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Is the expansion of oxygen minimum zones impacting the health of modern ocean basins? A review

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A B S T R A C T

Oxygen minimum zones (OMZ) are represented by sharply depleted oxygen concentrations in the modern ocean basins. The expansion of these zones is documented since 1960. They have been expanding globally in the world's oceans with profound implications for marine ecosystems and biogeochemical cycles. Under this review, we synthesize and integrate the current knowledge on the factors, dynamics and consequences of OMZ expansion in the modern ocean basins. We have explored the interplay of physical, chemical and biological factors conducive to OMZ formation and intensification, highlighting the role of ocean circulation patterns, nutrient enrichment from anthropogenic activities and augmenting influence of climate change. The impact of OMZs on marine ecology are explored with the focus on physiological stress on marine organisms, habitat compression, shifts in community structure and potential loss of biodiversity. We have also investigated their contribution to greenhouse gas emissions and the biogeochemical significance of OMZs, particularly in the context of nitrogen and other nutrient cycles. Further, this work emphasizes on the complex feedback loops between OMZ expansion and climate change underscoring the urgent need for mitigation and adaptation strategies. At the outset, the study discusses the future research scopes and management approaches crucial for addressing the challenges posed by expanding OMZs thereby ensuring the health and sustainability of modern ocean basins.

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1. Introduction

Over a geological past, ocean has evolved from being a sulphidic to sulphate in character with transformation from anaerobic hothouse of early life to well oxygenated nature supporting multicellular lifeforms (Kasting and Siefert, 2002). This transformation was interrupted by several extinction events followed by radiation of species leading to biological diversity (Henehan et al., 2019; Jurikova et al., 2020). However, during Anthropocene, the human activities have led to significant changes in the modern oceans. Recent studies observe that oceans have become more acidic and significantly warmer (Orr et al., 2005; Babila et al., 2022). As these changes continue and intensify, it will lead to severe disturbances in marine ecology affecting structure of marine biosphere with resulting effect on socio-economic benefits (Doney., 2010; Prada et al., 2017). Oxygen minimum zones (OMZs), also defined as oxygen deficient regions of ocean, are vital for these changes and represent a striking paradox within the world's oceans (Keeling et al., 2010). These zones are starkly juxtaposed to the oxygen-rich surface waters that support a flourishing marine life. OMZs are typically situated at depths ranging from 200 to 1000 m such as eastern tropical North and South Pacific (ETNP and ETSP), but are not necessarily restricted to these depths alone (Fig. 1; Lalli and Parsons, 1993). Local conditions, such as those reported in the Arabian Sea (AS) and Bay of Bengal (BoB), can lead to the formation of OMZs at shallower and mid depths respectively, sometimes as shallow as 50–100 m (Fig. 1; Morrison et al.,1999; McCreary et al., 2013; Al Azhar et al., 2017). This depth variability highlights the complex interaction of physical, chemical, and biological factors that control the distribution and characteristics of OMZs. This phenomenon forms in the ocean water column when oxygen requirement during decomposition of organic matter exceeds the oxygen availability in restricted regions of the oceans (Helm et al., 2011). OMZs are termed as being 'more intense' when oxygen concentration in its core is lower and this concentration even reaches as low as <1 micromole (μm). Water stratification occurs as ocean surface temperatures tend to increase, discouraging vertical mixing. The spatial extent of OMZs is projected to swell, particularly in the tropical regions where the effects of global warming are more pronounced, leading to a significant impact on marine ecosystems and nutrient cycling (Bindoff et al., 2019).

In spite of their uninhabitable nature, OMZs support a distinctive marine ecosystem that adapted to oxygen depleted conditions. It plays a crucial role in managing the global biogeochemical cycles, particularly the carbon and nitrogen cycles. As a matter of fact, these are identified as the foremost sites for nitrogen loss to the atmosphere aided by microbial processes such as denitrification and anammox (Arrigo, 2005; Paulmier and Ruiz-Pino, 2009). These processes transform the bioavailable nitrogen into forms unusable by most marine organisms thereby influencing the primary productivity and regulating the overall health of the ocean. Understanding the OMZ dynamics is critical for both comprehending the intricate web of marine life they support and for predicting the climate change impacts on these zones. There is recent evidence (Wright et al., 2012; Breitburg et al., 2018; Long et al., 2021) that global climate change, primarily through warming waters and increased stratification, has already or is poised to reduce oxygen levels of several modern ocean basins. This trend raises concerns about the potential expansion of existing OMZs and the formation of new ones with potentially far-reaching consequences for marine ecosystems challenging the socio-economic aspects of the ocean basins.

With this background, the study aims to provide an extensive, although not exhaustive, overview of main and most intense OMZs in the modern ocean basins (ETNP, ETSP, AS and BoB), delving into their characteristics, causes and effects on marine ecosystems and biodiversity. We also intend to explore the delicate balance of factors which contribute to their formation, the unique adaptations of organisms that flourish within these oxygen-depleted zones and critically compare their important characteristics to understand the implications of OMZ expansion for the future health of modern ocean basins. By shedding light on these critical aspects of OMZs, we hope to contribute to a thorough understanding of their significance in the context of a rising Earth's surface temperature and changing global climate.

2. Causes of OMZ

Oxygen saturation reaches to critically low levels in the regions of oxygen minimum zones. They are simply not a product of low oxygen supply, but rather interplay of physical, biological, and chemical processes that contribute to their formation and sustenance. Understanding of these intricate processes is vital for forecasting how OMZs might respond to a changing climate and the potential consequences for marine ecosystems.

2.1. Physical processes: limiting oxygen supply and ventilation

One of the primary physical processes influencing the formation of OMZ is ocean stratification. This stratification occurs when warmer, less dense water overlies cooler, denser water creating a barrier that inhibits vertical mixing (Singh et al., 2018). It is often exacerbated by temperature and salinity gradients which can lead to reduced oxygen replenishment in deeper waters (Canfield and Kraft, 2022; Beghoura et al., 2023). Unlike the surface layer, where direct contact with the atmosphere allows for continuous oxygen replenishment, deeper waters rely on a process called ventilation. This involves the transport of oxygen-rich surface waters to deeper depths through a complex interplay of currents, winds, and water density gradients usually known as Thermohaline Circulation. This global conveyor belt plays a crucial role in transporting oxygenated surface waters towards the ocean depths. In poorly ventilated regions such as Eastern Tropical Pacific and Arabian sea, sluggish circulation can lead to the accumulation of organic matter and resultant oxygen depletion (Figs. 2 and 3; Espinoza-Morriberon et al., 2021; Rangamaran et al., 2023). However, the sluggish nature of this circulation, often taking centuries to complete a cycle which indicates that oxygen consumed in the deep ocean is not quickly replenished (Yamamoto et al., 2015). Additionally, interaction of eddies with OMZs can influence nutrient cycling and the distribution of oxygen, as these features can trap and transport water masses with varying oxygen concentrations (Keil et al., 2016). As ocean temperatures rise further due to climate change, the density difference between warm surface waters and colder, deeper waters increases causing stratification of ocean water column, thus, preventing the mixing of surface and deep waters, thereby limiting the oxygen supply to bottom waters. Moreover, OMZs often form water mass boundaries between distinct water masses of different densities and oxygen concentrations (Rixen et al., 2020). These boundaries act as barriers to mixing and trapping oxygen-poor waters within specific depth ranges.

2.2. Biological processes: oxygen consumption and remineralization

While physical processes in the ocean restrict the oxygen supply, biological activity within the ocean water column plays a key role in consuming the available oxygen, thus contributing to the formation of OMZs. The oxygen concentration is primarily reduced through respiration when its rate overwhelms the rate of oxygen

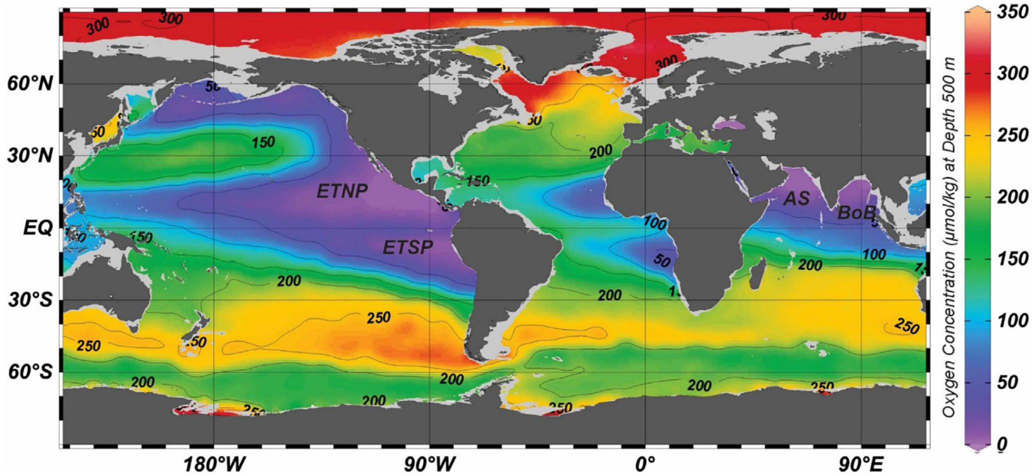

Fig. 1. World ocean map depicting dissolved oxygen concentrations at ~500 m depth. Note the significantly depleted oxygen concentrations in eastern tropical North and South Pacific (ETNP & ETSP), Arabian Sea (AS) and Bay of Bengal (BoB). Data source (Garcia et al., 2024a, 2024b) from NOAA World Ocean Database 2023 using all oxygen concentrations from 1965–2022 and was plotted using Ocean Data View.

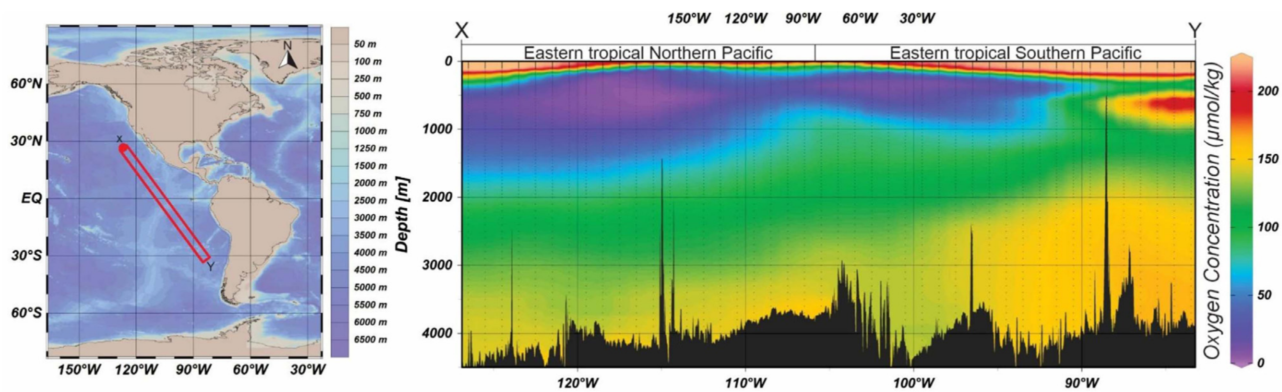

Fig. 2. Depth wise **c**ross section (X-Y) of dissolved oxygen profile of Eastern tropical North and South Pacific (ETNP & ETSP) oxygen minimum zones showing oxygen concentration from surface waters to the sea floor. Note the thickness of ETNP OMZ compared to ETSP OMZ.

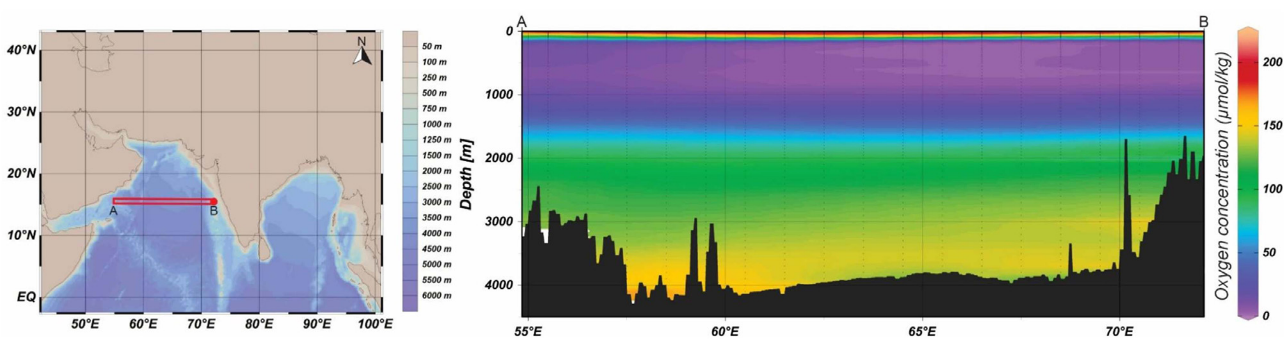

Fig. 3. Depth wise **e**ast-west **c**ross section (A-B) of dissolved oxygen profile of Arabian Sea (AS) showing wide extent and intensity of oxygen minimum zone.

supply (Rabalais et al., 2020). As organic matter sinks from the surface waters, it is ingested by archaea, bacteria and other microorganisms via microbial respiration (Ulloa et al., 2012; Baroni et al., 2020). This process utilizes oxygen and releases carbon dioxide, reducing oxygen concentration in the ocean water column. Further, the areas of the ocean with high primary productivity such as upwelling zones, often experience enhanced formation of OMZ. The abundance of phytoplankton in these regions of the oceans leads to an excess of organic matter sinking to deeper depths, steering microbial respiration (Paulmier et al., 2006; Fuenzalida et al., 2009; Thamdrup et al., 2012). The bacterial and microbial breakdown of this organic matter releases nutrients back into the ocean water column known as remineralization. This process, particularly in Bay of Bengal OMZ, gets enhanced due to the higher riverine supply from Indian landmass to Bay of Bengal thus facilitating the formation of OMZ (Figs. 1 and 4; Al Azhar et al., 2017). Though it is essential for nutrient cycling, this process further consumes oxygen exacerbating oxygen concentration in the OMZs (Giering et al., 2014; Limburg et al., 2020; Weber and Bianchi, 2020).

2.3. Chemical processes: oxygen depletion and nutrient cycling

The chemical environment within OMZs also plays a key role in shaping their characteristics and influencing the cycling of es-

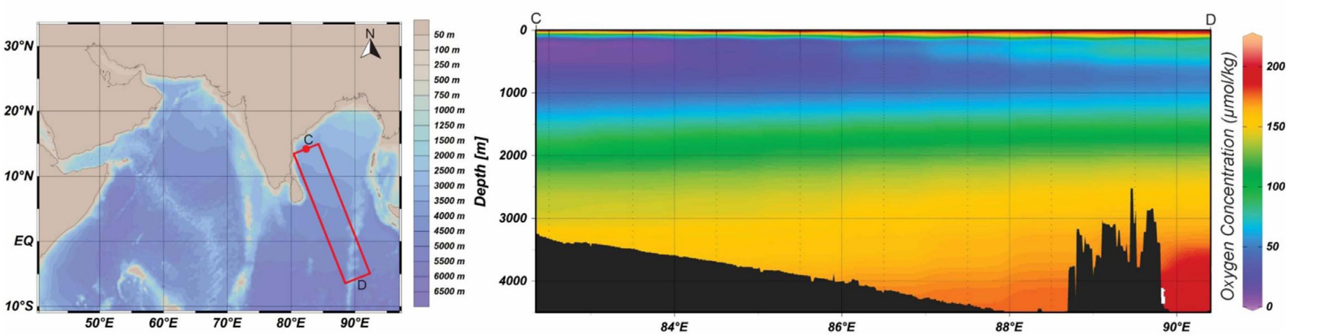

Fig. 4. Depth wise NW-SE **c**ross section (C-D) of dissolved oxygen profile of Bay of Bengal (BoB) oxygen minimum zone showing oxygen concentration from surface waters to the sea floor. Note the decreasing intensity and thickness towards south-east.

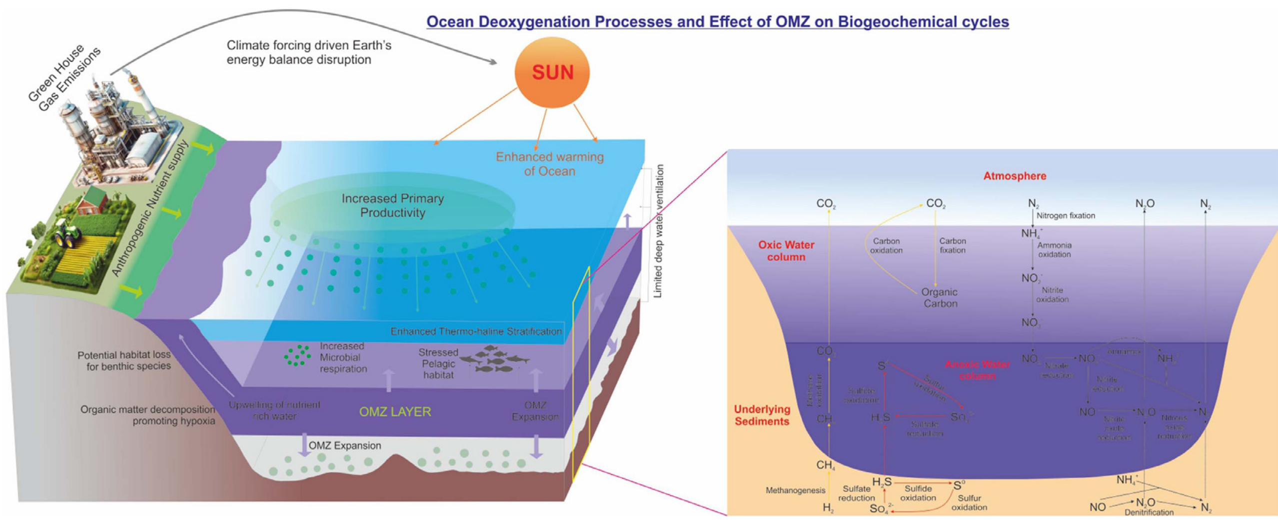

Fig. 5. Schematic cartoon (not to scale) of ocean deoxygenation processes and effects of OMZs on biogeochemical cycles viz. nitrogen, carbon and sulfur cycles in oxic and anoxic water column of ocean basin and their relations with underlying sediments. Note the upwelling, limited deep water ventilation and chemical transformations in three realms of the ocean.

sential nutrients. It plays an essential role in global nitrogen cycle in which different chemical species (NH_4^+, NO_3^-, NO_2^-, N_2O and N_2) intervene with various bacterial processes. The nitrification process converts ammonium (NH_4^+) into nitrate (NO_3^-) at upper boundary (oxycline) of OMZ under oxic condition, one of the vital regulating nutrients in the ocean (Fig. 5). However, OMZs are mainly associated with denitrification process which transforms NO_3^- into gaseous nitrogen (N_2) through a bacterial process in oxygen deficient regions. This gaseous nitrogen, then escapes to atmosphere thereby contributing to ocean nitrate deficit (Tyrrell, 1999; Seitzinger et al., 2006; Naqvi et al., 2008; Ward et al., 2009; Lam and Kuypers et al., 2011). Further, it has been observed that the ammonium ion (NH_4^+) converts directly into gaseous nitrogen and water, in the presence of nitrite ion (NO_2^-), an unknown anaerobic ammonium oxidation process defined as ‘anammox’. It has been first noted in the sediments and then in the water column in the OMZs which imposes an absolute revision of global nitrogen cycle (Fig. 5; Arrigo, 2005; Ward et al., 2009; Jensen et al., 2011; Kalvelage et al., 2013). The low oxygen levels in OMZs create unique chemical conditions that favor the accumulation of certain nutrients, such as phosphate and iron. These nutrients can fuel primary productivity when transported to surface waters, influencing global biogeochemical cycles (Fig. 5; Paulmier et al., 2006; Canfield and Kraft, 2022). OMZs are also responsible for cycle production of very important climatic gases such as H_2S, CH_4 and approximately 50% of oceanic N_2O and further plays pivotal role in the limitation of atmospheric CO_2 sequestration by the ocean (Fig. 5; Dugdale et al., 1977; Cicerone and Oremland, 1988; Bange et al., 1996; Paulmier et al., 2006; Naqvi et al., 2010). They are chemically characterized by acidification and reduced conditions favouring reduced chemical species such as Fe (II) or Cu(I) potentially aiding photosynthesis or N_2O production (Paulmier, 2005).

The complex interactions among physical, chemical and biological processes causes the formation and sustenance of OMZs. An understanding of these processes is crucial for predicting future trends of OMZs in response to a changing climate and the potential consequences for marine ecosystems and global biogeochemical cycles. The current expansion of OMZs present serious challenges to marine biodiversity with potential shifts in community composition and ecosystem function as many marine species (Zooplanktons, Phytoplanktons etc.) are adapted to specific oxygen levels and may be intolerant in fairly deoxygenated condition (Fernández Álamo and Färber Lorda, 2006 ; Limburg et al., 2020; Färber Lorda and Färber Data, 2023). This phenomenon of adaptation to specific oxygen levels by marine species came to be known as habitat compression hypothesis (HCH), first proposed by Fernández Álamo and Färber Lorda (2006) and later supported by Stramma et al. (2008) for the eastern tropical North Pacific and the equatorial pacific.

3. Classifying OMZs: A spectrum of oxygen depletion

OMZs are not homogeneous entities and display a range of characteristics relying on their geographic location, the interplay of physical and biological processes and the degree of oxygen reduction. Karstensen et al. (2008) dealt into the different types of OMZs describing their defining characteristics. OMZs are broadly classified based on the severity of oxygen depletion influencing the types of biogeochemical processes that may occur and the marine life they can support (Moffitt et al., 2015; Long et al., 2021; Liu et al., 2024).

3.1. Open ocean OMZs

These are the most extensive type, found in the interior regions of the ocean, typically at depth ranges of 200–1500 m They are characterized by oxygen concentrations below 45 µmol/kg, but rarely reaching anoxic conditions (completely devoid of oxygen; Fuenzalida et al., 2009; Canfield and Kraft, 2022). These OMZs are controlled by large scale circulation in ocean basins along with associated physical, chemical and biological processes (Fernández Álamo and Färber Lorda, 2006). The eastern tropical Pacific Ocean (ETP) host significant open ocean OMZs which comprises (a) eastern tropical North Pacific (ETNP) and (b) eastern tropical South Pacific (ETSP) oxygen minimum zones. They are primarily located between depths of approximately 200 to 1000 m (Figs. 1 and 2; Karstensen et al., 2008, 2015). ETNP extends from 0°−25°N latitude on the west of Mexico and United States of America (USA) covering a huge area of ∼12.4 million square km whereas ETSP has three main components extending from 0°−37°S on the west off Chile, Peru and near equator covering a relatively lower area of ∼5.7 million square km (Paulmier and Ruiz-Pino, 2009). The core depth of ETNP OMZ extends from 350–450 m with extensive horizontal width of ∼3500–5000 km offshore (Inferred horizontal extent from map boundaries) while it extends up to 600 m in ETSP OMZ and shoals to ∼40 m off Mexico and central America with broad & continuous horizontal extent of ∼3000 km offshore thereby indicating that ETNP OMZ is wider and more pronounced than that of ETSP (Fernández Álamo and Färber Lorda, 2006, see Fig. 3; Fiedler and Färber Lorda, 2008; Fuenzalida et al., 2009; Strama et al., 2010; Kwiecinski and Babbin, 2021). Staaf et al. (2010) further points that the oxygen levels within these OMZs can drop to critically low concentrations, often below 20 µM. The concentration has been recorded below 3–4 nM in the core of ETSP forming suboxic conditions compared to as low as 3.8 µM/kg in core of ETNP OMZ (Canfield and Kraft, 2022; Färber Lorda and Färber Data, 2023). The oxygen supply mechanism in ETNP is driven through zonal currents such as equatorial undercurrent (EUC), subsurface counter currents (SCCs) and intermediate countercurrents (ICCs) forming ventilation pathways which supply limited O_2 from the west due to shadow zones and stratification (Fiedler and Färber Lorda, 2008; Strammа et al., 2010). Compared to ETNP, ETSP OMZ gets its very limited O_2 supply through equatorial subsurface water (ESSW) transported by Peru-Chile undercurrent which becomes poorly ventilated due to increased stratification and barriers from Antarctic intermediate water (AIW; Feunzalida et al., 2009). The more detailed comparative analyses are described in Table 1. This dynamics of the ETP OMZ are controlled by ocean circulation patterns, upwelling processes and climatic variations. The critically low oxygen concentrations are largely controlled by elevated rates of organic matter generation in surface waters as upwelling of nutrient laden waters in these regions leads to higher microbial respiration and subsequent oxygen consumption in the water column (Figs. 1 and 2; Ito and Deutsch, 2013; Busecke et al., 2022). The mesoscale eddies in the eastern tropical Pacific, further, control the nitrous oxide distribution, an important greenhouse gas produced under low-oxygen conditions which in turn impacts the biogeochemical dynamics of the OMZ (Arévalo-Martínez et al., 2016).

3.2. Coastal OMZs

The depleted dissolved oxygen concentrations (commonly less than 20 µmol/kg) characterize these coastal OMZs and are usually located in the shallow coastal waters adjacent to the continental margins. These OMZs are intricately linked to the upwelling processes which transport nutrient laden water to the ocean surface leading to the high biological productivity in the form of phytoplankton blooms that gobbles up most of the oxygen during their decomposition thereby creating hypoxic (anoxic) conditions (Gilly et al., 2013; Espinoza-Morriberón et al., 2021). Coastal OMZs can undergo more severe oxygen depletion compared to their open ocean counterpart, occasionally leading to hypoxic conditions. The Peruvian OMZ (part of ETSP OMZ), for example, is known for its shallow depth and severe hypoxia with oxygen concentration in its core falling to nearly anoxic conditions (<1 µmol/L; Thomsen et al., 2016; Fig. 2). It is influenced by seasonal fluctuations in upwelling system and wind patterns that can lead to variations in oxygen concentrations and the distribution of marine life (Vergara et al., 2016). Moreover, the scenario of biogeochemical dynamics within the coastal OMZs are bit complex which involves significant sulfur and nitrogen cycling. Sulfur cycling is, particularly, active in such zones, where interaction of sulfide-rich sediments with the overlying water column contribute to a coupled benthic-pelagic sulfur cycle (Figs. 2, 3 and 5; Callbeck et al., 2021). Additionally, the microbial processes in such OMZs play a vital role in transforming fixed nitrogen into greenhouse gases, thus impacting both local ecosystems and global climate (Ulloa et al., 2012; Vuillemin et al., 2022). The anammox and denitrification processes are widespread in these environments that contribute to nitrogen loss, further exacerbating the hypoxic conditions (Bohlen et al., 2011).

3.3. Seasonal OMZs

These OMZs are temporary, forming and disappearing with seasonal shifts in the oceanographic conditions. They are marked by greatly reduced dissolved oxygen levels, which vary with changes in environmental conditions throughout the seasons. These zones are particularly prominent due to strong upwelling, such as the Arabian Sea and the eastern tropical Pacific. One of the defining features is their depth and the variability associated with seasonal upwelling. For instance, the OMZ is located beneath a strong and shallow thermocline in the eastern tropical Pacific, which can further rise to the depth range of 25–30 m during the dry season due to seasonal upwelling (Fig. 2; Logan, 2023). Similarly, the Arabian Sea (AS) exhibits a pronounced OMZ that can extend from 150 to 1250 m, with oxygen concentrations dropping below 2 µmol kg^{-1} forming anoxic conditions (Fig. 3; Schenau et al., 2000). On the other hand, Bay of Bengal (BoB) OMZ shows 200–700 m thickness with oxygen concentrations ranging between 5–20 µmol kg^{-1} exhibiting hypoxic condition (Fig. 4; Rixen et al., 2020; Vidhya et al., 2022). This depth variability is influenced by monsoonal winds that drive coastal and open-ocean upwelling, leading to high productivity and subsequent organic matter decomposition, which consumes oxygen (Schenau et al., 2000; Parvathi et al., 2023). Denitrification in AS OMZ is quite intense and widespread compared to BoB OMZ where it is virtually absent (Al Azhar et al., 2017). The seasonal dynamics of OMZs are also influenced by physical and biogeochemical processes. For example, the seasonal modulation of mesoscale activity significantly impacts the eddy flux of dissolved oxygen at the boundaries of the OMZs, leading to variations in oxygen levels throughout the year (Vergara et al., 2016).

Table 1
Comparative analyses of ETNP and ETSP Oxygen Minimum Zones.

Parameters	ETNP Oxygen Minimum Zones	ETSP Oxygen Minimum Zones	References
Geographical Extent	Off western Mexico, California and Central America	Off Peru and northern Chile	Paulmier and Ruiz-Pino, 2009
Core Depth	∼350–450; may extends up to 900 m	Extends up to 600 m and shoals as shallow as 30–50 m off Peru coast	Stramma et al., 2010; Davila et al., 2023
Horizontal Extent	Inferred range of ∼3500 to 5000 m offshore from western edge roughly around 140°−150°W	Broad and reaches up to more than 3000 m offshore and may continue even further	Feunzalida et al., 2009
Oxygen Concentration	<4 μmol/kg; often reaching near zero in the core	<3–4 nM in the core causing anoxic conditions	Canfield and Kraft, 2022
Oxygen supply & Ventilation Pathways	Zonal currents like Equatorial Undercurrents (EUC), Subsurface Counter Currents (SCCs), Intermediate Counter Currents (ICCs) supply moderate O_2 from the west, but limited by shadow zones and stratification	Equatorial Subsurface Water (ESSW) transported by Peru-Chile Under current; O_2 depleted on arrival due to poor ventilation & increased stratification and barriers from Antarctic Intermediate Water (AIW)	Feunzalida et al., 2009; Stramma et al., 2010
Water Mass Sources	Tropical and subtropical waters from both hemispheres	Primarily ESSW, but Antarctic Intermediate Water influence at depth	Davila et al., 2023
Nutrient Cycling and N_2 Loss	High denitrification; contributes ∼1/3rd of global pelagic N loss	Strong & Intense denitrification and anammox dominate; major contributor to N deficit	Ulloa and Pantoja, 2009; Tems and Tappa, 2024
Microbial Ecology	Zones of overlapping aerobic and anaerobic processes; active nitrifiers, denitrifiers & anammox bacteria; low diversity to benthic fauna due to hypoxia but presence of adapted macrofauna; high impact on fisheries	Similar microbial assemblages with adaptations to very low O2; low benthic fauna diversity; presence of large sulphur oxidizing bacteria & nitrate respiring protists; high impact on fisheries & crustaceans	Ulloa and Pantoja, 2009
Temporal changes & Climate sensitivity	Contractions & expansions of OMZ in past 2000 years due to strong ENSO & Pacific Decadal Oscillations (PDO); strong influence on productivity and OMZ intensity	Strongly impacted by ENSO; El Nino/La Nina causes rapid OMZ depth and thickness changes due to warming and stratification	Paulmier et al. 2009; Tems and Tappa, 2024

In the Arabian Sea, the interaction between monsoon driven upwelling and restricted ventilation forms one of the world's thickest OMZs globally, with seasonal blooms further contributing to the oxygen depletion due to high primary productivity compared to moderate productivity in BoB OMZ due to monsoon driven eddies and weak upwelling (Figs. 3 and 4; DiMarco, 2023; Parvathi et al., 2023). Also, the seasonal fluctuations in circulation patterns and water mass advection play a pivotal role in the intensity and distribution of Arabian sea OMZ in which it is found to be strongest and persistent during the winter monsoon whereas it is episodic and weak in BoB OMZ because of highly influenced by mesoscale eddies (Sarma, 2002; Queste et al., 2018; Schmidt et al., 2019). The seasonal OMZs, biologically, support the unique microbial communities that adapt to low-oxygen conditions (Fig. 4). These communities are involved in alternative electron acceptor processes, such as denitrification and anammox, which are critical for nitrogen cycling in these environments (Lam and Kuypers, 2011). Additionally, the interaction between the benthic and pelagic environments in OMZs can lead to complex biogeochemical cycles, including sulfur cycling, which is particularly active in highly productive coastal OMZs (Callbeck et al., 2021).

4. Variability and interconnectivity: a dynamic system

OMZs are influenced by multitude of factors including oceanographic conditions, biological processes and climate variability. The oceanographic conditions such as temperature, salinity and seasonal monsoon variations affect water column stratification and nutrient availability that further influence the variability within the OMZ (Sarma, 2002; Levine and Turner, 2012). One of the primary factors contributing to the variability of OMZs is the interaction between physical and biogeochemical processes including the dynamics of the mixed layer, nutrient cycling and denitrification (Figs. 1 and 5; Sarma, 2002). Montès et al. (2014), for example, highlights the representation of the Equatorial Current System which is crucial for accurately modeling the OMZ in the eastern tropical Pacific. This variability is, further, compounded by seasonal changes revealing that mesoscale activities play a critical role in influencing oxygen levels (Vergara et al., 2016). Moreover, the influence of climate variability, particularly through phenomena such as El Niño and La Niña, significantly affects the microbial community dynamics within OMZs. Pajares and Merino-Ibarra (2023) reported that prokaryotic assemblages and nitrogen-cycling genes are closely related to local physicochemical conditions and oceanographic fluctuations associated with these climate events, underscoring the importance of climate variability in shaping microbial dynamics in OMZs. This interplay of biological and climate processes demonstrates the interconnectedness of various factors that govern OMZ dynamics.

The interconnectivity of the Arabian Sea's ecosystems to atmosphere is evident that how atmospheric conditions and ocean currents influence the formation and expansion of OMZ. For instance, the Great Whirl, defined as a large anti-cyclonic eddy which forms every year after the onset of the summer monsoon, plays a crucial role in regulating sea surface temperature (SST) and meridional heat transport in the region (Schott and Quadfasel, 1982; Wirth et al., 2002). The fluctuations of the Great Whirl and its interactions with the Somali Current greatly influence the distribution of nutrients and dissolved oxygen levels in the OMZ which in turn affects the marine biodiversity and productivity (Figs. 1–3; McCreary et al., 1996; Melzer et al., 2019). Furthermore, the seasonal monsoonal winds drive the mixing of surface waters which can worsen OMZ conditions depending on the timing and strength of these winds (Sreekanth, 2016). Moreover, the Arabian Sea's OMZ is influenced by external factors such as aerosol loading and continental meteorology. Several workers (Nair et al., 2012; Jin et al., 2018) have also shown the fluctuations in aerosol optical depth (AOD) which may affect the regional climate and consequently the ocean's biogeochemical cycles. During the periods of high AOD, such as those linked to dust storms, changes in solar radiation can affect the primary productivity and influence the oxygen dynamics in the water column thereby highlighting the interconnectedness of atmospheric and oceanic processes in shaping the ecological landscape of the Arabian Sea (Fig. 3; Jin et al., 2018).

Also, OMZs are interconnected with other components of the Earth system which are influenced by global climate change, nutrient cycling and marine productivity. It is crucial to understand these complex interactions which becomes essential for forecasting the future of OMZs and their potential effects on marine ecosystems and global biogeochemical cycles. The ongoing research in this domain, is quite crucial for explaining these interdependencies and addressing the environmental challenges posed by the expansion of OMZs, especially in the light of anthropogenic effects on the ocean's health and climate dynamics (Paulmier and Ruiz-Pino, 2009). The implications of OMZ dynamics are particularly pronounced in regions like the Arabian Sea, where strong seasonal variability in circulation patterns significantly influences oxygen levels, indicating the need for comprehensive studies to unravel these complex relationships and their broader ecological consequences (Fernández Álamo and Färber Lorda, 2006; Paulmier and Ruiz-Pino, 2009; Schmidt et al., 2020; Färber Lorda and Färber Data, 2023).

5. Effects of expanding OMZs

The presence of oxygen minimum zones, marked by their depleted oxygen levels, have far-reaching influence on ocean-atmosphere system. Their expansion in the ocean has been linked to climate change, decreased oxygen supply due to warming and organic matter remineralization (Stramma et al., 2012; Tremblay and Abele, 2016; Croizier et al., 2020). The solubility of oxygen in ocean water reduces due to rise in global temperatures exacerbating the decline in oxygen levels thereby contributing to expansion of these zones (Getzlaff et al., 2016; Almendra, 2024). They play a crucial role in managing the nitrous oxide (N_2O) flux, a potential greenhouse gas, from the ocean to the atmosphere which has severe implications on marine ecology and marine biogeochemical cycles especially in the context of the nitrogen cycle, denitrification and nitrogen fixation processes (Lam and Kuypers, 2011; Vik et al., 2021). The oxygen consumption causes production of the nitrogen gas (N_2) and nitrous oxide (N_2O) in the OMZs which escapes into the atmosphere accounting for a substantial portion of global N_2O emissions, thereby controlling greenhouse gas concentrations (Fig. 5; Bristow et al., 2016; Fu et al., 2018; Boubonnais, 2023). The microbial communities in these regions adjust to conditions of reduced oxygen availability frequently depending on different electron acceptors for their respiratory processes which can additionally modify nutrient dynamics and functioning of the ecosystem (Lam and Kuypers, 2011; Kalvelage et al., 2015). OMZs are primarily responsible for the cycling of nitrogen through processes such as denitrification and annamox (Paulmier and Ruiz-Pino, 2009). Increase in nitrogen from human activities can further enhance denitrification in OMZs, potentially leading to higher N_2O emissions and exacerbating climate change.

Furthermore, it impacts the marine life by forming inhospitable conditions for several aerobic organisms. The species that are intolerant to depleted oxygen levels, either migrate to more oxygenated waters or experience declining in population (Fernández Álamo and Färber Lorda, 2006; Gilly et al., 2013; Färber Lorda and Färber Data, 2023; Parouffe et al., 2023). This physiological stress caused by hypoxia leads to metabolic suppression in marine organisms impacting their reproduction, growth and survival (Seibel, 2011; Tremblay and Abele, 2016). It has cascading effects on the marine food cycle particularly in the regions of upwelling nutrient rich waters leading to reduction in fish stocks and altered community structures (Fernández Álamo and Färber Lorda, 2006; Tremblay and Abele, 2016; Färber Lorda and Färber Data, 2023). Schubotz et al. (2018) reported that the microbial activity in Arabian sea OMZ removes ∼30–50% of ocean's fixed nitrogen. This nitrogen loss is intensified further through unique conditions present in OMZs where both aerobic and anaerobic processes coexist leading to complex interactions among microbial communities (Thamdrup et al., 2012; Beman and Carolan, 2013). In addition to this, the coupling of nitrogen and sulfur cycles in OMZs suggests that changes in one cycle can significantly affect the other cycle thereby controlling the larger ongoing biogeochemical processes in the ocean (Al Azhar et al., 2014; Carolan et al., 2015). The presence of sulfur reducing bacteria in OMZ can affect the availability of nitrogen compounds, further complicating the biogeochemical landscape (Fig. 5; Gazitúa et al., 2021). The low oxygen conditions in OMZs also influence the cycling of other elements, such as iron and phosphorus. These elements can accumulate in OMZs and, depending on ocean circulation patterns, may be transported to other regions, influencing primary productivity in those areas (Scholz, 2018; Xing et al., 2025).

The expansion of OMZs have significant implications for habitat loss in marine ecosystem. As the oxygen level declines, marine species, particularly those that are less tolerant to hypoxic conditions, experience habitat loss and compression that leads to shift in community composition and reduction in biodiversity (Fernández Álamo and Färber Lorda, 2006; Vaquer-Sunyer and Duarte, 2010; Lachkar et al., 2016; Färber Lorda and Färber Data, 2023). The direct relationship between oxygen depletion and habitat loss is evident in marine environments with high productivity and weak ventilation such as Arabian sea and eastern tropical pacific in which limited replenishment of oxygen leads to extensive OMZ formation that can displace or eliminate sensitive species (Figs. 2 and 3; Lachkar et al., 2016; Färber Lorda and Färber Data, 2023). This phenomenon becomes more severe when marine organisms including fish and invertebrates, have specific oxygen requirements for their sustenance and reproduction. As the overall biodiversity of the ocean's declines, it may cause loss of ecosystem services when organisms are pushed out of their preferred habitats (Vaquer-Sunyer and Duarte, 2010; Färber Lorda and Färber Data, 2023). The loss of biodiversity and habitat complexity further diminishes the resilience of the marine ecosystems to additional stressors such as climate change and pollution, further, amplifying the effects of habitat degradation (Breitburg et al., 2018). Bhuiyan (2024) recently noted that the expansion of OMZs impacts the critical habitats such as coral reefs, seagrass beds and coastal ecosystems which are already vulnerable to anthropogenic activities. The deterioration of these habitats leads to significant damage in marine biodiversity due to dependency of many species on these environments for breeding, feeding, and shelter (El-Naggar et al., 2022).

Further, the expansion is also largely attributed to anthropogenic activities, particularly the climate change and nutrient loading from the agricultural runoff which intensify the natural processes leading to the deoxygenation (Fig. 5). The ocean stratification, one of the primary causes of OMZ expansion, is aggravated by eutrophication phenomenon, especially in the semi-restricted basins like the Baltic Sea and Chesapeake Bay where nutrient enrichment leads to the algal blooms followed by hypoxic conditions because of decomposition of the organic matter (Fig. 5; Keeling et al., 2010; Lowery et al., 2018). The interaction of these factors leads to substantial reduction in oxygen levels, especially in coastal upwelling regions which are key hotspots for OMZ formation (Scholz, 2018). Oceanographic conditions such as upwelling and circulation patterns also affects the geographical distribution of OMZs. They cover a huge area in the Eastern Tropical Pacific and the Arabian Sea where nutrient rich waters rise to the surface to drive high primary productivity and therefore increase oxygen use at depth (Figs. 2, 3 and 5; Bristow et al., 2016). However, these regions are especially sensitive to changes by humans and these changes can amplify the spatial extent and intensity of OMZs by additional nutrient inputs and changed circulation patterns (Scholz, 2018). Gilly et al. (2013) reported that long term decreases in oxygen concentrations are evident throughout much of the ocean interior, especially in OMZs present in midwater and the extents of which have substantially increased during the past 50 years. Keeling et al. (2010) stated that forecasting statistical models indicate that as climate change continues, oxygen inventories around the globe will continue to decline and that the area and volume of OMZs will increase. The complex interaction among various factors characterizing these zones, makes it difficult to predict the precise impacts of climate change on OMZs and their downstream consequences. Nevertheless, understanding of these interactions is a prerequisite for the design of mitigation and adaptation strategies to protect marine ecosystems and the services they provide.

6. Current scenario and way forward

The expansion of OMZs, driven by a complex interaction of natural and anthropogenic factors, has a severe implication for marine ecosystems, global biogeochemical cycles and Earth's climate system. Understanding the current scenario and defining a future course, there needs to be a multidimensional approach involving the participation of scientific research, government policies and cooperation at global level. Moreover, most of the OMZs are expanding in geographical extent and intensifying in their hypoxic conditions, exacerbating marine biodiversity and ecosystem health in comparison to their past extent and intensity. Expanding OMZ is driven significantly by climate change. Reduced oxygen solubility in ocean warming and increased stratification prevent replenishment of oxygen to deeper waters. In turn, climate change strengthens the positive feedback loop of OMZ expansion in which perturbed biogeochemical cycle can further amplify the climate change. Consequently, OMZ expansion is driven in large part by anthropogenic nutrient loading, which in many cases, are caused by agricultural and wastewater feeding. The propagation of these nutrients led to the algal bloom and their subsequent decomposition utilize an enormous amount of oxygen, thus, depleting it in affected regions of the ocean.

The scientific research incorporating modern techniques is needed to further increase our knowledge on OMZ dynamics, their sensitivity to climate change and human impacts and ecological and biogeochemical consequences. It includes monitoring programs, modeling studies and experimental investigations to unravel the complex interplay of factors involved. As the climate change is a major driver of OMZ expansion, addressing this global challenge is paramount. Minimizing the nutrient run off from land-based sources is crucial to curb the excessive fertilization of coastal waters that contributes to OMZ formation. It involves implementing sustainable agricultural practices, improving wastewater treatment & management, and reducing industrial discharges. Implementation of marine protected areas and other conservation measures can help safeguard vulnerable ecosystems and species from impacts of OMZ expansion. These steps include identifying and protecting areas of high biodiversity and ecological importance. As OMZs are a global phenomenon, international cooperation is essential for effective monitoring, research and management efforts. Sharing of data, expertise and resources among nations and their scientific bodies is crucial to address this transboundary challenge.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Arvind Kumar Singh: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Aditya Abha Singh:** Conceptualization, Writing – review & editing. **Kumail Ahmad:** Data curation, Writing – review & editing.

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References

Al Azhar, M., Canfield, D.E., Fennel, K., Thamdrup, B., Bjerrum, C.J., 2014. A model-based insight into the coupling of nitrogen and sulfur cycles in a coastal upwelling system. J. Geophys. Research: Biogeosci. 119 (3), 264–285. doi:10.1002/2012JG002271.

Al Azhar, M., Lachkar, Z., Lévy, M., Smith, S., 2017. Oxygen minimum zone contrasts between the Arabian Sea and the Bay of Bengal implied by differences in remineralization depth. Geophys. Res. Letters. 44 (21), 11–106. doi:10.1002/2017gl075157.

Almendra, I., Dewitte, B., Garçon, V., Muñoz, P., Parada, C., Montes, I., Oschlies, A., 2024. Emergent constraint on oxygenation of the upper South Eastern Pacific oxygen minimum zone in the twenty-first century. Commun. Earth and Environ. 5 (1), 284. doi:10.1038/s43247-024-01427-2.

Arévalo-Martínez, D.L., Kock, A., Löscher, C.R., Schmitz, R.A., Stramma, L., Bange, H.W., 2016. Influence of mesoscale eddies on the distribution of nitrous oxide in the eastern tropical South Pacific. Biogeosci 13 (4), 1105–1118. doi:10.5194/bg-13-1105-2016, 2016.

Arrigo, K.R., 2005. Marine microorganisms and global nutrient cycles. Nature 437 (7057), 349–355. doi:10.1038/nature04159.

Babila, T.L., Penman, D.E., Standish, C.D., Doubrawa, M., Bralower, T.J., Robinson, M.M., Zachos, J.C., 2022. Surface Ocean warming and acidification driven by rapid carbon release precedes Paleocene-Eocene Thermal Maximum. Sci. Adv. 8 (11), eabg1025. doi:10.1126/sciadv.abg1025.

Bange, H.W., Rapsomanikis, S., Andreae, M.O., 1996. Nitrous oxide in coastal waters. Glob. Biogeochem. Cycles. 10 (1), 197–207. doi:10.1029/95GB03834.

Baroni, R., Palastanga, I.V., Slomp, C.P., 2020. Enhanced organic carbon burial in sediments of oxygen minimum zones upon ocean deoxygenation. Front. Marine Sci. 6, 839. doi:10.3389/fmars.2019.00839.

Beghoura, H., Gorgues, T., Fransner, F., Auger, P.A., Memery, L., 2023. Contrasting responses of the ocean's oxygen minimum zones to artificial re-oxygenation. Environment. Res. Letters. 18 (8), 084012. doi:10.1088/1748-9326/ace0cd.

Beman, J.M., Carolan, M.T., 2013. Deoxygenation alters bacterial diversity and community composition in the ocean's largest oxygen minimum zone. Nat. Commun. 4, 2705. doi:10.1038/ncomms3705.

Bhuiyan, M.M.U., Rahman, M., Naher, S., Shahed, Z.H., Ali, M.M., Islam, A.R.M.T., 2024. Oxygen declination in the coastal ocean over the twenty-first century: driving forces, trends, and impacts. Case Studies. Chem. and Environ. Eng. 9, 100621. doi:10.1016/j.cscee.2024.100621.

Bindoff, N.L., Cheung, W.W.L., Kairo, J.G., Arístegui, J., Guinder Valeria, Ana, et al., 2019. Changing Ocean, Marine Ecosystems, and Dependent Communities. Camb. Univ. Press, pp. 447–587. doi:10.1017/9781009157964.007.

Bohlen, L., Dale, A.W., Sommer, S., Mosch, T., Hensen, C., Noffke, A., Wallmann, K., 2011. Benthic nitrogen cycling traversing the Peruvian oxygen minimum zone. Geochim. Cosmochim. Acta 75 (20), 6094–6111. doi:10.1016/j.gca.2011.08.010.

Boubonnais, A., 2023. Editorial: recent developments in oxygen minimum zones biogeochemistry. Front. Mar. Sci. 10. doi:10.3389/fmars.2023.1333731.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., 2018. Declining oxygen in the global ocean and coastal waters. Science (1979) 359 (6371), eaam7240. doi:10.1126/science.aam7240.

Bristow, L., Dalsgaard, T., Tiano, L., Mills, D., Bertagnolli, A., Wright, J., Thamdrup, B., 2016. Ammonium and nitrite oxidation at nanomolar oxygen concentrations in

oxygen minimum zone waters. Proceed. Nat. Acad. Sci. 113 (38), 10601–10606. doi:10.1073/pnas.1600359113.
Busecke, J.J., Resplandy, L., Ditkovsky, S.J., John, J.G., 2022. Diverging fates of the Pacific Ocean oxygen minimum zone and its core in a warming world. AGU Adv 3 (6), e2021AV000470. doi:10.1029/2021AV000470.
Callbeck, C.M., Canfield, D.E., Kuypers, M.M., Yilmaz, P., Lavik, G., Thamdrup, B., Bristow, L.A., 2021. Sulfur cycling in oceanic oxygen minimum zones. Limnol. and Oceanogr. 66 (6), 2360–2392. doi:10.1002/lno.11759.
Canfield, D.E., Kraft, B., 2022. The 'oxygen' in oxygen minimum zones. Environ. Microbiol. 24 (11), 5332–5344. doi:10.1111/1462-2920.16192.
Carolan, M.T., Smith, J.M., Beman, J.M., 2015. Transcriptomic evidence for microbial sulfur cycling in the eastern tropical North Pacific oxygen minimum zone. Front. Microbiol. 6, 334. doi:10.3389/fmicb.2015.00334.
Cicerone, R.J., Oremland, R.S., 1988. Biogeochemical aspects of atmospheric methane. Glob. Biogeochem. Cycles 2 (4), 299–327. doi:10.1029/GB002i004p00299.
Davila, X., Olsen, A., Lauvset, S.K., McDonagh, E.L., Brakstad, A., Gebbie, G., 2023. On the origins of open ocean oxygen minimum zones. J. Geophys. Res.: Oceans 128 (8), e2023JC019677. doi:10.1029/2023JC019677.
Di Marco, S.F., Wang, Z., Chapman, P., al-Kharusi, L., Belabbassi, L., al-Shaqsi, H., Howard, M.K., 2023. Monsoon-driven seasonal hypoxia along the northern coast of Oman. Front. Marine Sci. 10, 1248005. doi:10.3389/fmars.2023.1248005.
Doney, S.C., 2010. The growing human footprint on coastal and open-ocean biogeochemistry. Science (1979) 328 (5985), 1512–1516. doi:10.1126/science.1185198.
Dugdale, R.C., Goering, J.J., Barber, R.T., Smith, R.L., Packard, T.T., 1977. Denitrification and hydrogen sulfide in the Peru upwelling region during 1976. Deep Sea Res 24 (6), 601–608. doi:10.1016/0146-6291(77)90530-6.
El-Naggar, H.A., Salem, E.S.S., El-Kafrawy, S.B., Bashar, M.A., Shaban, W.M., El-Gayar, E.E., Ahmed, H.O., Ashour, M., Abou-Mahmoud, M.E., 2022. An integrated field data and remote sensing approach for impact assessment of human activities on epifauna macrobenthos biodiversity along the western coast of Aqaba Gulf. Ecohydrol 15 (3), pe2400. doi:10.1002/eco.2400.
Espinoza-Morriberón, D., Echevin, V., Gutiérrez, D., Tam, J., Graco, M., Ledesma, J., Colas, F., 2021. Evidences and drivers of ocean deoxygenation off Peru over recent past decades. Scientific Rep 11 (1), 20292. doi:10.1038/s41598-021-99876-8.
Färber Lorda, J., Färber Data, B., 2023. Autumn vertical distribution of zooplankton in the oxygen minimum zone of the Eastern Tropical North Pacific. Marine Environ. Research 190, 106116. doi:10.1016/j.marenvres.2023.106116.
Fernández-Álamo, M.A., Färber-Lorda, J., 2006. Zooplankton and the oceanography of the eastern tropical Pacific: a review. Prog. in Oceanog. 69 (2–4), 318–359. doi:10.1016/j.pocean.2006.03.003.
Fiedler, P.C., Färber Lorda, J., 2008. Zooplankton night/day rations and the oxygen minimum layer in the eastern Pacific. NOAA Technical Memorandum NMFS-SWFSC 424. doi:10.13140/RG.2.2.31255.29603.
Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L., Lange, C., 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. Deep Sea Res. Part II: Trop. Stud. Oceanogr. 56 (16), 992–1003. doi:10.1016/j.dsr2.2008.11.001.
Fu, W., Primeau, F., Keith Moore, J., Lindsay, K., Randerson, J.T., 2018. Reversal of increasing tropical ocean hypoxia trends with sustained climate warming. Global. Biogeochem. Cycles. 32, 551–564. doi:10.1002/2017GB005788.
Garcia, H.E., Bouchard, C., Cross, S.L., Paver, C.R., Boyer, T.P., Reagan, J.R., Locarnini, R.A., Mishonov, A.V., Baranova, O.K., Seidov, D., Wang, Z., Dukhovskoy, D., 2024a. World Ocean Atlas 2023, Volume 4: Dissolved Inorganic Nutrients (Phosphate, Nitrate, Silicate). A. Mishonov Technical Editor. NOAA Atlas NESDIS 92, 79pp. https://doi.org/10.25923/39qw-7j08.
Garcia, H.E., Wang, Z., Bouchard, C., Cross, S.L., Paver, C.R., Reagan, J.R., Boyer, T.P., Locarnini, R.A., Mishonov, A.V., Baranova, O.K., Seidov, D., Dukhovskoy, D., 2024b. World Ocean Atlas 2023, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, Dissolved Oxygen Saturation, and 30-year Climate Normal. A. Mishonov Technical Editor. NOAA Atlas NESDIS 91, 109 pp. https://doi.org/10.25923/rb67-ns53.
Gazitúa, M.C., Vik, D.R., Roux, S., Gregory, A.C., Bolduc, B., Widner, B., Mulholland, M.R., Hallam, S.J., Ulloa, O., Sullivan, M.B., 2021. Potential virus-mediated nitrogen cycling in oxygen-depleted oceanic waters. The. ISMe J. 15 (4), 981–998. doi:10.1038/s41396-020-00825-6.
Getzlaff, J., Dietze, H., Oschlies, A., 2016. Simulated effects of southern hemispheric wind changes on the Pacific oxygen minimum zone. Geophys. Res. Lett. 43 (2), 728–734. doi:10.1002/2015GL066841.
Giering, S.L., Sanders, R., Lampitt, R.S., Anderson, T.R., Tamburini, C., Boutrif, M., Mayor, D.J., 2014. Reconciliation of the carbon budget in the ocean's twilight zone. Nature 507 (7493), 480–483. doi:10.1038/nature13123.
Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H., 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu. Rev. Marine Sci. 5 (1), 393–420. doi:10.1146/annurev-marine-120710-100849.
Helm, K.P., Bindoff, N.L., Church, J.A., 2011. Observed decreases in oxygen content of the global ocean. Geophys. Res. Lett. 38 (23). doi:10.1029/2011GL049513.
Henehan, M.J., Ridgwell, A., Thomas, E., Zhang, S., Alegret, L., Schmidt, D.N., Hull, P.M., 2019. Rapid ocean acidification and prrotracted Earth system recovery followed the end-Cretaceous Chicxulub impact. Proceed. Nat. Acad. Sci. 116 (45), 22500–22504. doi:10.1073/pnas.1905989116.
Ito, T., Deutsch, C., 2013. Variability of the oxygen minimum zone in the tropical North Pacific during the late twentieth century. Glob. Biogeochem. Cycles 27 (4), 1119–1128. doi:10.1002/2013GB004567.
Jensen, M.M., Lam, P., Revsbech, N.P., Nagel, B., Gaye, B., Jetten, M.S., Kuypers, M.M., 2011. Intensive nitrogen loss over the Omani Shelf due to anammox coupled with dissimilatory nitrite reduction to ammonium. ISMe J. 5 (10), 1660–1670. doi:10.1038/ismej.2011.44.
Jin, M., Deal, C., Maslowski, W., Matrai, P., Roberts, A., Osinski, R., Wang, S., 2018. Effects of model resolution and ocean mixing on forced ice-ocean physical and biogeochemical simulations using global and regional system models. J. Geophys. Research: Oceans 123 (1), 358–377. doi:10.1002/2017JC013365.
Jurikova, H., Gutjahr, M., Wallmann, K., Flögel, S., Liebetrau, V., Posenato, R., Eisenhauer, A., 2020. Permian–Triassic mass extinction pulses driven by major marine carbon cycle perturbations. Nature Geosci 13 (11), 745–750. doi:10.1038/s41561-020-00646-4.
Kalvelage, T., Lavik, G., Lam, P., Contreras, S., Arteaga, L., Löscher, C.R., Kuypers, M.M., 2013. Nitrogen cycling driven by organic matter export in the South Pacific oxygen minimum zone. Nature Geosci 6 (3), 228–234. doi:10.1038/ngeo1739.
Kalvelage, T., Lavik, G., Jensen, M., Revsbech, N., Löscher, C., Schunck, H., Kuypers, M., 2015. Aerobic microbial respiration in oceanic oxygen minimum zones. PLoS. One 10 (7), e0133526. doi:10.1371/journal.pone.0133526.
Karstensen, J., Stramma, L., Visbeck, M., 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. Prog. Oceanogr. 77 (4), 331–350. doi:10.1016/j.pocean.2007.05.009.
Karstensen, J., Fiedler, B., Schütte, F., Brandt, P., Körtzinger, A., Fischer, G., Wallace, D., 2015. Open ocean dead zones in the tropical North Atlantic Ocean. Biogeosci 12 (8), 2597–2605. doi:10.5194/bg-12-2597-2015.
Kasting, J.F., Siefert, J.L., 2002. Life and the evolution of Earth's atmosphere. Science (1979) 296 (5570), 1066–1068. doi:10.1126/science.1071184.
Keeling, R.F., Körtzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming world. Annu. Rev. Marine Sci. 2 (1), 199–229. doi:10.1146/annurev.marine.010908.163855.
Keil, R.G., Neibauer, J.A., Biladeau, C., van der Elst, K., Devol, A.H., 2016. A multiproxy approach to understanding the" enhanced" flux of organic matter through the oxygen-deficient waters of the Arabian Sea. Biogeosci 13 (7), 2077–2092. doi:10.5194/bg-13-2077-2016, 2016.
Kwiecinski, J.V., Babbin, A.R., 2021. A high-resolution atlas of the eastern tropical pacific oxygen deficient zones. Global. Biogeochem. Cyc. 35 (12), e2021GB007001. doi:10.1029/2021GB007001.
Lachkar, Z., Smith, S., Lévy, M., Pauluis, O., 2016. Eddies reduce denitrification and compress habitats in the Arabian Sea. Geophys. Res. Letters. 43 (17), 9148–9156. doi:10.1002/2016GL069876.
Lalli, C.M., Parsons, T.R., 1993. Biological Oceanography: An Introduction. Elsevier, p. 314.
Lam, P., Kuypers, M.M., 2011. Microbial nitrogen cycling processes in oxygen minimum zones. Annu. Rev. Marine Sci. 3 (1), 317–345. doi:10.1146/annurev-marine-120709-142814.
Le Croizier, G., Lorrain, A., Sonke, J.E., Hoyos-Padilla, E.M., Galván-Magaña, F., Santana-Morales, O., Point, D., 2020. The twilight zone as a major foraging habitat and mercury source for the great white shark. Environ. Sci. and Technol. 54 (24), 15872–15882. doi:10.1021/acs.est.0c05621.
Levine, R.C., Turner, A.G., 2012. Dependence of Indian monsoon rainfall on moisture fluxes across the Arabian Sea and the impact of coupled model sea surface temperature biases. Clim. Dyna. 38, 2167–2190. doi:10.1007/s00382-011-1096-z.
Limburg, K.E., Breitburg, D., Swaney, D.P., Jacinto, G., 2020. Ocean deoxygenation: a primer. One Earth. 2 (1), 24–29. doi:10.1016/j.oneear.2020.01.001.
Liu, J., Cui, Z., Luan, X., Wang, Z., Zhang, X., 2024. Expanding oxygen minimum zones in the northern Indian Ocean predicted by hypoxia-related bacteria. Frontiers in Marine Sci 11, 1396306. doi:10.3389/fmars.2024.1396306.
Logan, R.K., Vaudo, J.J., Wetherbee, B.M., Shivji, M.S., 2023. Seasonally mediated niche partitioning in a vertically compressed pelagic predator guild. Proceed. Royal Soc. B 2902012, 20232291. doi:10.1098/rspb.2023.2291.
Long, A.M., Jurgensen, S.K., Petchel, A.R., Savoie, E.R., Brum, J.R., 2021. Microbial ecology of oxygen minimum zones amidst ocean deoxygenation. Front. Microbiol. 12, 748961. doi:10.3389/fmicb.2021.748961.
Lowery, C.M., Leckie, R.M., Bryant, R., Elderbak, K., Parker, A., Polyak, D.E., Sterzinar, E., 2018. The Late Cretaceous Western Interior Seaway as a model for oxygenation change in epicontinental restricted basins. Earth. Sci. Rev. 177, 545–564. doi:10.1016/j.earscirev.2017.12.001.
McCreary Jr, J.P., Kohler, K.E., Hood, R.R., Olson, D.B., 1996. A four-component ecosystem model of biological activity in the Arabian Sea. Prog. in Oceanog. 37 (3–4), 193–240. doi:10.1016/S0079-6611(96)00005-5.
McCreary Jr, J.P., Yu, Z., Hood, R.R., Vinaychandran, P.N., Furue, R., Ishida, A., Richards, K.J., 2013. Dynamics of the Indian-Ocean oxygen minimum zones. Prog. Oceanogr. 112, 15–37. doi:10.1016/j.pocean.2013.03.002.
Melzer, B.A., Jensen, T.G., Rydbeck, A.V., 2019. Evolution of the Great Whirl using an altimetry-based eddy tracking algorithm. Geophys. Res. Lett. 46 (8), 4378–4385. doi:10.1029/2018GL081781.
Moffitt, S.E., Moffitt, R.A., Sauthoff, W., Davis, C.V., Hewett, K., Hill, T.M., 2015. Paleoceanographic Insights on Recent Oxygen Minimum Zone Expansion: lessons for Modern Oceanography. PLoS. One 10 (1), e0115246. doi:10.1371/journal.pone.0115246.
Montes, I., Dewitte, B., Gutknecht, E., Paulmier, A., Dadou, I., Oschlies, A., Garçon, V., 2014. High-resolution modeling of the Eastern Tropical Pacific oxygen minimum zone: sensitivity to the tropical oceanic circulation. J. Geophys. Res. Oceans. 119 (8), 5515–5532. doi:10.1002/2014JC009858.
Morrison, J.M., Codispoti, L.A., Smith, S.L., Wishner, K., Flagg, C., Gardner, W.D., Gundersen, J.S., 1999. The oxygen minimum zone in the Arabian Sea dur-

ing 1995. Deep Sea Res Part II: Trop. Stud. Oceanogr. 46 (8–9), 1903–1931. doi:10.1016/S0967-0645(99)00048-X.
Nair, M.P., Sujatha, C.H., 2012. Biogeochemical quality assessment of the sediments in Kerala coast. Int. J. Environ. Sci. 3 (1), 707–719. doi:10.1016/S0967-0645(99)00048-X.
Naqvi, S.W.A., Voss, M., Montoya, J.P., 2008. Recent advances in the biogeochemistry of nitrogen in the ocean. Biogeosci 5 (4), 1033–1041. doi:10.5194/bg-5-1033-2008.
Naqvi, S.W.A., Bange, H.W., Farías, L., Monteiro, P.M.S., Scranton, M.I., Zhang, J., 2010. Marine hypoxia/anoxia as a source of CH_4 and N_2O. Biogeosci 7 (7), 2159–2190. doi:10.5194/bg-7-2159-2010.
Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437 (7059), 681–686. doi:10.1038/nature04095.
Pajares, S., Merino-Ibarra, M., Farías, L., 2023. Prokaryotic community dynamics and nitrogen-cycling genes in an oxygen-deficient upwelling system during La Niña and El Niño conditions. Environ. Microbiol. 25 (7), 1281–1299. doi:10.1111/1462-2920.16362.
Parouffe, A., Garçon, V., Dewitte, B., Paulmier, A., Montes, I., Parada, C., Veliz, D., 2023. Evaluating future climate change exposure of marine habitat in the South East Pacific based on metabolic constraints. Front. Marine Sci. 9, 1055875. doi:10.3389/fmars.2022.1055875.
Parvathi, V., Lachkar, Z., Lévy, M., 2023. Shrinking of the Arabian Sea oxygen minimum zone with climate change projected with a downscaled model. Front. Marine Sci. 10. doi:10.3389/fmars.2023.1123739.
Paulmier, A., 2005. Zones de minimum d'oxygène (OMZs) de l'océan moderne: une étude focalisée dans l'OMZ du Pacifique Sud Est (Doctoral dissertation, Paris 6). DOI: 10.1016/j.pocean.2008.08.001.
Paulmier, A., Ruiz-Pino, D., Garcon, V., Farias, L., 2006. Maintaining of the eastern south Pacific oxygen minimum zone (OMZ) off Chile. Geophys. Res. Lett. 33 (20). doi:10.1029/2006GL026801.
Paulmier, A., Ruiz-Pino, D., 2009. Oxygen minimum zones (OMZs) in the modern ocean. Prog. Oceanogr. 80 (3–4), 113–128. doi:10.1016/j.pocean.2008.08.001.
Prada, F., Caroselli, E., Mengoli, S., Brizi, L., Fantazzini, P., Capaccioni, B., Goffredo, S., 2017. Ocean warming and acidification synergistically increase coral mortality. Sci. Rep. 7 (1), 40842. doi:10.1038/srep40842.
Queste, B.Y., Vic, C., Heywood, K.J., Piontkovski, S.A., 2018. Physical controls on oxygen distribution and denitrification potential in the North West Arabian Sea. Geophys. Res. Lett. 45 (9), 4143–4152. doi:10.1029/2017GL076666.
Rabalais, N.N., Baustian, M.M., 2020. Historical shifts in benthic infaunal diversity in the northern Gulf of Mexico since the appearance of seasonally severe hypoxia. Diversity. (Basel) 12 (2), 49. doi:10.3390/d12020049.
Rangamaran, V.R., Sankara Subramanian, S.H., Balachandran, K.R.S., Gopal, D., 2023. Vertical microbial profiling of Arabian Sea oxygen minimal zone reveals complex bacterial communities and distinct functional implications. Microb. Ecology 85 (2), 357–371. doi:10.1007/s00248-021-01952-z.
Rixen, T., Cowie, G., Gaye, B., Goes, J., Rosário, do, Gomes, H., Hood, R.R., Lachkar, Z., Schmidt, H., Segschneider, J., Singh, A., 2020. Reviews and syntheses: present, past, and future of the oxygen minimum zone in the northern Indian Ocean. Biogeosci 17 (23), 6051–6080. doi:10.5194/bg-17-6051-2020.
Sarma, V.V.S.S., 2002. An evaluation of physical and biogeochemical processes regulating the oxygen minimum zone in the water column of the Bay of Bengal. Glob. Biogeochem. cycles 16 (4), 46. doi:10.1029/2001GB001461, -1.
Schenau, S.J., Slomp, C.P., De Lange, G.J., 2000. Phosphogenesis and active phosphorite formation in sediments from the Arabian Sea oxygen minimum zone. Marine Geol 169 (1–2), 1–20. doi:10.1016/S0025-3227(00)00083-9.
Schmidt, H., Czeschel, R., Visbeck, M., 2019. Ventilation dynamics of the oxygen minimum zone in the Arabian Sea. Biogeosci. Discuss. 2019, 1–32. doi:10.5194/bg-2019-168.
Schmidt, H., Czeschel, R., Visbeck, M., 2020. Seasonal variability of the Arabian Sea intermediate circulation and its impact on seasonal changes of the upper oxygen minimum zone. Ocean Sci 16 (6), 1459–1474. doi:10.5194/os-16-1459-2020.
Scholz, F., 2018. Identifying oxygen minimum zone-type biogeochemical cycling in Earth history using inorganic geochemical proxies. Earth. Sci. Rev. 184, 29–45. doi:10.1016/j.earscirev.2018.08.002.
Schott, F., Quadfasel, D., 1982. Variability of the Somali Current and associated upwelling. Progr. in Oceanogr. 12, 357–381.
Schubotz, F., Xie, S., Lipp, J.S., Hinrichs, K., Wakeham, S.G., 2018. Intact polar lipids in the water column of the eastern tropical North Pacific: abundance and structural variety of non-phosphorus lipids. Biogeosci 15, 6481–6501. doi:10.5194/bg-15-6481-2018.
Seibel, B., 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J. Exp. Biology 214 (2), 326–336. doi:10.1242/jeb.049171.
Seitzinger, S., Harrison, J.A., Böhlke, J.K., Bouwman, A.F., Lowrance, R., Peterson, B., Drecht, G.V., 2006. Denitrification across landscapes and waterscapes: a synthesis. Ecological appl 16 (6), 2064–2090. doi:10.1890/1051-0761(2006)016[2064:dalawa]2.0.co;2.
Singh, A.K., Chakraborty, P.P., Sarkar, S., 2018. Redox structure of Vindhyan hydrosphere: clues from total organic carbon, transition metal (Mo, Cr) concentrations and stable isotope ($\delta^{13}C$) chemistry. Curr. Sci. 115 (7), 1334–1341. https://www.jstor.org/stable/26978407.
Sreekanth, V., 2016. Discussion on linear long-term trends in aerosol and cloud properties over India and its surrounding waters. Adv. Space Res. 57 (10), 2104–2114. doi:10.1016/j.asr.2016.02.015.
Staaf, D.J., Ruiz-Cooley, R.I., Elliger, C., Lebaric, Z., Campos, B., Markaida, U., Gilly, W.F., 2010. Ommastrephid squids Sthenoteuthis oualaniensis and Dosidicus gigas in the eastern Pacific show convergent biogeographic breaks but contrasting population structures. Marine Ecol. Prog. Series 418, 165–178. doi:10.3354/meps08829.
Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. Science (1979) 320 (5876), 655–658. http://doi.org/10.1126/science.1153847.
Stramma, L., Johnson, G.C., Firing, E., Schmidtko, S., 2010. Eastern Pacific oxygen minimum zones: supply paths and multidecadal changes. J. Geophys. Res. 115 (C9). doi:10.1029/2009JC005976.
Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Körtzinger, A., 2012. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat. Climate Change 2 (1), 33–37. doi:10.1038/nclimate1304.
Tems, C.E., Tappa, E., 2024. Regional Fluctuations in the Eastern Tropical North Pacific Oxygen Minimum Zone during the Late Holocene. Oceans 5 (2), 352–367. doi:10.3390/oceans5020021.
Thamdrup, B., 2012. New pathways and processes in the global nitrogen cycle. Annu. Rev. Ecology, Evol. Sys. 43 (1), 407–428. doi:10.1146/annurev-ecolsys-102710-145048.
Thomsen, S., Kanzow, T., Colas, F., Echevin, V., Krahmann, G., Engel, A., 2016. Do submesoscale frontal processes ventilate the oxygen minimum zone off Peru? Geophys. Res. Lett. 43 (15), 8133–8142. doi:10.1002/2016GL070548.
Tremblay, N., Abele, D., 2016. Response of three krill species to hypoxia and warming: an experimental approach to oxygen minimum zones expansion in coastal ecosystems. Marine Ecology 37 (1), 179–199. doi:10.1594/PANGAEA.835292.
Tyrrell, T., 1999. The relative influences of nitrogen and phosphorus on oceanic primary production. Nature 400 (6744), 525–531. doi:10.1038/22941.
Ulloa, O., Pantoja, S., 2009. The oxygen minimum zone of the eastern South Pacific. Deep Sea Res. Part II 56 (16), 987–991. doi:10.1016/j.dsr2.2008.12.004.
Ulloa, O., Canfield, D.E., DeLong, E.F., Letelier, R.M., Stewart, F.J., 2012. Microbial oceanography of anoxic oxygen minimum zones. Proceed. Nat. Acad. Sci. 109 (40), 15996–16003. doi:10.1073/pnas.1205009109.
Vaquer-Sunyer, R., Duarte, C.M., 2010. Sulfide exposure accelerates hypoxia-driven mortality. Limnol. and Oceanogr. 55 (3), 1075–1082. doi:10.4319/lo.2010.55.3.1075.
Vergara, O., Dewitte, B., Montes, I., Garçon, V., Ramos, M., Paulmier, A., Pizarro, O., 2016. Seasonal variability of the oxygen minimum zone off Peru in a high-resolution regional coupled model. Biogeosci 13 (15), 4389–4410. doi:10.5194/bg-13-4389-2016.
Vidhya, V., Jyothibabu, R., Jagadeesan, L., Rashid, C., Alok, K.T., Arunpandi, N., Thirumurugan, R., 2022. Oxygen minimum zone copepods in the Arabian Sea and the Bay of Bengal: their adaptations and status. Progr. in Oceanogr. 206, 102839. doi:10.1016/j.pocean.2022.102839.
Vik, D., Gazitúa, M.C., Sun, C.L., Zayed, A.A., Aldunate, M., Mulholland, M.R., Sullivan, M.B., 2021. Genome-resolved viral ecology in a marine oxygen minimum zone. Environ. Microbiol. 23 (6), 2858–2874. doi:10.1111/1462-2920.15313.
Vuillemin, A., Coskun, Ö.K., Orsi, W.D., 2022. Microbial activities and selection from Surface Ocean to subsea floor on the Namibian continental shelf. Appl. and Environ. Microbiol. 88 (9), e00216–e00222. doi:10.1128/aem.00216-22.
Ward, M.H., 2009. Too much of a good thing? Nitrate from nitrogen fertilizers and cancer. Rev. on Environ. Health 24 (4), 357–363. doi:10.1515/reveh.2009.24.4.357.
Ward, B.B., Devol, A.H., Rich, J.J., Chang, B.X., Bulow, S.E., Naik, H., Jayakumar, A., 2009. Denitrification as the dominant nitrogen loss process in the Arabian Sea. Nature 461 (7260), 78–81. doi:10.1038/nature08276.
Weber, T., Bianchi, D., 2020. Efficient particle transfer to depth in oxygen minimum zones of the Pacific and Indian Oceans. Front. Earth. Sci. 8, 376. doi:10.3389/feart.2020.00376.
Wirth, A., Willebrand, J., Schott, F., 2002. Variability of the Great Whirl from observations and models. Deep Sea Research Part II 49 (7–8), 1279–1295. doi:10.1016/S0967-0645(01)00165-5.
Wright, J.J., Konwar, K.M., Hallam, S.J., 2012. Microbial ecology of expanding oxygen minimum zones. Nature Rev. Microbio. 10 (6), 381–394. doi:10.1038/nrmicro2778.
Xing, J., Deng, Y., Ren, J., Hein, J.R., Xian, H., Li, L., Jiang, X., Yang, Y., He, G., Qiu, H., Zhu, J., 2025. Oxygen minimum-zone expansion controls critical metal enrichment and growth rates in a ferromanganese crust from the central Pacific Ocean. J. Geophys. Res: Oceans 130 (6), e2025JC022450. doi:10.1029/2025JC022450.
Yamamoto, A., Abe-Ouchi, A., Shigemitsu, M., Oka, A., Takahashi, K., Ohgaito, R., Yamanaka, Y., 2015. Global deep ocean oxygenation by enhanced ventilation in the Southern Ocean under long-term global warming. Glob. Biogeochem. Cycles 29 (10), 1801–1815. doi:10.1002/2015GB005181.