https://doi.org/10.5194/bg-2023-45
Preprint. Discussion started: 3 March 2023

Biogeosciences Discussions

Manuscript type: *Ideas and perspective*

Title:

Ideas and perspectives. The fluctuating nature of oxygen shapes the ecology of aquatic habitats and their biogeochemical cycles: the aquatic oxyscape

Authors

Marco Fusi[1,*], Sylvain Rigaud[2], Giovanna Guadagnini[3], Alberto Barausse[3], Ramona Marasco[4], Daniele Daffonchio[4], Julie Régis[2], Louison Huchet[2], Capucine Camin[2], Laura Pettit[1], Cristina Vina-Herbon[1], Folco Giomi[5,*]

[1]Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY

[2]Univ. Nîmes, EA 7352 CHROME, Rue Du Dr Georges Salan, 30021 Nîmes, France

[3]Department of Biology, University of Padova, Padova, Italy

[4]Biological and Environmental Sciences and Engineering Division (BESE), Red Sea Research Center (RSRC), King Abdullah University of Science and Technology (KAUST), Thuwal, Kingdom of Saudi Arabia

[5]Independent Researcher, Padua, Italy

*equal contribution and co-corresponding authors:

Marco Fusi: marco.fusi@jncc.gov.uk

Folco Giomi: folcog@gmailcom

https://doi.org/10.5194/bg-2023-45
Preprint. Discussion started: 3 March 2023

Abstract

Oxygen availability is a pivotal factor for ecosystem functioning and the resistance of organisms to the effect of climate change in aquatic habitats. Although extensive work has been made to assess the effect of oxygen on marine and freshwater biota, many studies did not capture the ecological importance of oxygen variations. Overlooking the fluctuating nature of oxygen may cause potential biases in the design and implementation of management policies of aquatic habitats. Conceptual perspectives on the dynamic nature of oxygen fluctuations have been raised in the scientific community to enhance the understanding of the effect of oxygen on the physiology and the ecology of aquatic species and the biogeochemical functioning of the ecosystems. A growing number of empirical works are outlining a novel conceptual framework that considers the magnitude of oxygen fluctuation as a key variable that explains adaptation to stress conditions. Oxygen in productive aquatic habitats shows large fluctuations at diel and seasonal scales, exposing aquatic species from conditions of extreme supersaturation to anoxia. Recent research indicates that such fluctuation tunes the physiological plasticity of the animal in response to thermal stresses. In this contribution, we provide compelling evidence based on current research that the fluctuating oxygen landscape, here defined as "*oxyscape*", has an important role in aquatic animal physiology and adaptation and the ecosystem biogeochemistry. We propose that the oxyscape should be considered in the modelling and managing policies of aquatic ecosystems.

Keyword

Biogeochemical cycles; Climate Change; Hyperoxia; Hypoxia; Marine Ecosystem Assessment; Microbial processes; Oxygen Fluctuations; Supersaturation

https://doi.org/10.5194/bg-2023-45
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1. Introduction to environmental dissolved oxygen variability and its ecological relevance

The actual assembly of organism communities in a given habitat is determined by the specific environmental conditions that select specific sets of species. Climate anomalies and changes raise concerns on ecosystem stability and habitat preservation, with consequences ranging from species substitution to species extinction (Antão et al., 2020). To model and predict such effects on community composition and stability, it is necessary to learn about the limits of the environmental conditions that challenge the different species (Bennett et al., 2021). However, in many cases, such conditions are resumed into averaged parameters that do not capture the whole range to which organisms are exposed to (Bernhardt et al., 2020).

In aquatic environments, chemical and physical parameters greatly vary at different time and spatial scales, following cyclical fluctuation or stochastic variations (Shaw et al., 2013; Kerrison et al., 2011; Vargas et al., 2017, 2022; Manzello, 2010; Challener et al., 2016; Duarte et al., 2013). The lack of details on such variations in time and space challenges our understanding of how the species adapt their physiology, limiting our estimation of their resilience to ongoing environmental changes (Booth et al., 2023). The perception of such knowledge gap is progressively moving the research interest on species' ecophysiological response to chemico-physical parameters, such as temperature, salinity or pH, and the associated biogeochemical cycles, toward more accurate assessments of their natural variability (Antão et al., 2020; Bernhardt et al., 2020). Increasing efforts are now devoted to upgrade eco-physiological approaches to integrate the relevant environmental background (Giomi et al., 2019; Marasco et al., 2023).

Oxygen variability exerts a deep effect on aquatic life yet remains underestimated. Most studies dealing with oxygen variation have addressed the decline of mean oxygen availability in oceans (Breitburg et al., 2018) and the occurrence and repercussions of events of environmental hypoxia (Diaz and Rosenberg, 2008; Bickler and Buck, 2007). How short-term oxygen variations shape aquatic life and biogeochemical processes remains largely overlooked. These variations are generally of greater amplitudes and more regular than seasonal ones (Limburg et al., 2020; Bates et al., 2018). We refer to deviation from the saturation of oxygen concentrations as the ratio between the actual concentration and the saturation concentration of oxygen that would be observed in water under equilibrium conditions between air and water. The fine measure of the range of variation of aquatic oxygen and its effect on organisms and biogeochemical cycles

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has the potential to elucidate unpredicted mechanisms of resilience and tolerance to ongoing climate change.

2. Oxygen trends and stochastic variations

A gradual decline of the total oxygen content of about 2% since the second half of the 20th century has been recently reported, with a further reduction of up to 7% predicted for the following century (Schmidtko et al., 2017; Breitburg et al., 2018). In parallel, open-ocean oxygen minimum zones (OMZs) have largely expanded (Stramma et al., 2010) together with the increasing occurrence of severe hypoxia events whose predictability has decreased as their occurrence spreads across all oceans (Diaz and Rosenberg, 2008). The main cause of deoxygenation is attributed to global warming and is exacerbated by the discharge of nutrients and pollutants (Ito et al., 2016). Topography of water basins also affects the incidence of hypoxia events influencing the rate of mixing of oxygenated layers and the resident time of water bodies. For example, in the Baltic Sea, the geomorphology of the coastline can explain up to 80% of the hypoxic phenomena (Virtanen et al., 2019).

The gradual decrease of total oxygen in oceans has been reported in several studies that analyse long time trends (Keeling et al., 2010; Schmidtko et al., 2017; Breitburg et al., 2018) and from reports at the global geographical scale (Laffoley and Baxter, 2016). However, unexpected oxygen profiles have also been reported in several specific habitats and at different time scales suggesting that different abiotic and biotic drivers modulate oxygen dynamics (Craig and Hayward, 1983). For instance, the alternation of oxygen biological production and consumption determines massive fluctuation of its availability in highly productive aquatic habitats, such as mangrove forests, salt marshes, coral reefs (Giomi et al., 2019; Fusi et al., 2021; Booth et al., 2021), kelp forests (Krause-Jensen et al., 2016), plankton blooms in the open oceans (Riser and Johnson, 2008; Benoiston et al., 2017), freshwater lakes (Andersen et al., 2017) or even in agricultural drainage channels (Booth et al., 2023). Stochastic variation of oxygen availability principally depends upon abiotic factors and may determine extensive conditions of uneven oxygenation on small and large spatial and temporal scales. Changes in wind, irradiance, temperature, and atmospheric pressure influence dissolved oxygen concentrations at the air-water interface (Emerson et al., 2002; Hull et al., 2008). The upwelling of nutrient-rich-poorly oxygenated waters affects oxygen concentrations in the ocean water

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column, ranging from undersaturation in the deep seawater to supersaturation in the mixing front, determined by an intensified biological activity (Emerson et al., 2002).

3. Seasonal and diel oxygen fluctuations

Technological advances in environmental monitoring by high-frequency logging allow capturing the seasonal and even the diel oxygen fluctuations (Bates et al., 2018). Seasonal diel oxygen variations are increasingly reported at all latitudes and habitats and occur in a vast range of water bodies independently of the scale, the hydrological features and the local biotic components (Figure 1). For example, fluctuations of 150% in spring and 30% in winter occur in the Venice lagoon (Figure 1, Location 5), and even more pronounced fluctuations occur in mangroves, corals and seagrasses (Figure 1, systems 10-12; Giomi et al., 2019). The magnitude of oxygen fluctuations is site-specific and depends, among other factors, on the solar radiation and water temperature and their effect on primary producers' photosynthetic and respiration activity, the cycles of water column stratification and mixing, and the nutrient loads. In highly productive marine environments, increased dissolved oxygen concentration may occur in spring due to the intensification of photosynthetic activity, followed by a decrease of available oxygen during the warmest months and a progressive recovery in autumn and winter (Cowan et al., 1996; Bartoli et al., 2001; Kim et al., 2019). Spatial differences in oxygen saturation occur between surface and bottom water masses because of isolation driven by water stratification, the decrease of light penetration, and the coupling with increased oxygen demand close to the sediments at the bottom of the water column (Figure 2). In summer, enhanced benthic respiration is determined by higher water temperature, which decreases oxygen solubility and enhances oxygen demand. Lower vertical mixing and higher water residence time, and higher turbidity due to higher concentration of organic matter, further decrease oxygen concentrations down to hypoxia in the deep water layers (Figure 2; Talke et al., 2009; Schmidt et al., 2019). Conversely, dissolved oxygen increases in the euphotic part of the water column because of the enrichment of photosynthetic communities (Spietz et al., 2015). The annual cycle of the ice cover regulates the seawater oxygen regime in polar environments, with depletion in winter and re-oxygenation during the spring (Deshpande et al., 2017; Zhan et al., 2014). Marked oxygen variations also occur at a diel scale driven by temperature and light diel cycles and by the balance between photosynthesis and respiration (Winter et al., 2019). The amplitude of diel oxygen variation

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can exceed the average seasonal variation, thus being variable with higher explanatory power for the physiology of aquatic life (Giomi et al., 2019). While water temperature is only linked to meteorological changes, the oxygen concentration in productive aquatic environments is also regulated by the biota component (Chapman, 2021). Community composition of primary producers (Power and Cardinale, 2009), rainfall level (Mallin et al., 1993), nutrients' runoff (Kinney and Roman, 1998), biotic networks (Graham et al., 2018; Breen and Mann, 1976), and bacterial community dynamics (Guo et al., 2022), govern, at a small scale, high spatial and temporal change in the concentrations of dissolved oxygen. The interaction of all these factors strongly affects dissolved oxygen fluctuations beyond the levels that can be predicted from just the meteorological trends.

4. The oxygen variation in the day-life of aquatic organisms

Oxygen availability plays an important role in the physiology of aquatic species (Pörtner, 2010; Hochachka, 1991; Stillman and Somero, 2000). In the design of experiments on the physiology of aquatic animals, oxygen is frequently treated as a fixed factor and maintained around the water saturation. However, organisms inhabiting aquatic environments experience ample diel oxygen fluctuations and are adapted to endure or respond to the experienced variation (Blewett et al., 2022; Morash et al., 2018). Oxygen may be systematically depleted at night and fully recovered during the day, changes that certainly have consequences on the tolerance to acute stressors such as hypoxia and warming. Dependent on the intensity of the photosynthetic activity, dissolved oxygen concentrations can reach levels far above the physical saturation (Giomi et al., 2019; McArley et al., 2020). Under such hyperoxic conditions, aquatic organisms experience oxygen availability well beyond their physiological needs, but the effects on their physiology and life history are largely unknown.

Hyperoxia benefits the metabolic performance of fishes and invertebrates, especially under acute warming that may be very intense in tidal ponds or shallow coastal habitats (Fusi et al., 2021; Booth et al., 2021; Giomi et al., 2019; McArley et al., 2020; Booth et al., 2023). It extends the upper thermal tolerance of aquatic animals during acute events of daily warming and their survival to anomalous heat waves (McArley et al., 2022). Within the current trend of climate change, the beneficial effect of hyperoxia against extreme heating events can have underestimated positive consequences on the survival of the animals. For instance,

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an important consequence of exposure to the hyperoxic conditions experienced during the daytime under high heating regimes is the enhanced capability to extract oxygen from the poorly oxygenated water during the night and endure hypoxic or even anoxic periods (Giomi et al., 2019; Booth et al., 2021).
Oxygen fluctuations are also appreciated as a factor contributing to the structuring of organismal networks and in the synchronization of life history dynamics such as spawning or larval recruitment (Garzke et al., 2019; Viaroli and Christian, 2004).

5. The role of oxygen fluctuation in coastal biogeochemical cycles

5.1 Biogeochemical cycles in the pelagic compartment in relation to oxygen fluctuation

Fixation of CO_2 and nutrients and the consequent accumulation of organic matter is the main natural process that occurs along coastal areas and transfer excess carbon, nitrogen and phosphorous from the surface layers to the sediment, atmosphere, and open ocean (Rabouille et al., 2001). The transfer of carbon, nitrogen and phosphorous are regulated by multiple processes involving a smaller space-time scale where oxygen availability is the strongest driver (Figure 3). The concentration of oxygen and the horizontal surface distribution of nutrients together with surface phytoplankton and zooplankton are influenced by currents which are affected by the winds combined with the Earth's rotation, *i.e.*, the Coriolis effect, and by inputs from coastal zones (Legendre, 2014; Lévy et al., 2018; Rabouille et al., 2001). The daily and/or seasonal water column stratification, determined by the vertical gradient of the chemical-physical parameters, influences primary production. In the euphotic zone (global average depth, 65 m), phytoplankton is responsible for carbon fixation and the biogeochemical cycles of nitrogen, phosphorus, and silicates and modulates the daily fluctuations of dissolved oxygen in the superficial layers (Litchman et al., 2015; Le Quéré et al., 2016). The concentration of sinking organic material is influenced by the activity of the autotrophic components (production of oxygen and sinking of organic material in the form of phytoplankton) and of the heterotrophic components (faster sinking of marine snow and single cells with higher density and consumption of organic material with consequent reduction of dissolved oxygen) (Falkowski, 1994; Litchman et al., 2015; Howarth et al., 2011). This varies on a daily and/or seasonal scale, depending on the stratification of the water column and the dissolved oxygen fluctuations that influence the nychthemeral displacement, the permanence of zooplankton and the consumption of organic matter.

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On a global scale, the difference in density of the water column caused by the chemical-physical vertical gradient induces the thermohaline circulation of the water mass and consequently may enrich the concentrations of dissolved oxygen and nutrients on the seabed (Legendre, 2014; Ulloa and Pantoja, 2009). Some areas do not have a temporal regularity, such as upwelling areas (Eastern Boundary Upwelling Systems EBUS) and/or areas characterized by weak currents (*e.g.*, lagoons) in which the increase in primary productivity that follows nutrient increase, favours an oxygen increase followed by hypoxic and anoxic conditions of the waters. Algal blooms combined with stratification of the water column inhibit daily dissolved oxygen fluctuations and favour the permanence of anoxic conditions of the more superficial layers of the OMZs (Ulloa and Pantoja, 2009). As a result, the uptake of nutrients by the autotrophic component is inhibited, and the rate of oxygen production and consumption and the consumption of organic matter are reduced, thus affecting the biogeochemical feedback, especially in coastal ecosystems.

5.2 Biogeochemical cycles in the benthic environments in relation to oxygen fluctuation

5.2.1. General aspect of the coastal benthic biogeochemistry. Coastal areas are generally characterized by relatively limited water column height and biogeochemical cycles in these environments are tightly coupled to benthic processes and associated chemical transfers at the sediment-water interface (Soetaert et al., 2000). The physico-chemistry of the water column strongly impacts the biogeochemical reactions occurring in surface sediment and chemical transfers at the sediment-water interface, which in return impacts the water column biogeochemistry. In coastal environments, sediment is the main reservoir of organic matter (OM) from pelagic productivity. Most sedimentary OM is re-mineralized by biogeochemical pathways depending on the availability of electron acceptors, from the most to the least energetically favourable: oxygen, nitrate, Mn oxides, Fe oxides and sulfate (Burdige, 2005). These reactions are biologically mediated by heterotrophic organisms, which promotes aerobic respiration when oxygen is present, anaerobic respiration by denitrification in the presence of nitrate, particulate Mn and Fe oxyhydroxides reduction when they are available, and sulphate reduction (see also section 6). Those reactions consume OM and oxidants to release chemicals from the degradation of OM (CO_2, NH_4^+, PO_4^{3-}) and by-products of each reaction (N_2, Mn and Fe, H_2S) that accumulate in porewaters. Because the availability of oxidants decreases in the sediment during burial, the biogeochemical reactions are vertically zoned in the sediment, with concentration gradients occurring between the water column and the different layers of the sediment (Konhauser, 2007). These gradients govern the direction of the dissolved chemical species migration (Schulz, 2006). Oxygen availability also affects the structure and composition of the benthic macrofauna community and related bioturbation processes that, by sediment reworking, impact the efficiency of biogeochemical reactions and the nature and the intensity of the chemical transfers at the sediment-water interface by bio-irrigation process (Sturdivant et al., 2012). In the sediments exposed to the tidal range, such as those where mangroves thrive, the burrowing and sediment reworking activity of crabs and other animals expose the deeper parts of the sediment to oxygen, creating a "halo effect" where the redox potential is increased respect to the undisturbed sediments and the availability of energetically favourable electron acceptors, such as oxygen and nitrate, is higher (Booth et al., 2019a, b). As oxygen is the most energetically favourable oxidant involved in the mineralization pathways and directly involved in the micro- and macro-biological communities and activities in surface sediment, its availability in overlying water thus appears as the most important driver of the biogeochemical cycles and transfer in the benthic environment.

5.2.2. Impact on benthic environment biogeochemistry at the seasonal steady-state scale. At the seasonal scale, it is well known that the decrease of oxygen concentrations in the water column lower the oxygen penetration depth in the sediment and the relative contribution of aerobic processes in the OM mineralization (Middelburg and Levin, 2009). It induces an upward migration of anaerobic processes and release of Mn, Fe and nutrients (PO_4^{3-} and NH_4^+ and other redox-sensitive trace elements) to the water column (Konhauser, 2007). The occurrence of long and strong O_2 depletion (*i.e.*, anoxia) in the water column may induce the release of toxic H_2S (Rigaud et al., 2013). Under low oxygen conditions, macrofauna density, diversity and activity are also generally reduced, along with reworking processes, affecting negatively O_2 penetration depth and solute transfer (Diaz and Rosenberg, 1995). In contrast, when the water column is well oxygenated, aerobic processes are favoured in the surface sediment and anaerobic processes remain deeper in sediment, preventing the release of reduced chemical species to the water column (Middelburg and Levin, 2009). When oxygen is non-limiting, high macrofauna diversity and activity are favoured, promoting oxygen penetration in the sediment and the associated aerobic processes. In such situations, higher oxygen concentrations enhance OM remineralization rates and chemical release rates. At the seasonal scale, high

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oxygen concentrations are generally encountered in winter with lower temperatures, while the lowest oxygen concentrations occur in summer with high temperatures (Figure 2). Temperature not only governs biogeochemical reaction kinetics, molecular diffusive transport rates and biological activity, but in synergy with oxygen concentration in the water column, it also drives the nature and intensity of the biogeochemical reactions at the seasonal scale.

5.2.3. Impact on benthic environment biogeochemistry at diurnal scale. When temperature and oxygen concentration in the water column fluctuate at short daily time scale, yet with very large amplitude (from anoxia/hypoxia to hyperoxia), the impact on biogeochemical cycles and chemical transfers is mostly unknown. Based on the trends observed at seasonal "steady-state" conditions, a conceptual model on the location of the major benthic processes in the sediment and the resulting fluxes at the sediment-water interface within the diurnal temporal scale can be drawn (Figure 4).

As oxygen penetration depth and concentration in sediment is known to rapidly evolve in response to the oxygen concentration in the overlying water (Glud, 2008), the importance of aerobic process in surface sediment is also expected to fluctuate at the diurnal timescale, with higher contribution during the day than during the night. The fast kinetics of the reductive dissolution/oxidative precipitation of Mn and Fe oxy-hydroxides and the redox cycle of S chemical species (*i.e.*, H_2S/SO_4^{2-}) suggests that those chemical species should evolve with a similar trend over daily timescales, with a reasonable short term (minutes-hours) delay (Rigaud et al., 2018). Consequently, we expect a vertical fluctuation of those biogeochemical redox processes in the sediment and related fluxes under diel oxygen fluctuation (Figure 4). The low oxygen concentration at night should induce a lower oxygen penetration depth and an upward distribution of NO_3^-, Mn and Fe oxyhydroxides and SO_4^{2-} reductions. If the oxygen concentration is low enough, the reductive dissolution of Mn and Fe oxyhydroxides may directly occur at the sediment-water interface, inducing their release to the water column with other chemical species associated with these phases (*i.e.*, PO_4^{3-} and most trace elements). In the specific case of anoxia, the sulfate-reduction process may occur at the sediment surface, releasing H_2S to the water column. It is expected that in such a condition, the release of dissolved metals (Fe, Mn and trace elements), which also present a rapid kinetic for metal sulfide formation in the presence of S(-II), can be reduced and likely reverted (Figure 4). In contrast, the increase of oxygen

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concentration during the day promotes oxygen penetration in the sediment and the oxidation of reduced species accumulated during the night, such as dissolved Mn, Fe, NH_4^+ and eventually H_2S, preventing their release from the sediment. The reconstitution of the Mn/Fe oxyhydroxide reservoir in surface sediment favours the trapping of PO_4^{3-} and trace elements associated with Fe and Mn cycles. The oxidation of NH_4^+ induces the formation of NO_2^- and NO_3^- that may be released from the sediment.

In shallow coastal areas, the light radiation may also reach the sediment surface allowing the photosynthetic activity of the microphytobenthos to occur in surface sediment (Figure 4). The local source of oxygen at the sediment surface occurs because photosynthesis strongly enhances the biogeochemical processes described above (Denis et al., 2012; Rigaud et al., 2018). The oxygen released in the water column enhances the water hyperoxia and consumes nutrients and CO_2 during photosynthesis. This creates a very peculiar situation that modifies the direction and intensity of chemical fluxes at the sediment-water interface and the chemical composition of water and surface sediment in coastal areas at the diurnal scale. For those rapid redox-sensitive chemical species, processes and fluxes are thus expected to evolve, between such extreme night/day fluctuations, with a transient response related to the reaction kinetics and transport within the sediment surface.

For OM mineralization processes, the effects of short-term oxygen fluctuation are more challenging to predict. It will also be dependent on the capacity of heterotrophs to react/adapt to the changing oxygen concentrations and eventually shift between different metabolic processes (for microorganisms where variables metabolic pathways coexist) or to activate/cease the process in relation to physicochemical conditions and oxidant availability (for microorganisms with specialized metabolisms). Consequently, the dynamic response of the microbial community to short-term oxygen and chemical fluctuations needs to be investigated in more detail in relation to microbial communities' resilience and adaptation capacity (see section 6).

In productive coastal areas, the benthic organisms, including macro and meiofaunal species, adapt to large and rapid daily oxygen variation by modifying their behaviour. The bioturbating activity may be favoured during high oxygen concentration and lowered during conditions of low oxygen availability. We expect that, during the night oxygen deficiency, the benthic organism activity is reduced, inducing a decrease in the sediment reworking intensity. This is accompanied by a reduction of the biologically-mediated solute fluxes

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at the sediment-water interface and oxygen penetration depth in the sediment. In contrast, during oxygen supersaturation occurring in the day, bioturbation is intensified and may induce a short-term change in the contribution of biologically-mediated reactions and transfers. Here also, a delay between the oxygen fluctuation in the water column and the biogeochemical response of the sediment, related to the biological activity, would depend on site characteristics (oxygen concentration and range of fluctuation, bioturbating species). For instance, in areas where anoxia events are recurrent, the absence of macrofauna prevents bioturbation and its influence on the benthic biogeochemistry (Nilsson and Rosenberg, 1997).

In response to large amplitude and diel oxygen fluctuations, the sediment' biogeochemical cycles are also expected to fluctuate (Figure 4). However, as the resulting benthic biogeochemistry cycles are associated with the dynamics of three interdependent compartments (*i.e.*, geochemical composition, microbial communities, bioturbating-faunal communities), each presenting its kinetics and responses to oxygen fluctuations, we expect the sediment to be permanently maintained under unsteady-state conditions. This makes it difficult to quantitatively predict the resulting OM mineralization rates, the proportion of involved processes, and the chemical transfers at the sediment-water interface. The recent development of tools which can measure the chemical composition and sediment-water fluxes over the short-term scale (*i.e.*, microsensors, eddy covariance technic, gradient-flux method), in addition to benthic microbial and macrofaunal activity (*e.g.*, improved sediment profile imaging), may be beneficial to produce experimental data that will help to fill these gaps in understanding. At the same time, specific efforts should be focused on assessing the isolated response to those three different compartments. Those data should then be implemented to appropriately calibrate non-steady-state coupled pelagic-benthic biogeochemical models, which can predict the resulting biogeochemical functioning of productive coastal ecosystems and, thus, to predict their fate under climatic changes.

6. The interrelationship of oxygen fluctuation and aquatic microbial communities

Oxygen is a two-faced element that acts as the terminal electron acceptor in aerobic respiration (by far the most efficient energy metabolism) and as an element of toxicity because the reduction of O_2 molecules partly results in reactive oxygen species. For this reason, oxygen remains a strong evolutionary force dominating functional interactions and the spatial structure of many microbial communities (Fenchel and

Finlay, 2008). Oxygen availability determines microbial metabolism, and many studies have been carried out to elucidate the different kinds of communities and metabolisms occurring under anaerobic or aerobic conditions (Sandrin et al., 2009). Marine microorganisms in productive coastal environments also experience large oxygen diel fluctuations, especially at the boundary layer between sediment/primary producers and water (Pacherres et al., 2022).

Assessing the full environmental oxygen variability in aquatic habitats using high-resolution temporal and spatial scales relevant to microorganisms can reveal in detail the complexity of the patterns of community dynamics and diversity in such oxygen-variable environments (Berg et al., 2022). For example, oxygen largely varies during the day in tropical clear shallow waters because of the photosynthetic activity of seagrasses, corals and mangroves (Giomi et al., 2019). Therefore, the microbial communities in these ecosystems can experience environmental conditions ranging from hyperoxia to anoxia (see the oxygen profile in Figure 2). These fluctuations imply that the microbial communities have to shift their composition and function according to the oxygen availability (Fenchel and Finlay, 2008). Microorganisms generally have a short generation time (and high turnover) that favour timely adaptation to new conditions in a changing environment (Steiner et al., 2019). During low oxygen availability at night-time, bacterial communities will shift their composition and function toward anaerobic function. End products of anaerobic metabolisms such as ammonium, sulphur and methane are consumed when oxygen becomes available again during the daylight and the recovery of photosynthesis, re-establishing aerobic respiration as the central metabolism of the microbial communities (Fenchel and Finlay, 2008). For example, in the Bohai Sea (China), under oxygen concentration lower than 4.2 mg/L the microbial communities were dominated by bacteria of the *Anaerolineaceae* (Guo et al., 2022). In Chilean coast ecosystems, the composition of the bacterial communities is regulated by the seasonality of the upwelling waters, with the partitioning of community composition driven by dissolved oxygen. *Bacteroidetes*, SAR11, SAR86 and *Alphaproteobacteria* dominated in waters containing dissolved oxygen concentrations higher than 70 µM. In contrast, taxonomic groups such as Arctic96BD-19, SUP05, SAR324 and *Desulfobacterales* were observed at dissolved oxygen concentrations below 70 µM to undetectable levels (Aldunate et al., 2018). The continuous variation of oxygen concentration enhances the diel cycling of nutrients in productive coastal environments,

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highlighting the importance of assessing the ecologically relevant oxygen fluctuations to determine the effective microbial functionality of the marine coastal ecosystem (Trowbridge et al., 2017).

The heterogeneity of oxygen availability that drives microbial communities' composition is not only temporal but also spatial. In shallow-productive marine environments, animal bioturbation is one of the main forces that allows oxygen to penetrate in waterlogged anoxic sediment and change the physico-chemical conditions, reshaping the microbial community assembly and functionality. Local accumulations of particulate OM and ventilated animal burrows mimic a mosaic of anaerobic and aerobic patches at a centimetre to sub-millimetre scale that changes the composition of the microbial assemblages, determining a significant consistent zonation around the burrow (Booth et al., 2019a, b). Incorporating methods to assess the ecologically relevant variability of oxygen availability, intensity and synchronicity in future experimental designs will generate a more accurate prediction of the response of bacterial communities and therefore their potential for biogeochemical cycling to climate change, better informing the development of management strategies to mitigate detrimental stressor impact on ecosystems effectively.

The current challenge in microbial ecology is to understand the widespread temporal and spatial environmental oxygen variability and switch from the "mean conditions paradigm" often used for investigations of microbial ecological processes to a dynamic model able to capture the microbial changing and functional potential under oxygen fluctuating conditions (Fusi et al., 2022).

7. Implications for marine assessment and management

Oxygen production is considered an ecosystem service (https://cices.eu/) because of the benefits humans receive, but, to date, there is limited inclusion of the impacts of deoxygenation or oxygen fluctuation in marine environmental policies. As such, there has been a lack of oxygen dynamics' integration into the computation of biodiversity indicators that assess aquatic communities (Breitburg et al., 2019; Chen et al., 2022).

Policies on pollution or nutrient control had a positive effect on the oxygen level in ocean water, however, there is still a clear missing link on specific policies to monitor and manage oxygen. While attention has been given to ocean warming and acidification, oxygen dynamics have been overlooked in assessing marine habitat or species' sensitivity to climate changes and anthropogenic disturbances. Including ecologically

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relevant variations of oxygen availability into aquatic biodiversity indicators, in addition to continuous and high temporal resolution oxygen and chemical concentration measurements in the sediment and water column, offers a great opportunity to refine and produce more robust predictors that will be able to disentangle better the response of aquatic ecosystems to climate change and anthropogenic disturbances (Dafforn et al., 2012). This would allow changes to be detected and identify areas where climate change's effects are (will) likely more severe. Managing or addressing the impacts of deoxygenation could also help to enhance biodiversity.

Understanding the rules that govern primary producers and their role in controlling the diel oxygen provision in aquatic habitats becomes pivotal to protect or restore the oxygen regime that can benefit aquatic ecosystems. Accurate investigation of oxygen cycles can have direct implications for management. For example, it can help early detection of oxygen disruption and therefore understand the vulnerability of many aerobic species. It can also help to understand the probability of shifts to anaerobic metabolisms that can significantly affect many components of marine ecosystems. For example, it could provide information on how to engineer anthropogenic structures (for example, offshore energy power plants; *e.g.*, Inger et al., 2009) to increase the growth of primary producers. Off-shore facilities are proliferating in high-energy environments, like the North Sea, following the huge demand for renewable energy. Beyond energy production platforms, they can serve as artificial habitats for marine fauna by cultivating marine macrophytes (Duarte et al., 2022; Koschorreck et al., 2020). They can attract marine fauna by providing shelter, but at the same time, they can provide thermal resistance by enhancing the oxygen level of the adjacent waters. Primary producers can provide habitat protection; for example, Maerl beds are important spawning grounds for anchovies in cold water and Maerl photosynthetic activity can benefit the development of the anchovy embryos (Berg et al., 2022). Along with other important functional roles, such as providing a pH buffer Field (Duarte et al., 2013) and pathogen protection Field (Lamb et al., 2017), aquatic primary producers can enrich the oxygen and be used to ameliorate and also protect aquatic biodiversity. Moreover, the value of oxygen production can be aggregated with carbon sequestration by blue carbon ecosystems, one of the most important buffers against climate change (Macreadie et al., 2021). Monitoring oxygen dynamics will need the effective implementation of a data management system, with

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rigorous quality control and leadership by a globally recognized oceanography data centre that provides open access for use in science and policy.

Moving forward, ecological research incorporating the role of oxygen variation in aquatic habitats will offer valuable progress, bringing together scientists and stakeholders to develop natural-based solutions to human impact (Gattuso et al., 2018). In this contribution, based on recent research, we provide evidence that the fluctuating oxygen creates a spatial and temporal heterogeneous aquatic oxygen landscape that we have defined here as "oxyscape". The oxyscape—having an important role for aquatic animal physiology and adaptation and the ecosystem biogeochemistry—should be considered in the modelling and managing policies of aquatic ecosystems to capture the ecologically relevant oxygen fluctuation. Understanding the oxyscape can help to reconsider the dynamics of many productive aquatic ecosystems and we, therefore, call on ecologists to rethink their models and experiments in this light. This would increase understanding of variations and resilience of communities to changes in environmental conditions at the scales of space and time relevant to individual components.

Author contributions

MF and FG conceived the study and wrote sections 1 to 4. AB, GG, SR, FG wrote section 5.1 and 5.2 and provided data for the Mediterranean sites. MF, RM and DD wrote section 6 and provided data for the Red Sea. MF, LP and CVH wrote section 7. All the authors discussed and reviewed the final version.

Competing interests

The contact author has declared that none of the authors have competing interests.

Financial support

D.D. acknowledge the financial support of King Abdullah University of Science and Technology (KAUST) through the Circular Carbon Economy initiative (grant no. REI/1/4483-01-01). D.D also acknowledge the Competitive Research Grant (CRG-7-3739), "The role of the bacterial symbiome at the gill-water (air) interface in the evolution toward territorialisation (Microlanding)," 1 April 2019 to 31 March 2022. We are very grateful to the LabEx DRIIHM, French Programme "Investissements d'Avenir" (ANR-11-LABX-

https://doi.org/10.5194/bg-2023-45
Preprint. Discussion started: 3 March 2023

0010), which is managed by the French ANR, under the Human- Environment Observatory "Mediterranean coast" (OHM Littoral Méditerranéen) for its funding that allowed to collect data from the Prevost lagoon, the Excellence Initiative of Aix-Marseille University - A*MIDEX, a French "Investissements d'Avenir" programme (reference number ANR-11-IDEX-0001- 02), the PACA region and the CNRS-INSU-EC2CO program (PREDHYP- O2 program) for its funding that allowed to collect data from the Berre lagoon, and the Occitanie region and the University of Nîmes for the funding of PhD Thesis of Julie Régis. We also thank all the members who allowed us to collect data from the coastal Mediterranean lagoons in France (syndicat mixte GIPREB, Mairie de Chateauneuf-les-Martigues, Compagnons de Maguelone). The PREDHYPO program has received funding from Excellence Initiative of Aix-Marseille University - A*MIDEX, a French "Investisse- ments d'Avenir" programme (reference number ANR-11-IDEX-0001- 02), the PACA region and the CNRS-INSU-EC2CO program (PREDHYP- O2 program).

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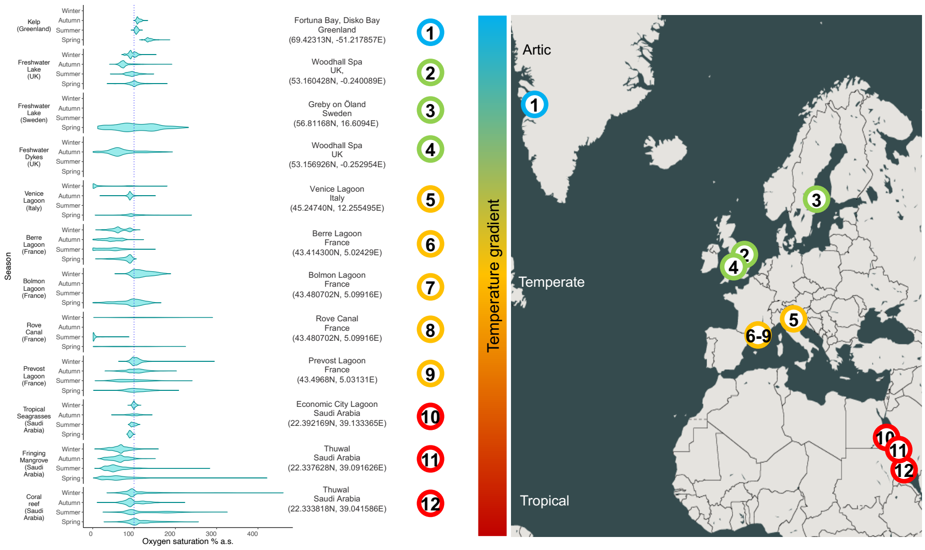
Preprint. Discussion started: 3 March 2023

Figure captions

Figure 1. Range of oxygen saturations in several productive aquatic habitats. The dashed line represents 100% oxygen saturation. The violin plots report the densities of the frequencies of oxygen saturation measured at each ecosystem across different season (based on data availability). Data source is specified for each environment in the Supplementary Dataset for Figure 1 and 2.



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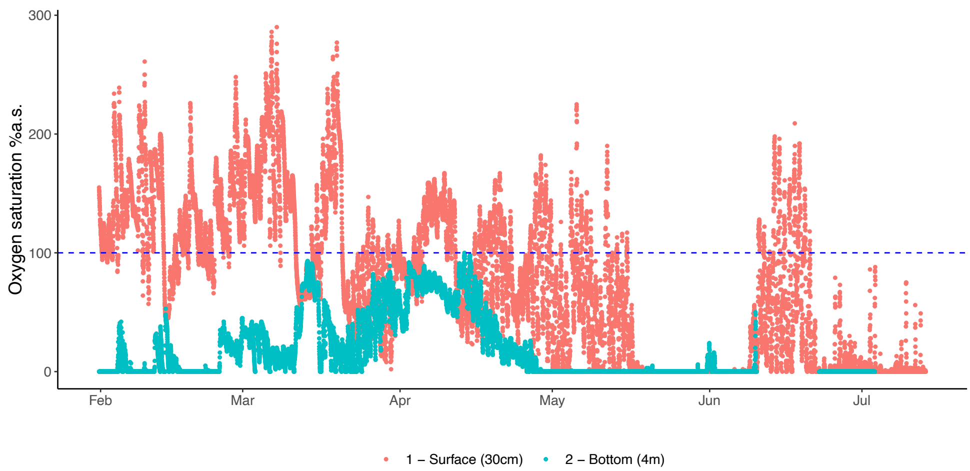
Preprint. Discussion started: 3 March 2023

Figure 2. Fluctuation of oxygen saturation measured at the bottom (4 m) and surface (30 cm) oxygen saturation of the Rove canal in France that highlight the contrast between the two depths of eutrophicated coastal environment from the winter to summer. The analysis of these case studies revealed different power to predict oxygen variation.



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Preprint. Discussion started: 3 March 2023

Figure 3. Concentration of nitrate and phosphate and their interdependence correlation with oxygen concentration in the water column at three latitudes, polar, tropical and temperate. At the three latitudes three different regimes of dissolved oxygen/nutrient concentration occur. Data analysis was performed from the CCHDO dataset. Each point on the map represents a single bottle closure from the same cruise that sampled water quality at increasing depths. We consider data from the warmer seasons: polar data were sampled in May 2009 (polar), tropical data in January 2002 (tropical) and temperate data in September 2014 (temperate). Polar water has higher concentrations of oxygen and less pronounced fluctuations. The denser water sinks to the ocean floor and enters the thermohaline circulation. The deep waters of the temperate zone show the passage of this circulation with oxygen concentrations in the bathypelagic water (depth > 1000 m) higher than in mesopelagic water. In the euphotic zone of the coastal area (temperate and tropical water on the map) there is a greater variability and reduction of oxygen with the increase of nutrients assimilated by autotrophs and consequently by the heterotrophs. The temperate zone of the Pacific Ocean shows a strong correlation between dissolved oxygen and nutrients that increases the productivity of these areas which may lead to eutrophication. The maps has been generated using © Google Earth (2023) accessed the 22nd February 2023).

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Preprint. Discussion started: 3 March 2023

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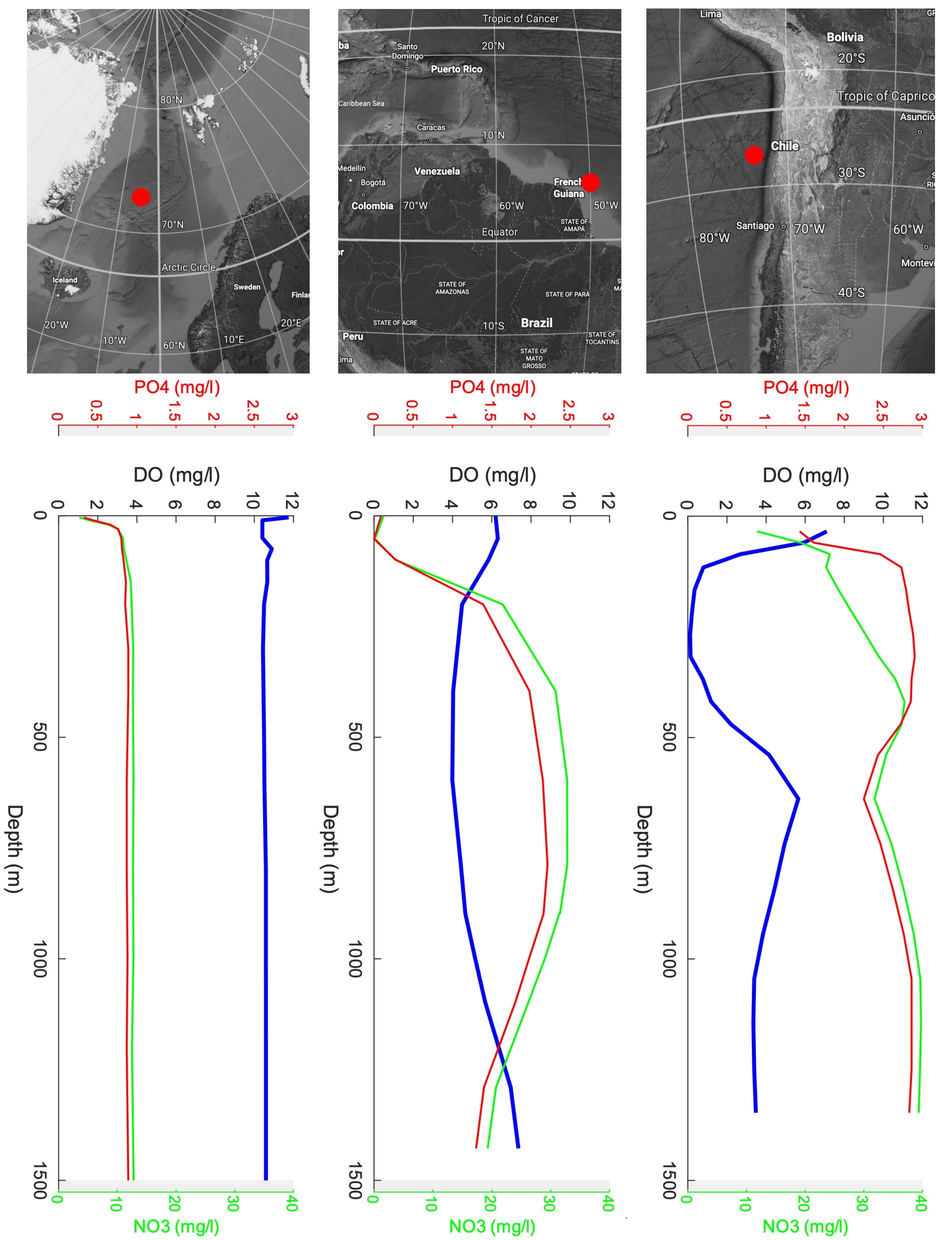

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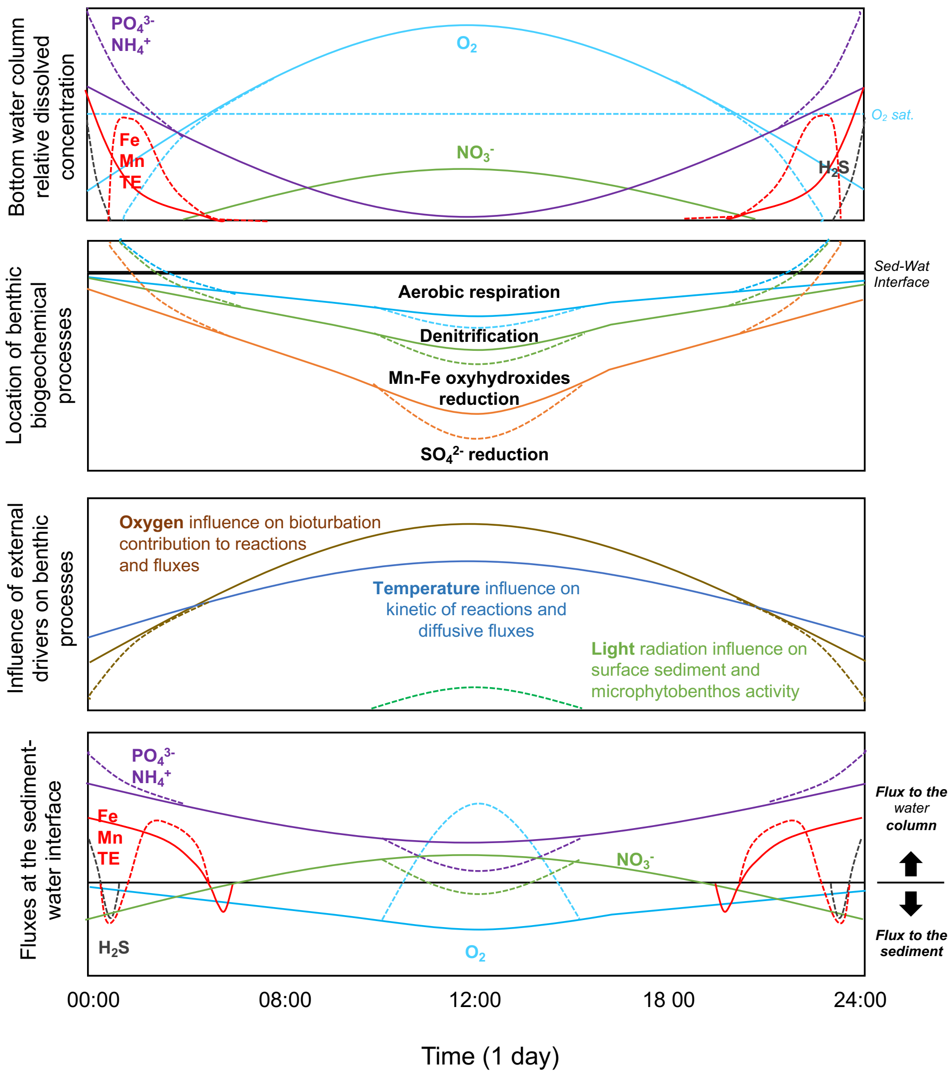
Preprint. Discussion started: 3 March 2023

Figure 4. Scheme of the benthic biogeochemical cycle in relation to diel oxygen fluctuation. (A) The relative evolution of the bottom water chemical composition, (B) evolution of the location of the most important biogeochemical processes in the benthic compartment. (C) Relative influence of external drivers on benthic processes. (D) Relative evolution of resulting flux direction and intensity. Note that the graphs are not drawn to scale. Although concentrations of PO_4^{3-} and NH_4^{+} and of Mn and Fe may behave differently, they are represented as similar in this figure for simplification.



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Preprint. Discussion started: 3 March 2023

Figure 5. Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of microbial community controlled by the oxygen availability that control the ratio between aerobic and anaerobic taxa and their relative function. Oxygen fluctuation is important to determine the diel cycling of the bacterial communities that in turn affect the biogeochemistry and the overall functioning of the aquatic ecosystems. Note that the graphs are not drawn to scale.