 (Zouhair Lachkar), section 5 (Birgit
1289 Gaye and Joachim Segschneider), section 6 (Henrike Schmidt and Raleigh R.
1290 Hood), section 7.1 (Joaquim Goes, Helga do Rosário Gomes and Arvind Singh), and
1291 section 7.3 (Greg Cowie).

1292 **10 Competing interests**

1293 The authors declare that they have no conflict of interest.

1294 **Acknowledgment**

1299

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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: Oxygen profile which were obtained during the RV Meteor cruise M74/1b (Station 450) in 2007 at around 64°E and 15°N in the Arabian Sea (see Rixen et al. (2014) for further details). Blue arrows indicate processes controlling the oxygen concentrations in the OMZ such as the respiration of organic matter, fluxes of oxygen across the air-sea interface, upwelling and lateral inputs of oxygen-enriched waters, as well as the outflow of OMZ water balancing the inflow of water.

Figure 5: (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 6: Conceptual illustration of the meridional overturning circulation the Indian Ocen according to Rahaman et al. (2020) and Bange et al. (2000), including the supply of oxygen via air-sea fluxes and upwelling of oxygen-enriched deep waters. The oxygen profiles were obtained during the RV Meteor cruise M74/1b and the RV

Sonne cruise SO270 in 2007 and 2019, respectively at 15°N and 15°S and approximately the same longitude (~ 64°E). ICW means Indian Ocean Central Water.

Figure 7: (a) The seasonal mean areal extension and the depth 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 8: (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 OMZ thickness. The data are the same as shown in figure 7.

Figure 9: 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 10: 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 11: Schematic sketch illustrating the role of mesoscale eddies in ventilating the Arabian Sea OMZ (a) by enhancing isopycnal mixing and water stirring (based on results from Lachkar et al (2016). (b) In the absence of eddies (e.g., in coarse-resolution global models) the along-isopycnal ventilation is reduced and the OMZ is larger and more intense, leading to potentially stronger denitrification and more compressed marine habitats.

Figure 12: (a) Locations of high resolution cores (circles) and areas of model simulations (boxes). (b) Increasing δ^{15}N values in high resolution cores from the Arabian Sea (note inverted scale) show increasing denitrification since about 6000 – 8000 years BP; data from the northern (yellow; light brown), eastern (red), western (blue) and southwestern (black) Arabian Sea. Sediment cores: 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 13: 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 14: (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 15: 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

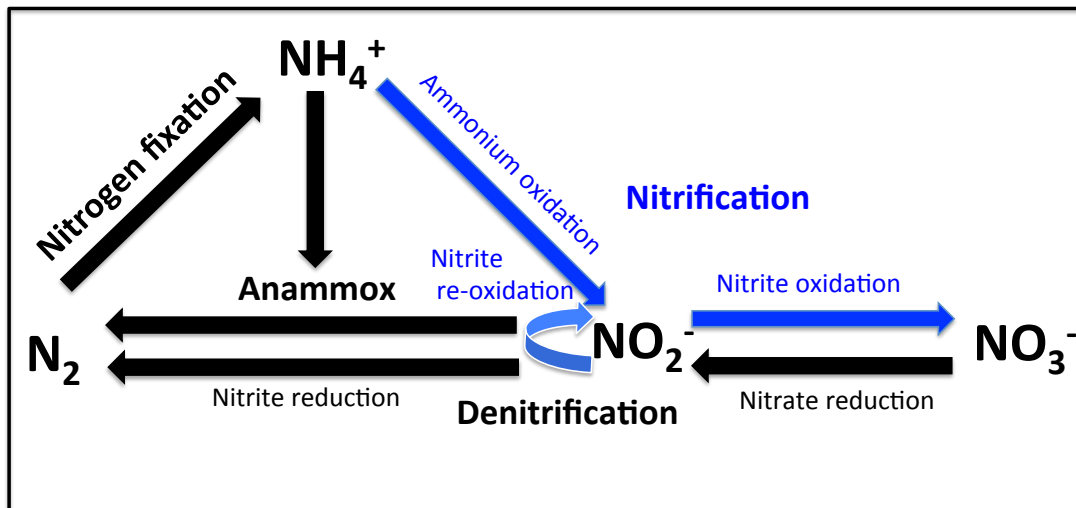boundary shoals during the summer monsoon season. Faunal classes are as defined by Gooday et al (2009).
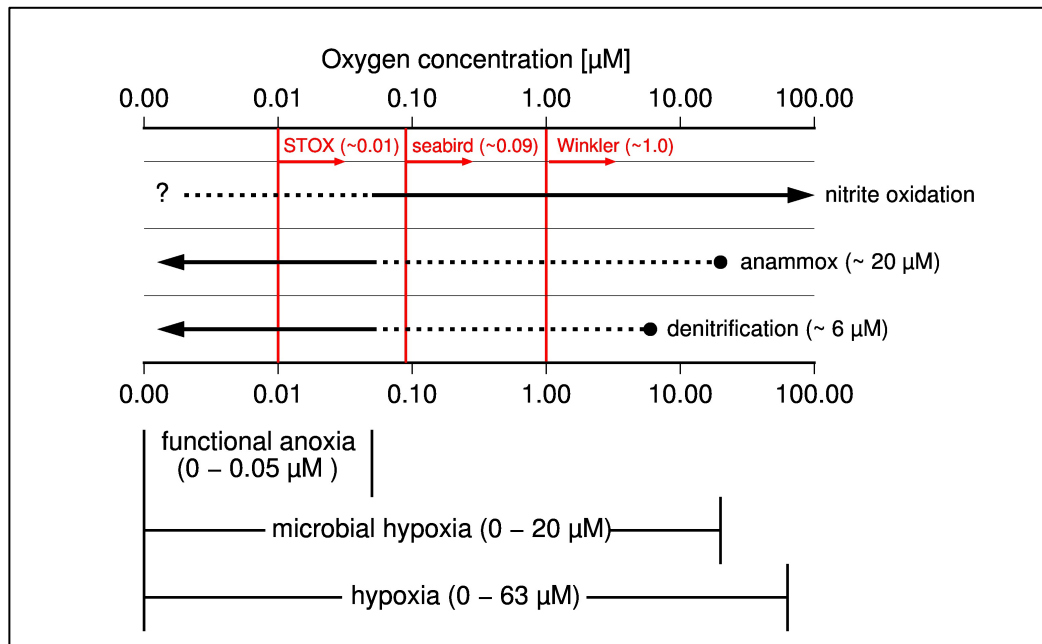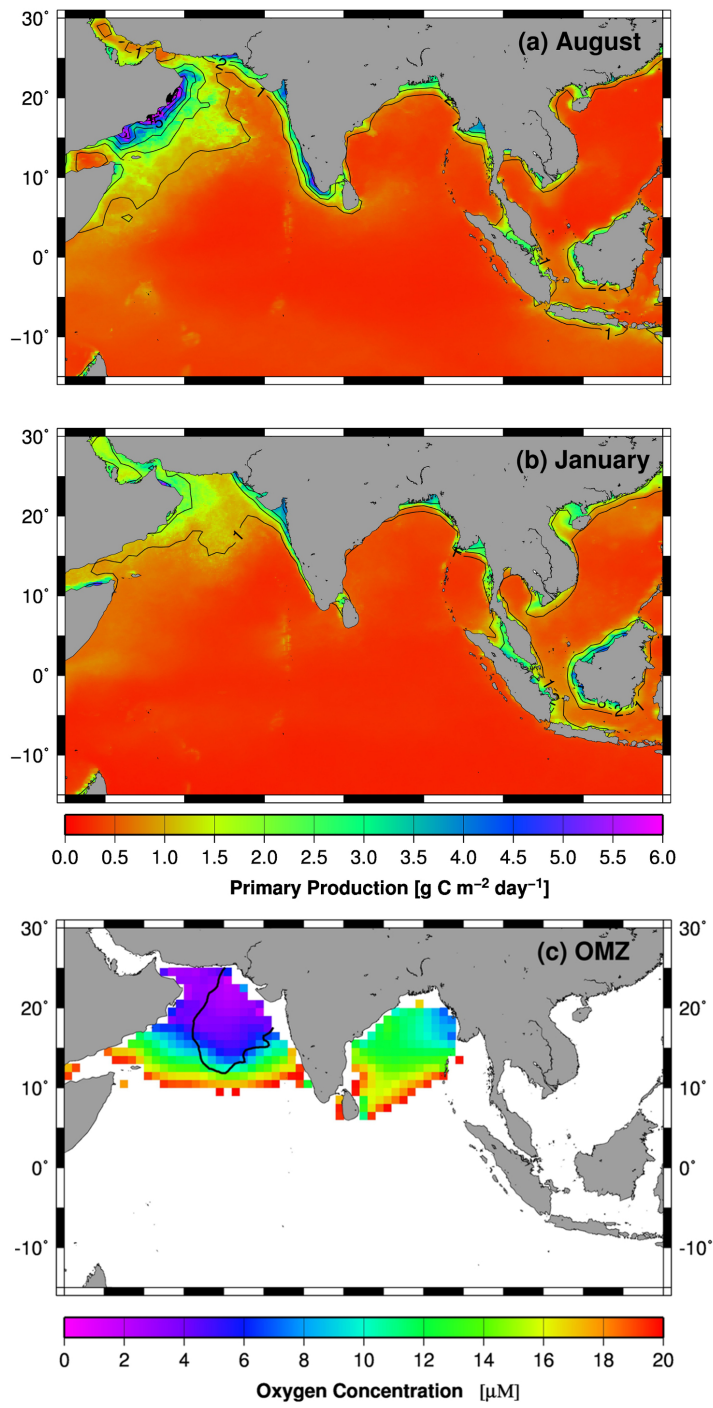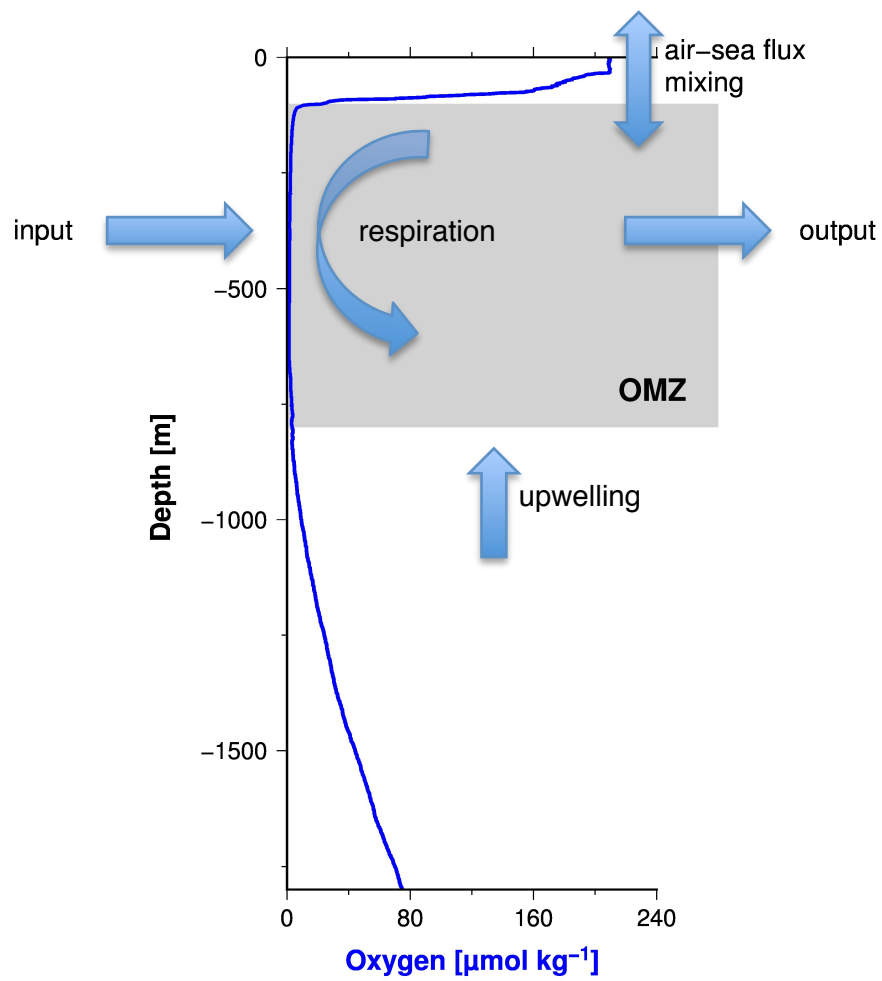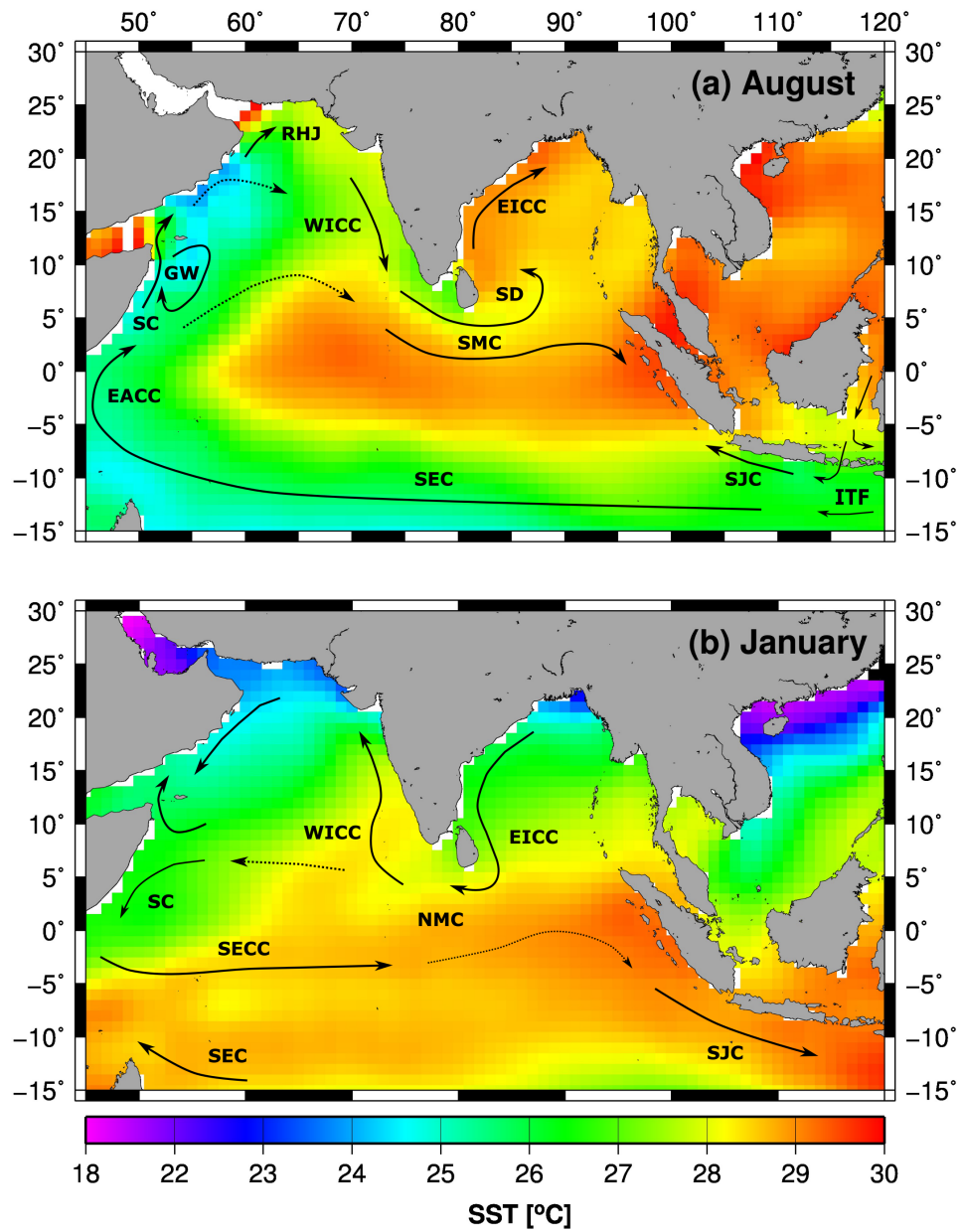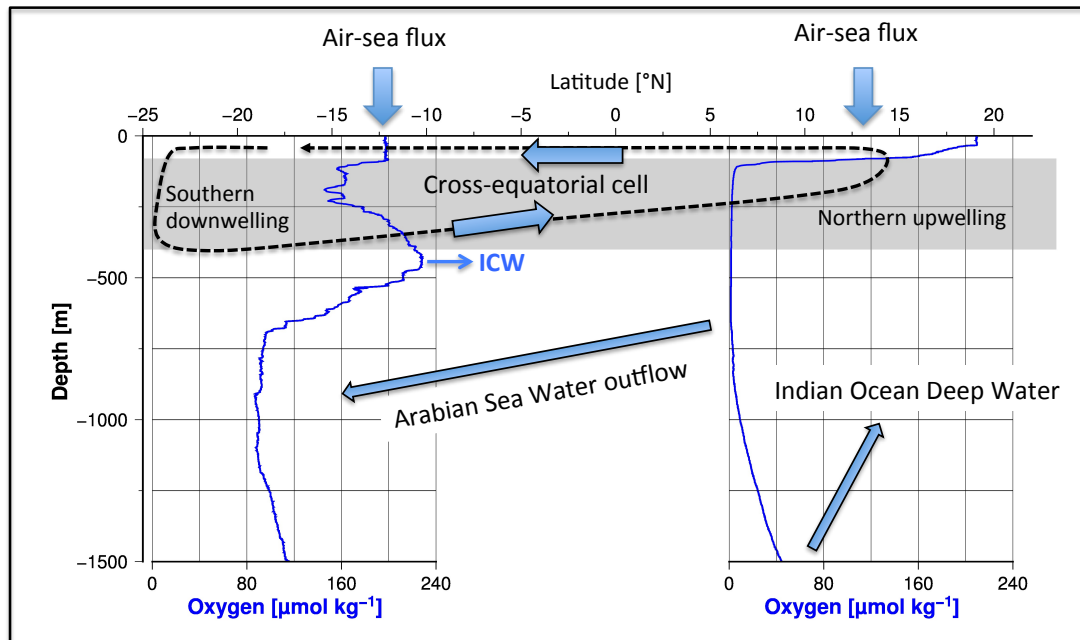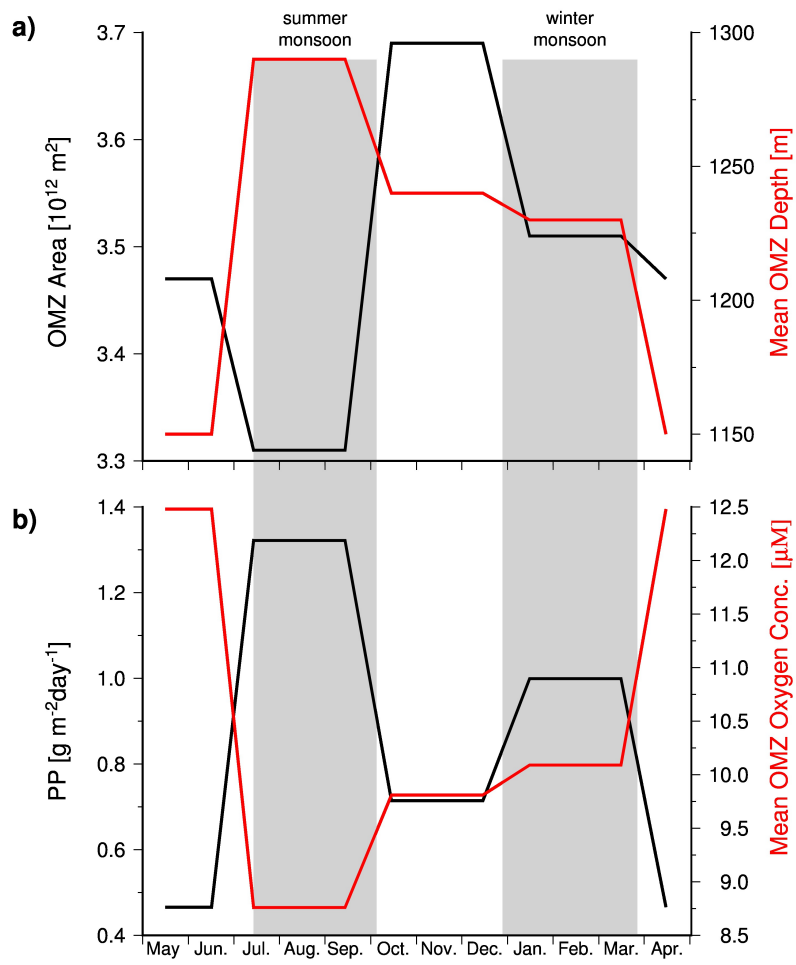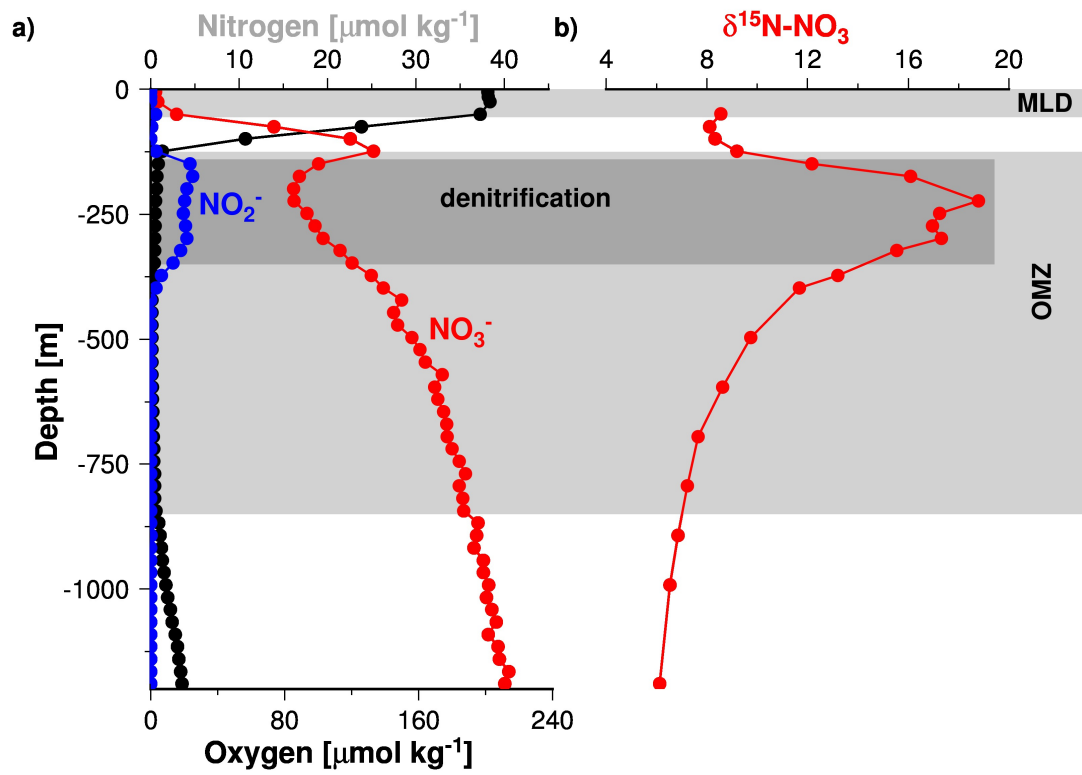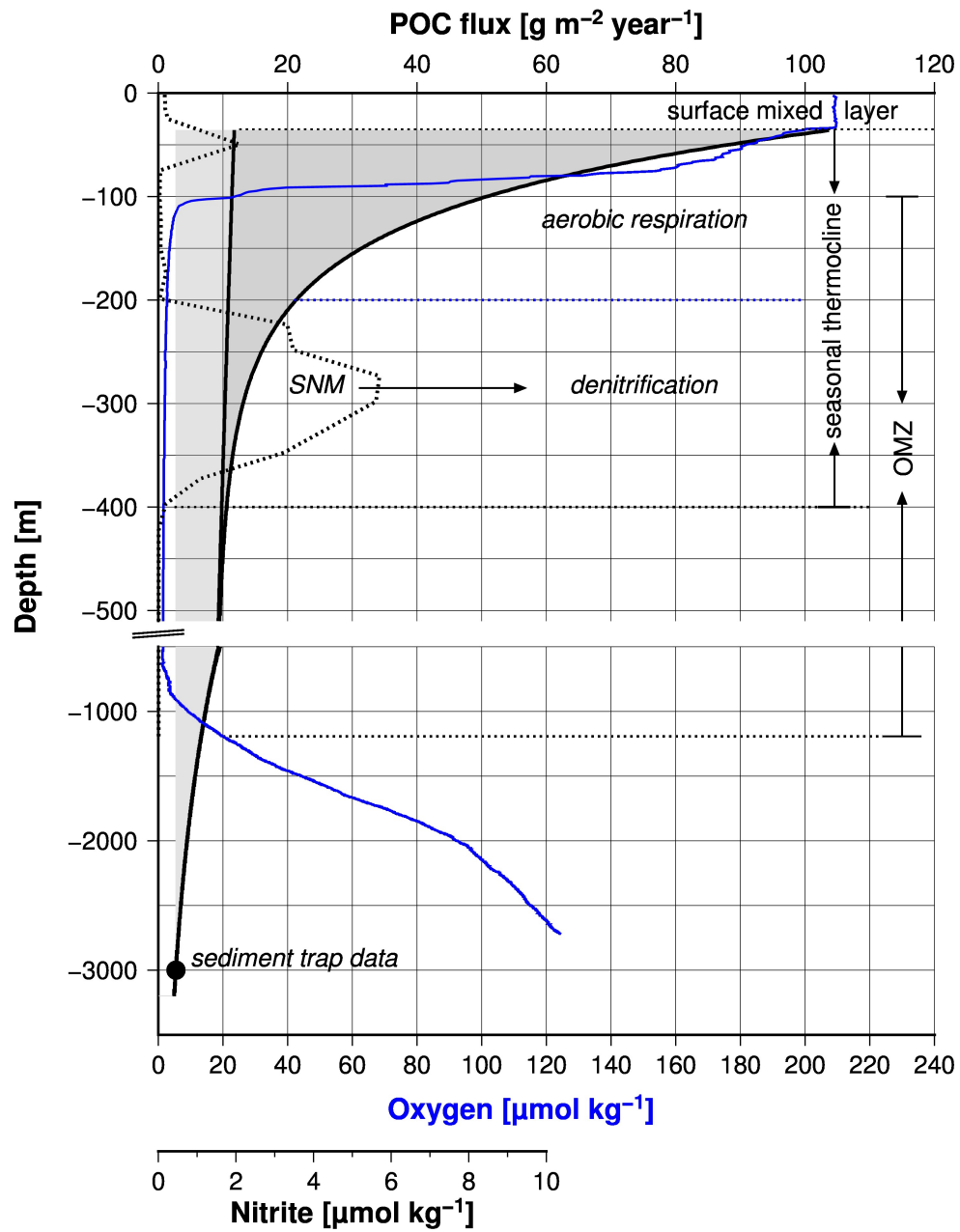
Figure 1
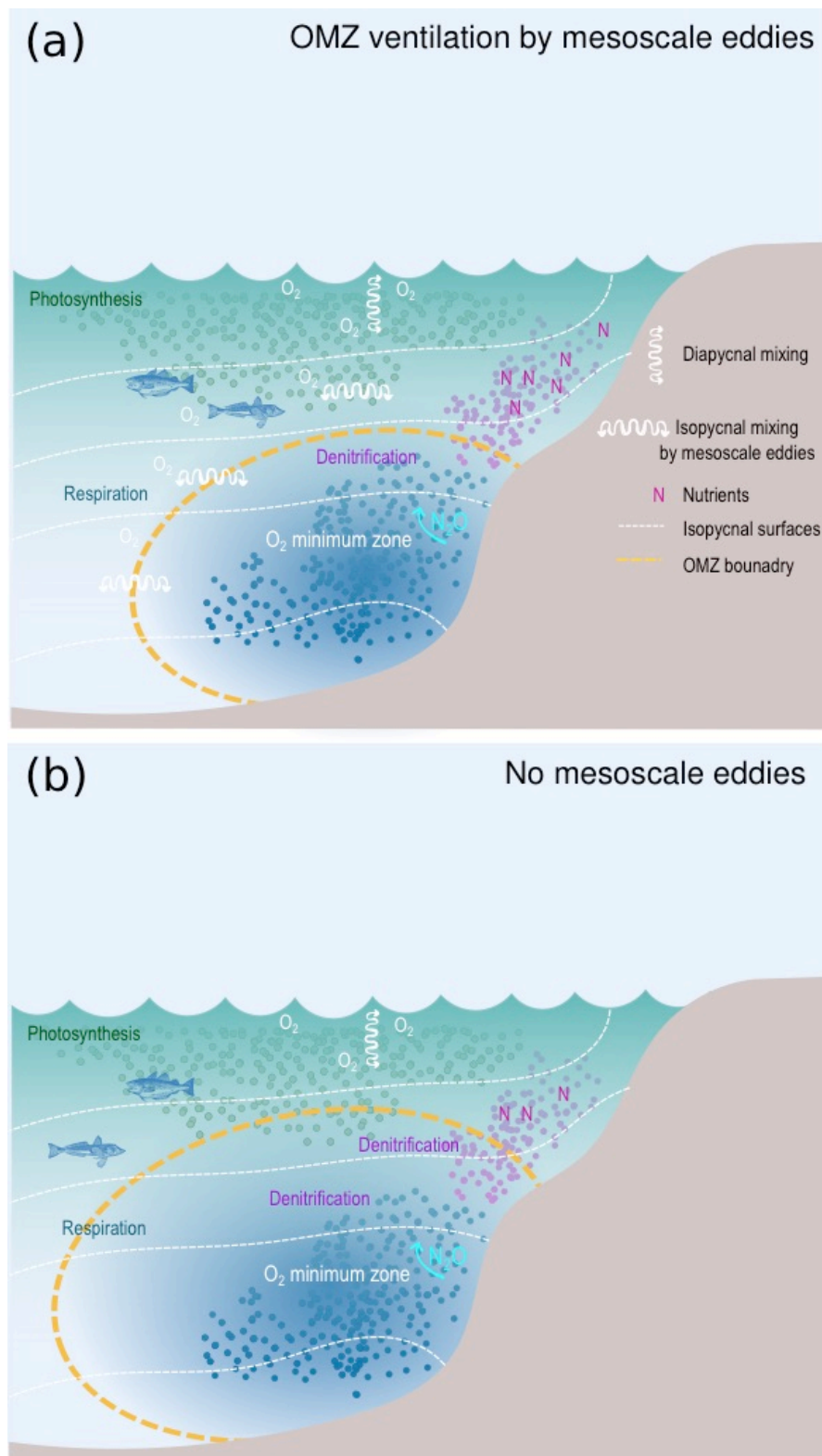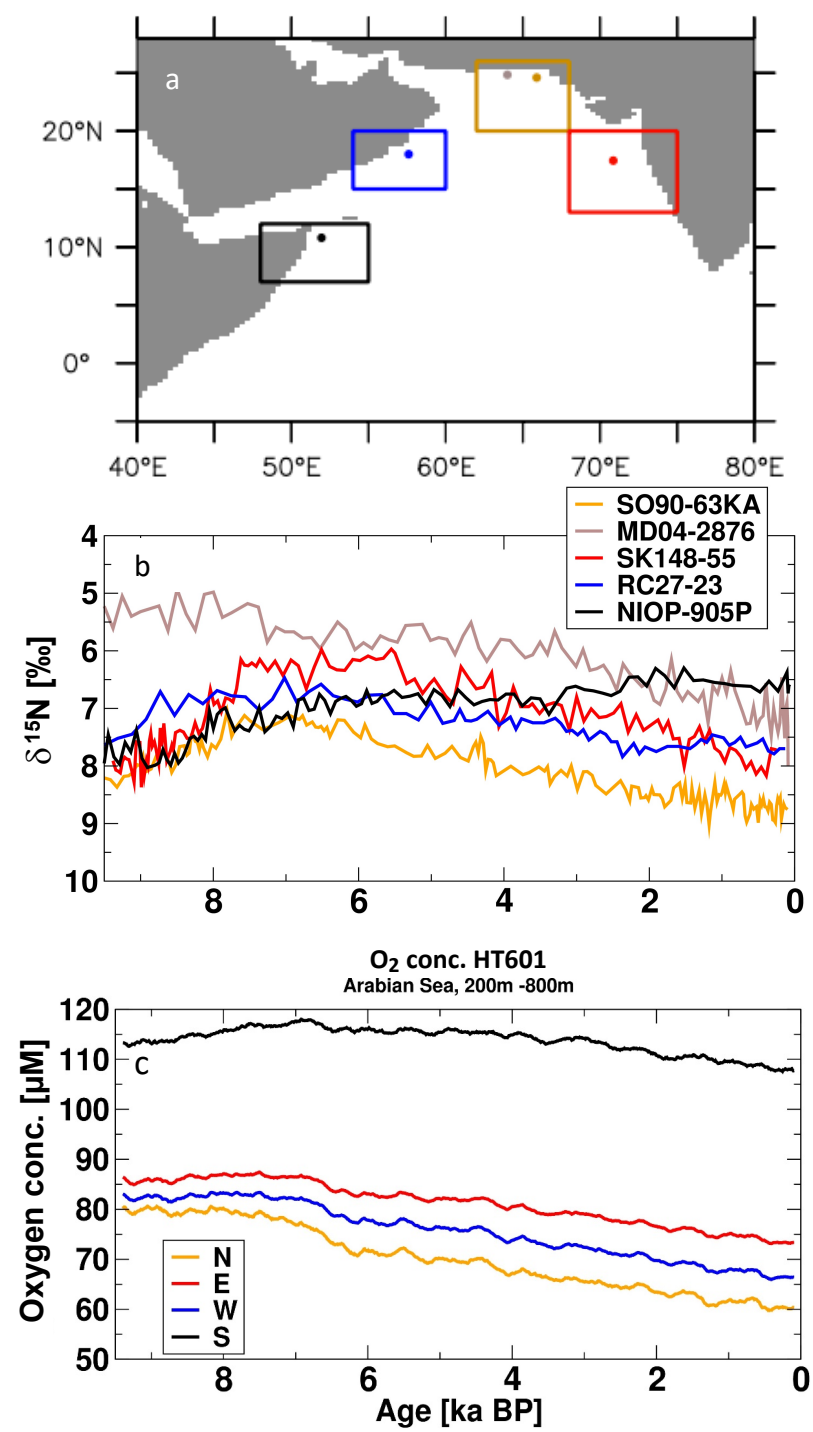
Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

a)

y = −4.35x + 14.49 r^2=0.999

OMZ Oxygen Conc. [μM] vs PP [g m^{-2}day^{-1}]

b)

y = −36.7x + 1605, r^2=0.990

OMZ Thickness [m] vs OMZ Oxygen Conc. [μM]   [μM]

Figure 9

Figure 10

POC flux [g m⁻² year⁻¹]

surface mixed layer

aerobic respiration

SNM → *denitrification*

sediment trap data

Depth [m]

seasonal thermocline

OMZ

Oxygen [µmol kg⁻¹]

Nitrite [µmol kg⁻¹]
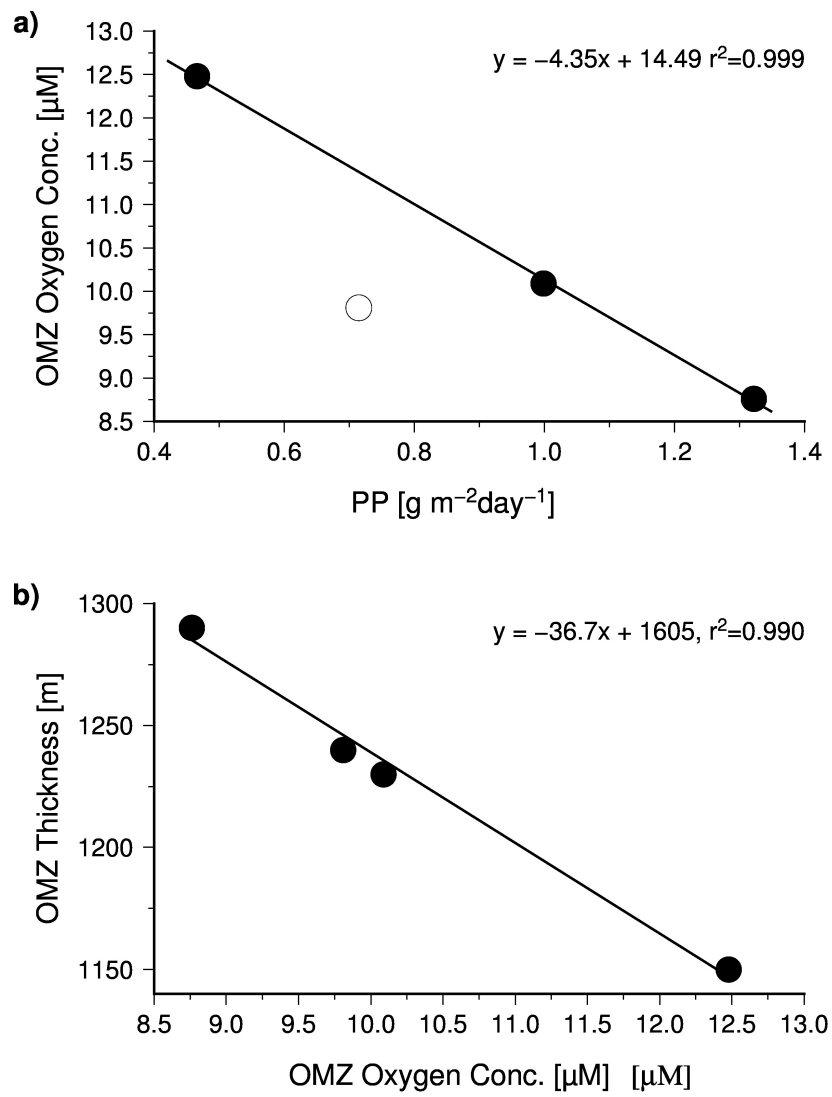
Figure 11

Figure 12

Figure 13

Figure 14

Figure 15