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

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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 scale, 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

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., 2023a). The perception of such knowledge gap is progressively moving the research interest on species' eco-physiological response to chemical and 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; Bitter et al., 2018, 2021; Pörtner 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 (i.e., daily) 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 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 (Breitburg and Grégoire, 2018; Laffoley and Baxter, 2019). 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). The seasonal variation of diel oxygen fluctuations is 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, Locations 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, 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).

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

Marked oxygen variations 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 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.

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., 2023a). 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, 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).

4. The role of oxygen fluctuation in coastal biogeochemical cycles

4.1 Biogeochemical cycles in the pelagic compartment in relation to oxygen fluctuation at daily scale

In productive coastal ecosystems the biogeochemical cycles of key chemical elements are strongly interconnected with oxygen dynamics. Nitrogen and phosphorus are typically key elements which limit primary production in shallow coastal-marine ecosystems, whose emissions from river basins (or other sources, such as previously enriched sediments) can lead to eutrophication with detrimental effects on biodiversity and human welfare (Palmeri et al., 2013). The biogeochemical cycles of nitrogen and phosphorus are composed of multiple physical, chemical and biological processes, of which some are accelerated by oxygen availability, such as nitrification and mineralization, while some others are enhanced by its absence, such as denitrification and P release from sediments. The regular daily alternation of contrasting conditions of below- and above-saturation dissolved oxygen concentrations in the water column, particularly in the euphotic zone, promotes changes in the relative abundance of different nutrient forms (Figure 3). This becomes clear when looking, for example, at the nitrogen cycle in the water column and its complex relationship with oxygen availability: the presence of dissolved oxygen speeds up the mineralization of organic nitrogen to ammonium as well as nitrification, i.e., the microbial oxidation of ammonium into nitrites and then nitrates. The absence of oxygen makes denitrification possible, i.e., the reduction of nitrates into inert gaseous nitrogen is promoted by facultative aerobic bacteria which, in the absence of anoxia, will prefer oxygen to nitrates as an electron acceptor (Palmeri et al., 2013). Ammonium, nitrites and nitrates are important nitrogen forms which are bioavailable to primary producers, and oscillating oxygen conditions in the water column at the diel scales can promote their removal via the nitrification-denitrification chain. High oxygen concentrations are also associated with high photosynthetic activity (e.g., planktonic) and, therefore, with the fast removal of dissolved inorganic nutrients from water through uptake by primary producers (Caron, 1994). The picture is made more complex by the typically non-linear dependence of biogeochemical reactions on oxygen concentration (e.g., nitrification and denitrification) and on temperature (in the case of most biogeochemical processes), which can both change strongly throughout the day, especially in shallow productive ecosystems, altering reaction rates at sub-daily scales in a way which cannot be appreciated if only the daily mean in dissolved oxygen is considered, but which needs to be quantified if we are to mechanistically predict future biogeochemical cycling under climate change (Caballero-Alfonso et al., 2015). A further source of complexity is given by the feedbacks between abiotic and biotic components of pelagic ecosystems. The growth of primary producers, both microscopic and macroscopic, is on the one hand affected by the presence of bioavailable nutrient forms, and on the other hand their biomass can reduce light availability by increasing shading or turbidity, limiting light penetration and, so, oxygen production and warming in deeper waters. These examples highlight the importance of higher frequency measurements of oxygen fluctuations, nutrient concentrations, and microbial community abundance, composition and activity in the water column at sub-daily scales, to get a better, more quantitative grasp of biogeochemical cycling in coastal water bodies (Meire et al., 2013). A general framework to assess the short-term (hourly) oxygen fluctuations in relation to the movement and related physical properties of water masses, i.e., of processes such as stratification, residence time, thermohaline flows, in addition to other processes (photosynthesis, respiration, solubility changes, etc.) is important to future oxygen modelling.

Of course, the intertwined oxygen and nutrient dynamics in the water column cannot be understood, at least in relatively shallow aquatic ecosystems, without looking also at the interactions between the pelagic and the benthic compartment. This takes place through vertical transport of matter (settling, resuspension, convection, upwelling currents, etc.) and is also affected by stratification, gradient-driven diffusive fluxes, and organism movements and vertical migrations.

4.2 Biogeochemical cycles in the benthic compartment in relation to oxygen fluctuation at daily 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 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 5).

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 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.

5. 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; Booth et al., 2023b, 2019). 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 (Figure 5). 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, 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). 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).

6. 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. There are only few areas whose oxygen dynamics has been extensively monitored like in North America (i.e., Cheaspeake bay, Gulf of Mexico, Long Island Sound) and included in management plans for environmental protections (e.g., https://coastalscience.noaa.gov/project/operational-gulf-of-mexico-hypoxia-monitoring/). However, globally, 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), and in particular the oxygen dynamic at a daily scale remains largely neglected is marine assessment and management. 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 daily oxygen variability. While attention has been given to ocean warming and acidification, daily oxygen dynamics have been overlooked in assessing marine habitat or species' sensitivity to climate changes and anthropogenic disturbances. Including ecologically 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).

Current hypoxic thresholds for aquatic ecosystem management are generally calculated on averages and minima oxygen concentrations in water and they risk overlooking the effect of the oxygen fluctuation which are more relevant for communities' physiology (Tomasetti and Gobler, 2020). Enhancing monitoring programs by capturing the daily oxygen fluctuation will allow detection of when night-time low oxygen content is followed by a daytime recovery period, often reaching oxygen supersaturation. This alternation allows the aquatic communities to sustain their homeostasis in a fluctuating environment. Therefore, proper monitoring can inform a correct management to conserve, protect, and restore coastal water mosaic patterns of primary producers to ensure the ecological relevant fluctuations of dissolved oxygen.

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 3. AB, GG, SR, FG wrote section 4.1 and 4.2 and provided data for the Mediterranean sites. MF, RM and DD wrote section 5 and provided data for the Red Sea. MF, LP and CVH wrote section 6. All the authors discussed and reviewed the final version.

Competing interests

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

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References

Aldunate, M., De la Iglesia, R., Bertagnolli, A. D., and Ulloa, O.: Oxygen modulates bacterial community composition in the coastal upwelling waters off central Chile, Deep. Res. Part II Top. Stud. Oceanogr., 156, 68–79, https://doi.org/10.1016/j.dsr2.2018.02.001, 2018.

Andersen, M. R., Kragh, T., and Sand-Jensen, K.: Extreme diel dissolved oxygen and carbon cycles in shallow vegetated lakes., Proceedings. Biol. Sci., 284, 20171427, https://doi.org/10.1098/rspb.2017.1427, 2017.

Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., Dornelas, M., and Schipper, A. M.: Temperature-related biodiversity change across temperate marine and terrestrial systems, Nat. Ecol. Evol., 4, 927–933, https://doi.org/10.1038/s41559-020-1185-7, 2020.

Bartoli, M., Castaldelli, G., Nizzoli, D., Gatti, L. G., and Viaroli, P.: Benthic Fluxes of Oxygen, Ammonium and Nitrate and Coupled-uncoupled Denitrification Rates within Communities of Three Different Primary Producer Growth Forms, Mediterr. Ecosyst., 225–233, https://doi.org/10.1007/978-88-470-2105-1_29, 2001.

Bates, A. E., Helmuth, B., Burrows, M. T., Duncan, M. I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros, A. M., Seabra, R., Marsh, R., Belmaker, J., Bensoussan, N., Dong, Y., Mazaris, A. D., Smale, D., Wahl, M., and Rilov, G.: Biologists ignore ocean weather at their peril, Nature, 560, 299–301, 2018.

Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar, A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., and Olalla-Tárraga, M. Á.: The evolution of critical thermal limits of life on Earth, Nat. Commun., 12, 1–9, https://doi.org/10.1038/s41467-021-21263-8, 2021.

Benoiston, A. S., Ibarbalz, F. M., Bittner, L., Guidi, L., Jahn, O., Dutkiewicz, S., and Bowler, C.: The evolution of diatoms and their biogeochemical functions, Philos. Trans. R. Soc. B Biol. Sci., 372, https://doi.org/10.1098/rstb.2016.0397, 2017.

Berg, P., Huettel, M., Glud, R. N., Reimers, C. E., and Attard, K. M.: Aquatic Eddy Covariance: The Method and Its Contributions to Defining Oxygen and Carbon Fluxes in Marine Environments, Ann. Rev. Mar. Sci., 14, 431–455, https://doi.org/10.1146/annurev-marine-042121-012329, 2022.

Bernhardt, J. R., O'Connor, M. I., Sunday, J. M., and Gonzalez, A.: Life in fluctuating environments, Philos. Trans. R. Soc. Lond. B. Biol. Sci., 375, 20190454, https://doi.org/10.1098/rstb.2019.0454, 2020.

Bickler, P. E. and Buck, L. T.: Hypoxia tolerance in reptiles, amphibians, and fishes: Life with variable oxygen availability, Annu. Rev. Physiol., 69, 145–170, https://doi.org/10.1146/annurev.physiol.69.031905.162529, 2007.

Bitter, M. C., Wong, J. M., Dam, H. G., Donelan, S. C., Kenkel, C. D., Komoroske, L. M., Nickols, K. J., Rivest, E. B., Salinas, S., Burgess, S. C., Morash, A. J., Neufeld, C., MacCormack, T. J., and Currie, S.: The importance of incorporating natural thermal variation when evaluating physiological performance in wild species, J. Exp. Biol., 221, https://doi.org/10.1242/JEB.164673, 2018.

Bitter, M. C., Wong, J. M., Dam, H. G., Donelan, S. C., Kenkel, C. D., Komoroske, L. M., Nickols, K. J., Rivest, E. B., Salinas, S., Burgess, S. C., and Lotterhos, K. E.: Fluctuating selection and global change: A synthesis and review on disentangling the roles of climate amplitude, predictability and novelty, Proc. R. Soc. B Biol. Sci., 288, https://doi.org/10.1098/rspb.2021.0727, 2021.

Blewett, T. A., Binning, S. A., Weinrauch, A. M., Ivy, C. M., Rossi, G. S., Borowiec, B. G., Lau, G. Y., Overduin, S. L., Aragao, I., and Norin, T.: Physiological and behavioural strategies of aquatic animals living in fluctuating environments, J. Exp. Biol., 225, jeb242503, https://doi.org/10.1242/jeb.242503, 2022.

Booth, J., Fusi, M., Giomi, F., Chapman, E., Diele, K., and McQuaid, C.: Diel oxygen fluctuation drives the thermal response and metabolic performance of coastal marine ectotherms, Proc. R. Soc. B Biol. Sci., 288, 20211141, 2021.

Booth, J. M., Fusi, M., Marasco, R., Mbobo, T., and Daffonchio, D.: Fiddler crab bioturbation determines consistent changes in bacterial communities across contrasting environmental conditions, Sci. Rep., 9, https://doi.org/10.1038/s41598-019-40315-0, 2019.

Booth, J. M., Giomi, F., Daffonchio, D., Mcquaid, C. D., and Fusi, M.: Disturbance of primary producer communities disrupts the thermal limits of the associated aquatic fauna, Sci. Total Environ., 872, 162135, https://doi.org/10.1016/j.scitotenv.2023.162135, 2023a.

Booth, J. M., Fusi, M., Marasco, R., and Daffonchio, D.: The microbial landscape in bioturbated mangrove sediment: A resource for promoting nature-based solutions for mangroves, Microb. Biotechnol., in press, https://doi.org/10.1111/1751-7915.14273, 2023b.

Breen, P. A. and Mann, K. H.: Changing lobster abundance and the destruction of kelp beds by sea urchins, Mar. Biol., 34, 137–142, https://doi.org/10.1007/BF00390755, 1976.

Breitburg, D. and Grégoire, M.: The ocean is losing its breath, Unesco, 11, 1–43, 2018.

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., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., Telszewski, M., Yasuhara, M., and Zhang, J.: Declining oxygen in the global ocean and coastal waters, Science (80-.)., 359, eaam7240, https://doi.org/10.1126/science.aam7240, 2018.

Breitburg, D. L., Conley, D., Isensee, K., Levin, L. A., Limburg, K. E., and Williamson, P.: What can we do? Adaptation and solutions to declining ocean oxygen, Ocean deoxygenation everyone's Probl. Causes, impacts, consequences Solut., 545–562, 2019.

Caballero-Alfonso, A. M., Carstensen, J., and Conley, D. J.: Biogeochemical and environmental drivers of coastal hypoxia, J. Mar. Syst., 141, 190–199, https://doi.org/10.1016/j.jmarsys.2014.04.008, 2015.

Caron, D. A.: Inorganic nutrients, bacteria, and the microbial loop, Microb. Ecol. Ecol., 28, 295–298, https://doi.org/10.1007/BF00166820, 1994.

Challener, R. C., Robbins, L. L., and Mcclintock, J. B.: Variability of the carbonate chemistry in a shallow, seagrass-dominated ecosystem: Implications for ocean acidification experiments, Mar. Freshw. Res., 67, 163–172, https://doi.org/10.1071/MF14219, 2016.

Chapman, D.: Water Quality Assessments - A Guide to Use of Biota, Sediments and Water in Environmental Monitoring - Second Edition, E&FN Spon, London, 2021.

Chen, H., Costanza, R., and Kubiszewski, I.: Legitimacy and limitations of valuing the oxygen production of ecosystems, Ecosyst. Serv., 58, 101485, https://doi.org/10.1016/j.ecoser.2022.101485, 2022.

Cowan, J. L. W., Pennock, J. R., and Boynton, W. R.: Seasonal and interannual patterns of sediment-water nutrient and oxygen fluxes in Mobile Bay, Alabama (USA): Regulating factors and ecological significance, Mar. Ecol. Prog. Ser., 141, 229–245, https://doi.org/10.3354/meps141229, 1996.

Craig, H. and Hayward, T.: Oxygen Supersaturation in the Ocean: Biological Versus Physical Contributons, 735, 1983–1986, 1983.

Dafforn, K. a., Simpson, S. L., Kelaher, B. P., Clark, G. F., Komyakova, V., Wong, C. K. C., and

Johnston, E. L.: The challenge of choosing environmental indicators of anthropogenic impacts in estuaries, Environ. Pollut., 163, 207–217, https://doi.org/10.1016/j.envpol.2011.12.029, 2012.

Denis, L., Gevaert, F., and Spilmont, N.: Microphytobenthic production estimated by in situ oxygen microprofiling: Short-term dynamics and carbon budget implications, J. Soils Sediments, 12, 1517–1529, https://doi.org/10.1007/s11368-012-0588-8, 2012.

Diaz, R. J. and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science (80-.)., 321, 926–929, https://doi.org/10.1126/science.1156401, 2008.

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., and Marbà, N.: The role of coastal plant communities for climate change mitigation and adaptation, Nat. Clim. Chang., 3, 961–968, https://doi.org/10.1038/nclimate1970, 2013.

Fenchel, T. and Finlay, B.: Oxygen and the spatial structure of microbial communities, Biol. Rev., 83, 553–569, https://doi.org/10.1111/j.1469-185X.2008.00054.x, 2008.

Fusi, M., Daffonchio, D., Booth, J., and Giomi, F.: Dissolved Oxygen in Heterogeneous Environments Dictates the Metabolic Rate and Thermal Sensitivity of a Tropical Aquatic Crab, Front. Mar. Sci., 8, 1–9, https://doi.org/10.3389/fmars.2021.767471, 2021.

Fusi, M., Marasco, R., Ramond, J., Barausse, A., and Baldanzi, S.: Editorial : Fluctuating Habitats : Ecological Relevance of Environmental Variability and Predictability on Species , Communities , and Ecosystems, Front. Ecol. Evol., 10, 1–4, https://doi.org/10.3389/fevo.2022.907622, 2022.

Garzke, J., Connor, S. J., Sommer, U., and O'connor, M. I.: Trophic interactions modify the temperature dependence of community biomass and ecosystem function, PLoS Biol., 17, 1–27, https://doi.org/10.1371/journal.pbio.2006806, 2019.

Giomi, F., Barausse, A., Duarte, C. M., Booth, J., Agusti, S., Saderne, V., Anton, A., Daffonchio, D., and Fusi, M.: Oxygen supersaturation protects coastal marine fauna from ocean warming, Sci. Adv., 5, 1–8, https://doi.org/10.1126/sciadv.aax1814, 2019.

Glud, R. N.: Oxygen dynamics of marine sediments, Mar. Biol. Res., 4, 243–289, https://doi.org/10.1080/17451000801888726, 2008.

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., and MacNeil, M. A.: Seabirds enhance coral reef productivity and functioning in the absence of invasive rats, Nature, 559, 250–253, https://doi.org/10.1038/s41586-018-0202-3, 2018.

Guo, X., Song, G., Li, Y., Zhao, L., and Wang, J.: Switch of Bacteria Community Under Oxygen Depletion in Sediment of Bohai Sea, Front. Mar. Sci., 9, 1–13, https://doi.org/10.3389/fmars.2022.833513, 2022.

Hochachka, P. W.: Temperature: the ectothermy option, in: Phylogenetic and biochemical perspectives: Biochemistry and molecular biology of fishes, 1, vol. 1, 313–322, https://doi.org/10.1016/B978-0-444-89124-2.50016-6, 1991.

Ito, T., Nenes, A., Johnson, M. S., Meskhidze, N., and Deutsch, C.: Acceleration of oxygen decline in the tropical Pacific over the past decades by aerosol pollutants, Nat. Geosci., 9, 443–447, https://doi.org/10.1038/ngeo2717, 2016.

Keeling, R. F., Körtzinger, A., and Gruber, N.: Ocean deoxygenation in a warming world, Ann. Rev. Mar. Sci., 2, 199–229, https://doi.org/10.1146/annurev.marine.010908.163855, 2010.

Kerrison, P., Hall-Spencer, J. M., Suggett, D. J., Hepburn, L. J., and Steinke, M.: Assessment of pH variability at a coastal CO2 vent for ocean acidification studies, Estuar. Coast. Shelf Sci., 94, 129–137, https://doi.org/10.1016/j.ecss.2011.05.025, 2011.

Kim, H., Takayama, K., Hirose, N., Onitsuka, G., Yoshida, T., and Yanagi, T.: Biological modulation in the seasonal variation of dissolved oxygen concentration in the upper Japan Sea, J. Oceanogr., 75, 257–271, https://doi.org/10.1007/s10872-018-0497-6, 2019.

Kinney, E. H. and Roman, C. T.: Response of primary producers to nutrient enrichment in a shallow estuary, Mar. Ecol. Prog. Ser., 163, 89–98, https://doi.org/10.3354/meps163089, 1998.

Krause-Jensen, D., Marba, N., Sanz-Martin, M., Hendriks, I. E., Thyrring, J., Carstensen, J., Sejr, M. K., and Duarte, C. M.: Long photoperiods sustain high pH in Arctic kelp forests, Sci. Adv., 2, e1501938–e1501938, https://doi.org/10.1126/sciadv.1501938, 2016.

Laffoley, D. and Baxter, J. M.: Explaining Ocean Warming: Causes, scale, effects and consequences, 458 pp., https://doi.org/http://dx.doi.org/10.2305/IUCN.CH.2016.08.en, 2016.

Laffoley, D. D. A. and Baxter, J. M.: Ocean Deoxygenation: Everyone's Problem-Causes, Impacts, Consequences and Solutions, 2019.

Limburg, K. E., Breitburg, D., Swaney, D. P., and Jacinto, G.: Ocean Deoxygenation: A Primer, One

Earth, 2, 24–29, https://doi.org/10.1016/j.oneear.2020.01.001, 2020.

Mallin, M. A., Paerl, H. W., Rudek, J., and Bates, P. W.: Regulation of estuarine primary production by watershed rainfall and river flow, Mar. Ecol. Prog. Ser., 93, 199–203, https://doi.org/10.3354/meps093199, 1993.

Manzello, D. P.: Ocean acidification hot spots: Spatiotemporal dynamics of the seawater CO2 system of eastern Pacific coral reefs, Limnol. Oceanogr., 55, 239–248, https://doi.org/10.4319/lo.2010.55.1.0239, 2010.

Marasco, R., Fusi, M., Coscolín, C., Barozzi, A., Almendral, D., Bargiela, R., Gohlke, C., Christopher, P., Dittrich, J., Gohlke, H., Matesanz, R., Sanchez-carrillo, S., Mapelli, F., Chernikova, T. N., Golyshin, P. N., Ferrer, M., and Daffonchio, D.: Enzyme adaptation to habitat thermal legacy microbiomes, Nat. Commun., in press, https://doi.org/10.1038/s41467-023-36610-0, 2023.

McArley, T. J., Sandblom, E., and Herbert, N. A.: Fish and hyperoxia—From cardiorespiratory and biochemical adjustments to aquaculture and ecophysiology implications, Fish Fish., 1–32, https://doi.org/10.1111/faf.12522, 2020.

McArley, T. J., Morgenroth, D., Zena, L. A., Ekström, A. T., and Sandblom, E.: Experimental hyperoxia (O2 supersaturation) reveals a gill diffusion limitation of maximum aerobic performance in fish, Biol. Lett., 18, 20220401, https://doi.org/10.1098/rsbl.2022.0401, 2022.

Meire, L., Soetaert, K. E. R., and Meysman, F. J. R.: Impact of global change on coastal oxygen dynamics and risk of hypoxia, Biogeosciences, 10, 2633–2653, https://doi.org/10.5194/bg-10-2633-2013, 2013.

Morash, A. J., Neufeld, C., MacCormack, T. J., and Currie, S.: The importance of incorporating natural thermal variation when evaluating physiological performance in wild species, J. Exp. Biol., 221, https://doi.org/10.1242/JEB.164673, 2018.

Nilsson, H. C. and Rosenberg, R.: Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images, J. Mar. Syst., 11, 249–264, https://doi.org/10.1016/S0924-7963(96)00111-X, 1997.

Pacherres, C. O., Ahmerkamp, S., Koren, K., Richter, C., and Holtappels, M.: Ciliary flows in corals ventilate target areas of high photosynthetic oxygen production, Curr. Biol., 32, 4150-4158.e3, https://doi.org/10.1016/j.cub.2022.07.071, 2022.

Palmeri, L., Barausse, A., and Jorgensen, S. E.: Ecological processes handbook, edited by: Palmeri, L., Barausse, A., and Jorgensen, S. E., CRC Press, Boca Raton FL, 375 pp., 2013.

Pörtner, H.-O.: Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems., J. Exp. Biol., 213, 881–893, 2010.

Pörtner, H.-O., Scholes, R. J., Arneth, A., Barnes, D. K. A., Burrows, M. T., Diamond, S. E., Duarte, C. M., Kiessling, W., Leadley, P., Managi, S., McElwee, P., Midgley, G., Ngo, H. T., Obura, D., Pascual, U., Sankaran, M., Shin, Y. J., and Val, A. L.: Overcoming the coupled climate and biodiversity crises and their societal impacts, Science (80-.)., 380, eabl4881, https://doi.org/10.1126/science.abl4881, 2023.

Power, L. D. and Cardinale, B. J.: Species richness enhances both algal biomass and rates of oxygen production in aquatic microcosms, Oikos, 118, 1703–1711, https://doi.org/10.1111/j.1600-0706.2009.17585.x, 2009.

Rigaud, S., Deflandre, B., Maire, O., Bernard, G., Duchêne, J. C., Poirier, D., and Anschutz, P.: Transient biogeochemistry in intertidal sediments: New insights from tidal pools in Zostera noltei meadows of Arcachon Bay (France), Mar. Chem., 200, 1–13, https://doi.org/10.1016/j.marchem.2018.02.002, 2018.

Riser, S. C. and Johnson, K. S.: Net production of oxygen in the subtropical ocean, Nature, 451, 323–325, https://doi.org/10.1038/nature06441, 2008.

Sandrin, T. R., Dowd, S. E., Herman, D. C., and Maier, R. M.: Aquatic environments., in: Environment Microbiology, Elsevier, 103–122, 2009.

Schmidt, S., Diallo, I. I., Derriennic, H., Fallou, H., and Lepage, M.: Exploring the susceptibility of turbid estuaries to hypoxia as a prerequisite to designing a pertinent monitoring strategy of dissolved oxygen, Front. Mar. Sci., 6, 1–8, https://doi.org/10.3389/fmars.2019.00352, 2019.

Schmidtko, S., Stramma, L., and Visbeck, M.: Decline in global oceanic oxygen content during the past five decades, Nature, 542, 335–339, https://doi.org/10.1038/nature21399, 2017.

Shaw, E. C., Munday, P. L., and McNeil, B. I.: The role of CO2 variability and exposure time for biological impacts of ocean acidification, Geophys. Res. Lett., 40, 4685–4688, https://doi.org/10.1002/grl.50883, 2013.

Spietz, R. L., Williams, C. M., Rocap, G., and Horner-Devine, M. C.: A dissolved oxygen threshold for shifts in bacterial community structure in a seasonally hypoxic estuary, PLoS One, 10, 1–18, https://doi.org/10.1371/journal.pone.0135731, 2015.

Steiner, P. A., De Corte, D., Geijo, J., Mena, C., Yokokawa, T., Rattei, T., Herndl, G. J., and Sintes, E.: Highly variable mRNA half-life time within marine bacterial taxa and functional genes, Environ. Microbiol., 21, 3873–3884, https://doi.org/10.1111/1462-2920.14737, 2019.

Stillman, J. H. and Somero, G. N.: A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus Petrolisthes: influences of latitude, vertical zonation, acclimation, and phylogeny., Physiol. Biochem. Zool., 73, 200–208, https://doi.org/10.1086/316738, 2000.

Stramma, L., Schmidtko, S., Levin, L. A., and Johnson, G. C.: Ocean oxygen minima expansions and their biological impacts, Deep. Res. Part I Oceanogr. Res. Pap., 57, 587–595, https://doi.org/10.1016/j.dsr.2010.01.005, 2010.

Talke, S. A., De Swart, H. E., and De Jonge, V. N.: An idealized model and systematic process study of oxygen depletion in highly turbid estuaries, Estuaries and Coasts, 32, 602–620, https://doi.org/10.1007/s12237-009-9171-y, 2009.

Tomasetti, S. J. and Gobler, C. J.: Dissolved oxygen and pH criteria leave fisheries at risk, Science (80-.)., 368, 372–373, https://doi.org/10.1126/science.aba4896, 2020.

Trowbridge, C. D., Davenport, J., Cottrell, D. M., Harman, L., Plowman, C. Q., Little, C., and McAllen, R.: Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough, Reg. Stud. Mar. Sci., 11, 9–16, https://doi.org/10.1016/j.rsma.2017.01.008, 2017.

Vargas, C. A., Lagos, N. A., Lardies, M. A., Duarte, C., Manríquez, P. H., Aguilera, V. M., Broitman, B., Widdicombe, S., and Dupont, S.: Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity, Nat. Ecol. Evol., 1, 1–7, https://doi.org/10.1038/s41559-017-0084, 2017.

Vargas, C. A., Cuevas, L. A., Broitman, B. R., San Martin, V. A., Lagos, N. A., Gaitán-Espitia, J. D., and Dupont, S.: Upper environmental pCO2 drives sensitivity to ocean acidification in marine invertebrates, Nat. Clim. Chang., 12, 200–207, https://doi.org/10.1038/s41558-021-01269-2, 2022.

Viaroli, P. and Christian, R. R.: Description of trophic status, hyperautotrophy and dystrophy of a coastal lagoon through a potential oxygen production and consumption index - TOSI: Trophic Oxygen Status Index, Ecol. Indic., 3, 237–250, https://doi.org/10.1016/j.ecolind.2003.11.001, 2004.

Virtanen, E. A., Norkko, A., Nyström Sandman, A., and Viitasalo, M.: Identifying areas prone to coastal hypoxia - The role of topography, Biogeosciences, 16, 3183–3195, https://doi.org/10.5194/bg-16-3183-2019, 2019.

Winter, G., Hetzel, Y., Huang, P., Hipsey, M. R., Mulligan, R. P., and Hansen, J.: Coastal processes, extreme events and forecasting, in: Marine Extreme, Routledge, 17, 2019.

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.

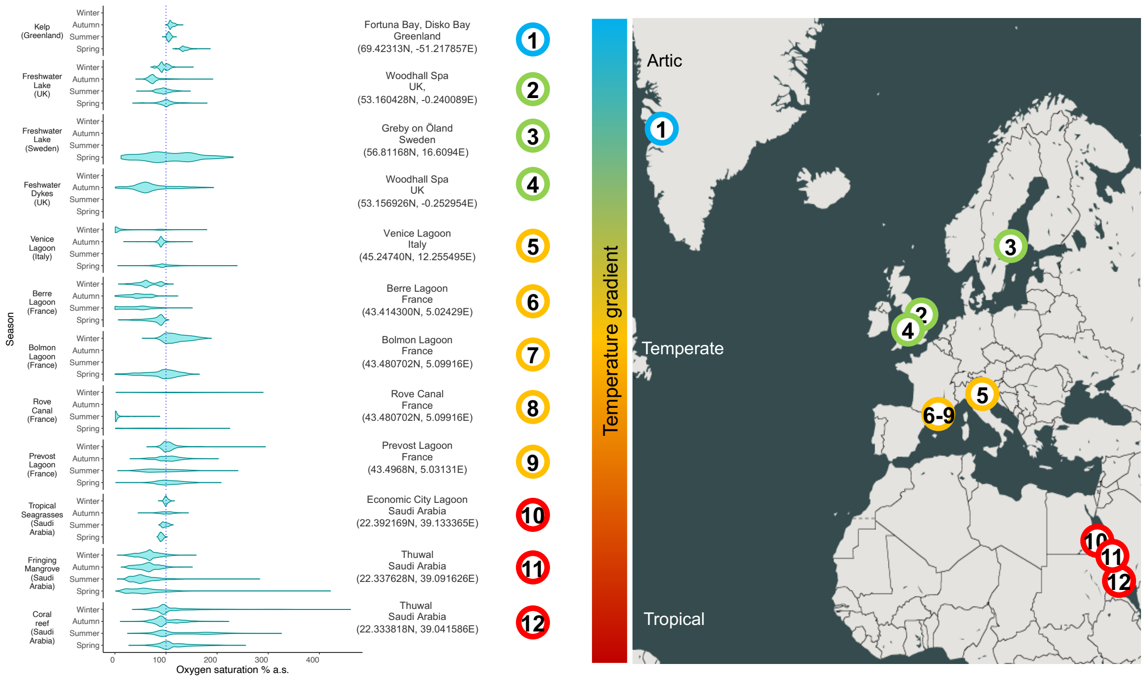

Figure 2. Fluctuation of oxygen saturation measured at the bottom (4 m) and surface (30 cm) oxygen saturation of the Rove canal in France that highlight the contrast between the two depths of eutrophicated coastal environment from the winter to summer. The analysis of these case studies revealed different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

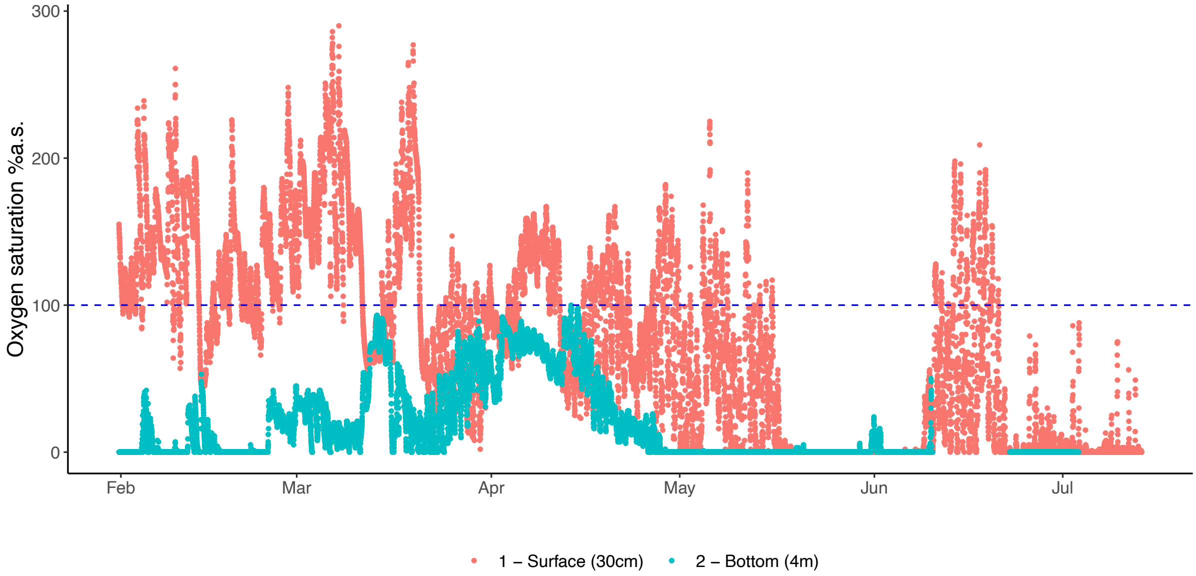

Figure 3. Nutrient concentration, dissolved oxygen and water temperature measurements made in the water of a salt marsh of the Northern Venice Lagoon (Italy) on August 13th, 2015. A) Concentration of different nitrogen forms in the marsh water (notice the two different vertical axes) over time in the central part of the day. Measurements are made in the water entering the marsh (flood phase, left of the vertical gray line which indicates the tidal peak) and quitting from the salt marsh (ebb phase, right of the vertical gray line). After some time spent in the marsh, which is flooded by tide twice per day, water becomes depleted in inorganic nutrients, presumably due to the uptake by primary producers, exchanges with the sediments, and (in the case of ammonium) nitrification. Concurrently, water is enriched with dissolved organic nitrogen related to the intense biological activity within the marsh. B) Dissolved oxygen and temperature of the water entering the marsh (flood phase, left of the vertical gray line which indicates the tidal peak) and quitting from the salt marsh (ebb phase, right of the vertical gray line) over time in the central part of the day. While in the marsh, which is a biologically productive habitat compared to the surrounding waters, the water becomes enriched with dissolved oxygen paralleled by an increase in water temperature.

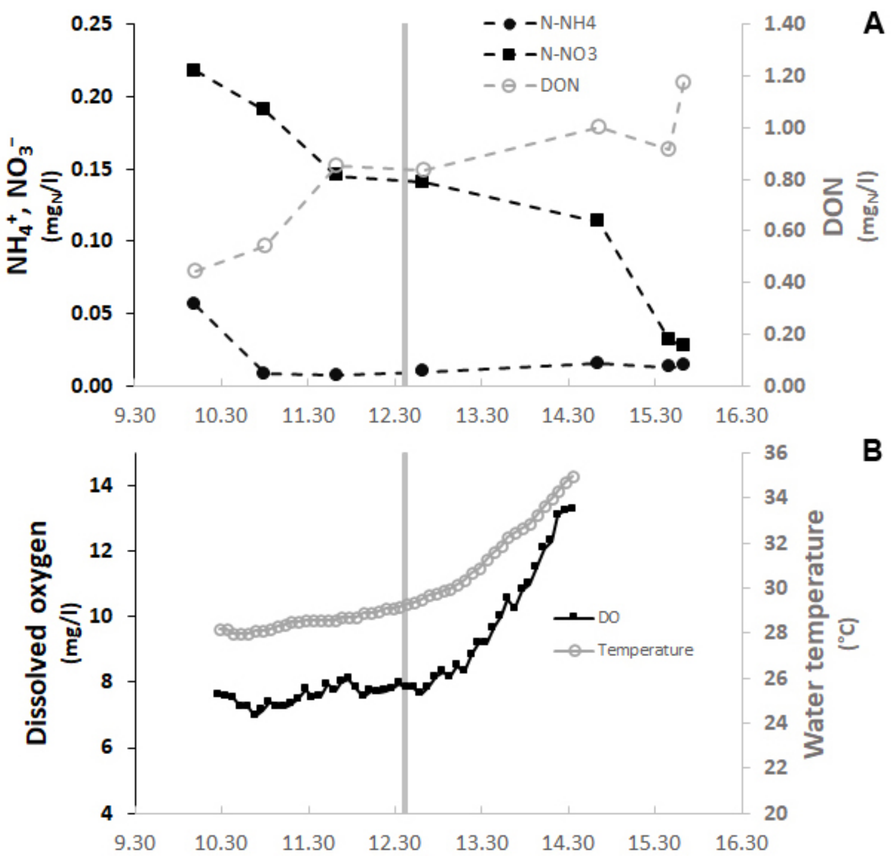

Figure 4. Scheme of the benthic biogeochemical cycle in relation to diel oxygen fluctuation. (A) The relative evolution of the bottom water chemical composition, (B) evolution of the location of the most important biogeochemical processes in the benthic compartment. (C) Relative influence of external 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.

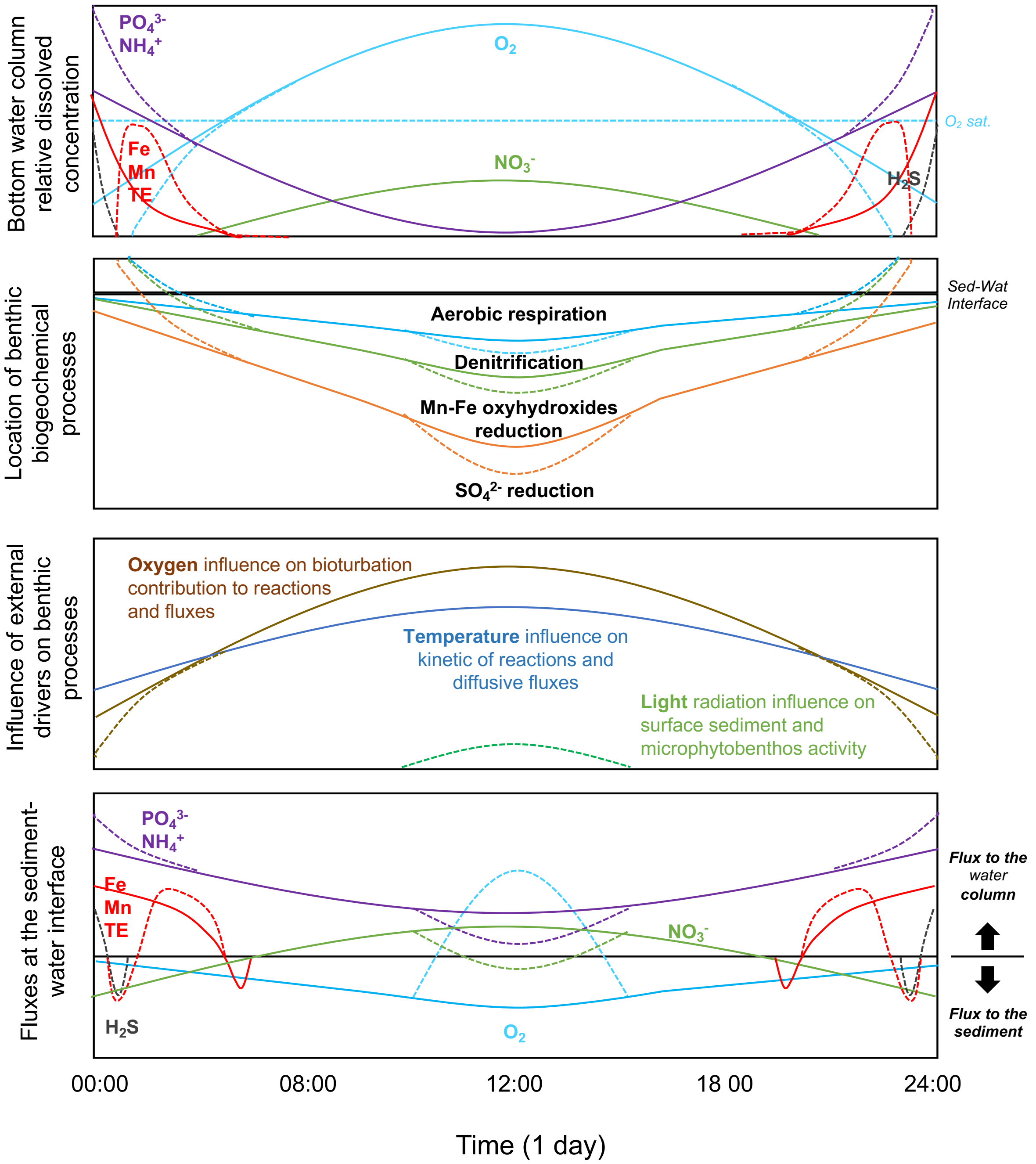

Figure 5. Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of microbial community controlled by the oxygen availability that control the ratio between aerobic and anaerobic taxa and their relative function. Oxygen fluctuation is important to determine the 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.