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Editorial: Recent developments in oxygen minimum zones biogeochemistry

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Editorial on the Research Topic
Recent developments in oxygen minimum zones biogeochemistry

Marine Oxygen Minimum Zones (OMZs) modulate biogeochemical cycles, and directly impact climate dynamics by influencing air-sea fluxes of the potent greenhouse gases methane and nitrous oxide (Levin, 2018). OMZs are formed in regions of weak oxygen (O_2) supply from physical ventilation and high integrated microbial O_2 demand fueled by downward organic flux from overlying surface waters. The ocean's major OMZs are found in the Eastern Tropical South and North Pacific Ocean and the Arabian Sea and Bay of Bengal in the Indian Ocean (Karstensen et al., 2008; Stramma et al., 2008). OMZs are especially prevalent along eastern boundary upwelling systems (EBUS) where high nutrient water is upwelled along the coast to the surface, sustaining high primary productivity (e.g., off Chile, Peru, and South Africa). Other low-O_2 or hypoxic regions (also called dead zones, with hypoxia being less than 2 mg/L O_2) occur in the tropical Atlantic, the Gulf of Mexico, the Baltic Sea and isolated fjords and basins. Recent observations suggest an ongoing expansion and intensification of OMZs. Global warming is recognized as the main driver causing global ocean deoxygenation due to decreased oxygen solubility and increased water-column stratification (Keeling et al., 2010; Helm et al., 2011; Schmidtko et al., 2017). Global warming also causes changes in respiration, ocean circulation and wind patterns, which affect the development of OMZs (Levin, 2018). Declining O_2 concentrations greatly impact marine ecosystems, with consequences for fisheries and the global economy. There is thus a pressing need to better understand future OMZs distribution and biogeochemistry.

This Research Topic presents 14 original research articles with the goal of reviewing current knowledge on OMZ biogeochemistry, the impact of climate change and global warming on OMZ expansion, and novel approaches informing future research directions.

Several contributions to the Research Topic (6 out of 14 manuscripts) cover temporal variability in distribution and volume of OMZs, in both the past and present. Soetaert et al. investigated the mechanisms causing deep-water renewal events in Saanich inlet, a seasonally anoxic basin in British Columbia, Canada, which serves as a natural laboratory to understand OMZs. They found that these events were characterized by a complex layering of water masses with different densities and controlled by a combination of easily predictable (tidal current speeds) and less predictable (the intensity of coastal upwelling) factors.

Muñoz et al. showed a strong temporal variability of the upper part of the OMZ along the Chilean continental margin over the last 2000 years using redox-sensitive metals and $\delta^{15}N$ from sediment cores. The OMZ was more intense before 1400 AD, then oxygenated waters mostly prevailed afterward, including for the last 50 years, except between 1925 and 1970, corresponding with low amplitude of the Pacific Decadal Oscillation and reduced El Niño Southern Oscillation (ENSO). Additionally, Pizarro-Koch et al. observed a strong temporal variability of the subtropical OMZ off central Chile using a coupled physical-biogeochemical regional model during a period dominated by two cold La Niña events (2001 and 2007). Changes in oxygenation were attributed to transport of waters by the oxygen poor Peru-Chile undercurrent, quasi-zonal jets, and mesoscale eddies.

The mechanism explaining the geographic decoupling between the highly productive western boundary and the OMZ in the northeastern part of the Arabian Sea is still a topic up for debate (e.g., Kim et al., 2001; Sarma, 2002; McCreary et al., 2013; Sarma et al., 2020). Zhang et al. attributed this decoupling to the region's ocean circulation and its impact on particle flux. Their model showed enhanced ventilation from the northward circulation of oxygen-rich intermediate waters in the west as well as transport of particulate organic matter (POM) from the productive western region toward the eastern part of the Arabian Sea during summer. Future oxygen evolution in response to climate change in the Arabian Sea is unclear, with contrasting Earth System Model simulations, such as in Vallivattathillam et al., predicting shrinking of the OMZ and other studies observing an expansion (e.g., Lachkar et al., 2019; Lachkar et al., 2021). The findings by Vallivattathillam et al. show the importance of correcting model biases using observational data, especially in regions where local forcing dominates. Lachkar et al. further reviews the current literature on the recent and future evolution of the Arabian Sea OMZ. They discuss the reasons for observed discrepancies in model projections, challenges to predict changes and next research directions.

OMZs greatly impact biogeochemical cycling, with 6 out of 14 submitted manuscripts focused on this topic. Aldunate et al. found that the secondary chlorophyll maximum (SCM) significantly contributed to the particulate organic carbon (POC) pool in the Eastern Tropical North and South Pacific. The SCM develops just below the oxycline in the anoxic portion of OMZs, where nutrient concentrations are generally elevated and light intensity only 1% of incident light. The $\delta^{13}C$ of the POC was enriched by up to 3‰ in the SCM, mostly reflecting net heterotrophy. More depleted $\delta^{13}C$ of POC in the absence of a SCM was attributed to the dominance of chemoautotrophic bacteria (e.g., anammox and sulfur-oxidizing bacteria). Further, Henríquez-Castillo et al. showed, using metagenomics, that gammaproteobacteria of the genus *Alteromonas* are abundant in suboxic waters, peaking at the SCM and significantly impacting carbon cycling in OMZs.

Low-O_2 concentrations in OMZs are the on-switch for hypoxic and anaerobic processes such as nitrogen loss by denitrification and anammox. Up to 30-50% of fixed nitrogen loss occur in OMZs, which represent only 0.1% of total oceanic volume, and affects global marine primary productivity on longer time scales (Codispoti et al., 2001; Gruber and Galloway, 2008; DeVries et al., 2012; Eugster et al., 2013). Chuang et al. used a biogeochemical model in the Benguela Upwelling System and showed the significant role of large sulfur bacteria for benthic nitrogen (and possibly phosphorus) fluxes to the water-column. Denitrification rates were over two times higher than DNRA (dissimilatory nitrate reduction to ammonium) in the presence of these bacteria. Dale et al. used benthic chamber measurements and a numerical model to investigate sedimentary oxygen, carbon, and nutrient fluxes, with a focus on nitrogen, in the Mauritanian upwelling OMZ. The authors estimated a larger net benthic isotope effect of nitrogen loss compared to other marine oxygenated environments, with possible implications for our understanding of the global marine nitrogen budget.

Conversely, OMZs also provides suitable conditions for N_2-fixing organisms, since the key enzyme involved in this process, *nifH*, coding for the Mo-Fe nitrogenase, is inhibited at high oxygen levels. There is however an increasingly recognized discrepancy between low N_2 fixation rates and high diazotrophic diversity in OMZs (Jayakumar and Ward, 2020), including the Northern Benguela Upwelling System (NBUS; Reeder et al.). Reeder and Löscher further explore the causes of this discrepancy by looking at alternative types of nitrogenase, which have been overlooked in previous studies: the Fe-Fe nitrogenase *Anf* and the V-Fe nitrogenase *Vnf*. Diazotrophs with the genetic potential for using these alternative nitrogenases were detected in metagenomes and transcriptomes of OMZs off Peru, the Bay of Bengal and Saanich Inlet. The authors suggest that, while these alternative nitrogenase genes are likely not active in present OMZs due to low trace metal concentrations, their role for N_2 fixation might change under future climate scenarios.

Finally, greenhouse gas production, e.g., nitrous oxide and methane, is enhanced under hypoxic and anoxic conditions, accelerating global warming, putatively creating a positive feedback loop for ocean deoxygenation. Bourbonnais et al. present a N_2O concentration, stable isotopic composition, and isotopomer dataset of unprecedented high spatial and depth resolution in the eastern Pacific Ocean. Different N_2O sources were identified under different oxygen regimes, with the largest N_2O accumulations mostly from denitrification at low oxygen concentrations near the oxycline.

Future research directions emerge from the topics covered in this Research Topic. Novel approaches, such as long-term monitoring using sensors installed on autonomous platforms, which is the goal of programs such as Biogeochemical Argo (BGC-ARGO) or Ocean Observatories Initiative (OOI), will allow increasing spatial and temporal resolution and extent of observations (e.g., Margolskee et al., 2019; Kwiecinski and Babbin, 2021). In this context, 1 manuscript in the Research Topic (McNeil et al.) presents a gas tension device to study denitrification in the anoxic core of the Eastern Tropical North Pacific OMZ. This device measures total dissolved gas pressure, which allowed obtaining the first autonomous biogenic N_2 profiles in the open ocean. This high-resolution data is necessary to validate numerical models and better understand the evolution of OMZs in the past and future in relation to climate change and global warming. Further, *in-situ* microbial ecology approaches (e.g., Edgcomb et al., 2016) could help better understand biogeochemical cycling and pathways in OMZs and resolve current unknowns, such as the paradigm regarding N_2 fixation in low-oxygen environments.

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Conflict of interest

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