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3   **Title:**

4   Ideas and perspectives. The fluctuating nature of oxygen shapes the ecology of aquatic habitats and their

5   biogeochemical cycles: the aquatic oxyscape

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24   **Abstract**

25   Oxygen availability is a pivotal factor for ecosystem functioning and the resistance of organisms to the

26   effect of climate change in aquatic habitats. Although extensive work has been made to assess the effect of

27   oxygen on marine and freshwater biota, many studies did not capture the ecological importance of oxygen

28   variations. Overlooking the fluctuating nature of oxygen may cause potential biases in the design and

29   implementation of management policies for aquatic habitats. Conceptual perspectives on the dynamic

30   nature of oxygen fluctuations have been raised in the scientific community to enhance the understanding

31   of the effect of oxygen on the physiology and the ecology of aquatic species and the biogeochemical

32   functioning of the ecosystems. A growing number of empirical works are outlining a novel conceptual

33   framework that considers the magnitude of oxygen fluctuation as a key variable that explains adaptation to

34   stress conditions. Oxygen in productive aquatic habitats shows large fluctuations at diel scale, exposing

35   aquatic species from conditions of extreme supersaturation to anoxia. Recent research indicates that such

36   fluctuation tunes the physiological plasticity of the animal in response to thermal stresses. In this

37   contribution, we provide compelling evidence based on current research that the fluctuating oxygen

38   landscape, here defined as "*oxyscape*", has an important role in aquatic animal physiology and adaptation

39   and the ecosystem biogeochemistry. We propose that the oxyscape should be considered in the modelling

40   and managing policies of aquatic ecosystems.

41

42   **Keyword**

43   Biogeochemical cycles; Climate Change; Hyperoxia; Hypoxia; Marine Ecosystem Assessment; Microbial

44   processes; Oxygen Fluctuations; Supersaturation

45

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 upgrading 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 great 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

74 biogeochemical cycles has the potential to elucidate unpredicted mechanisms of resilience and tolerance to

75 ongoing climate change.

76

77 **2. Oxygen trends and stochastic variations**

78 A gradual decline of the total oxygen content of about 2% since the second half of the 20th century has

79 been recently reported, with a further reduction of up to 7% predicted for the following century (Schmidtko

80 et al., 2017; Breitburg et al., 2018). In parallel, open-ocean oxygen minimum zones (OMZs) have largely

81 expanded (Stramma et al., 2010) together with the increasing occurrence of severe hypoxia events whose

82 predictability has decreased as their occurrence spreads across all oceans (Diaz and Rosenberg, 2008). The

83 main cause of deoxygenation is attributed to global warming and is exacerbated by the discharge of nutrients

84 and pollutants (Ito et al., 2016). The topography of water basins also affects the incidence of hypoxia events

85 influencing the rate of mixing of oxygenated layers and the resident time of water bodies (Breitburg and

86 Grégoire, 2018; Laffoley and Baxter, 2019). For example, in the Baltic Sea, the geomorphology of the

87 coastline can explain up to 80% of the hypoxic phenomena (Virtanen et al., 2019).

88 The gradual decrease of total oxygen in oceans has been reported in several studies that analyse long time

89 trends (Keeling et al., 2010; Schmidtko et al., 2017; Breitburg et al., 2018) and from reports at the global

90 geographical scale (Laffoley and Baxter, 2016). However, unexpected oxygen profiles have also been

91 reported in several specific habitats and at different time scales suggesting that different abiotic and biotic

92 drivers modulate oxygen dynamics (Craig and Hayward, 1983). For instance, the alternation of oxygen

93 biological production and consumption determines massive fluctuation of its availability in highly

94 productive aquatic habitats, such as mangrove forests, salt marshes, coral reefs (Giomi et al., 2019; Fusi et

95 al., 2021; Booth et al., 2021), kelp forests (Krause-Jensen et al., 2016), plankton blooms in the open oceans

96 (Riser and Johnson, 2008; Benoiston et al., 2017), freshwater lakes (Andersen et al., 2017) or even in

97 agricultural drainage channels (Booth et al., 2023). The seasonal variation of diel oxygen fluctuations is

98 increasingly reported at all latitudes and habitats and occurs in a vast range of water bodies independently

99 of the scale, the hydrological features, and the local biotic components (Figure 1). For example, fluctuations

100 of 150% in spring and 30% in winter occur in the Venice lagoon (Figure 1, Location 5), and even more

101 pronounced fluctuations occur in mangroves, corals and seagrasses (Figure 1, Locations 10-12; Giomi et

102   al., 2019). The magnitude of oxygen fluctuations is site-specific and depends, among other factors, on the

103   solar radiation and water temperature and their effect on primary producers' photosynthetic and respiration

104   activity, the cycles of water column stratification and mixing, and the nutrient loads. Spatial differences in

105   oxygen saturation also occur between surface and bottom water masses because of isolation driven by water

106   stratification, the decrease of light penetration, and the coupling with increased oxygen demand close to

107   the sediments at the bottom of the water column (Figure 2). In summer, enhanced benthic respiration is

108   determined by higher water temperature, which decreases oxygen solubility and enhances oxygen demand.

109   Lower vertical mixing, higher water residence time, and higher turbidity due to higher concentration of

110   organic matter further decrease oxygen concentrations down to hypoxia in the deep water layers (Figure 2;

111   Talke et al., 2009; Schmidt et al., 2019). Conversely, dissolved oxygen increases in the euphotic part of the

112   water column because of the enrichment of photosynthetic communities (Spietz et al., 2015).

113

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

115   Marked oxygen variations occur at a diel scale, driven by temperature and light diel cycles and the balance

116   between photosynthesis and respiration (Winter et al., 2019). The amplitude of diel oxygen variation can

117   exceed the average seasonal variation, thus being variable with higher explanatory power for the physiology

118   of aquatic life (Giomi et al., 2019). While water temperature is only linked to meteorological changes, the

119   oxygen concentration in productive aquatic environments is also regulated by the biota component

120   (Chapman, 2021). Community composition of primary producers (Power and Cardinale, 2009), rainfall

121   level (Mallin et al., 1993), nutrients' runoff (Kinney and Roman, 1998), biotic networks (Graham et al.,

122   2018; Breen and Mann, 1976), and bacterial community dynamics (Guo et al., 2022), govern, at a small

123   scale, high spatial and temporal change in the concentrations of dissolved oxygen. The interaction of all

124   these factors strongly affects dissolved oxygen fluctuations beyond the levels that can be predicted from

125   just the meteorological trends.

126   Oxygen availability plays an important role in the physiology of aquatic species (Pörtner, 2010; Hochachka,

127   1991; Stillman and Somero, 2000). In the design of experiments on the physiology of aquatic animals,

128   oxygen is frequently treated as a fixed factor and maintained around the water saturation. However,

129   organisms inhabiting aquatic environments experience ample diel oxygen fluctuations and are adapted to

130 endure or respond to the experienced variation (Blewett et al., 2022; Morash et al., 2018). Oxygen may be

131 systematically depleted at night and fully recovered during the day, changes that certainly have consequences

132 on the tolerance to acute stressors such as hypoxia and warming. Dependent on the intensity of the

133 photosynthetic activity, dissolved oxygen concentrations can reach levels far above the physical saturation

134 (Giomi et al., 2019; McArley et al., 2020). Under such hyperoxic conditions, aquatic organisms experience

135 oxygen availability well beyond their physiological needs, but the effects on their physiology and life history

136 are largely unknown.

137 Hyperoxia benefits the metabolic performance of fishes and invertebrates, especially under acute warming

138 that may be very intense in tidal ponds or shallow coastal habitats (Fusi et al., 2021; Booth et al., 2021;

139 Giomi et al., 2019; McArley et al., 2020; Booth et al., 2023a). It extends the upper thermal tolerance of

140 aquatic animals during acute events of daily warming and their survival to anomalous heat waves (McArley

141 et al., 2022). Within the current trend of climate change, the beneficial effect of hyperoxia against extreme

142 heating events can have underestimated positive consequences on the survival of the animals. For instance,

143 an important consequence of exposure to the hyperoxic conditions experienced during the daytime under

144 high heating regimes is the enhanced capability to extract oxygen from the poorly oxygenated water during

145 the night and endure hypoxic or even anoxic periods (Giomi et al., 2019; Booth et al., 2021).

146 Oxygen fluctuations are also appreciated as a factor contributing to the structuring of organismal networks

147 and in the synchronisation of life history dynamics such as spawning or larval recruitment (Garzke et al.,

148 2019; Viaroli and Christian, 2004).

149

150 **4. The role of oxygen fluctuation in coastal biogeochemical cycles**

151 *4.1 Biogeochemical cycles in the pelagic compartment in relation to oxygen fluctuation at daily scale*

152 In productive coastal ecosystems, the biogeochemical cycles of key chemical elements are strongly

153 interconnected with oxygen dynamics. Nitrogen and phosphorus are typically key elements which limit

154 primary production in shallow coastal-marine ecosystems, whose emissions from river basins (or other

155 sources, such as previously enriched sediments) can lead to eutrophication with detrimental effects on

156 biodiversity and human welfare (Palmeri et al., 2013). The biogeochemical cycles of nitrogen and

157 phosphorus are composed of multiple physical, chemical and biological processes, of which some are

158   accelerated by oxygen availability, such as nitrification and mineralisation, while others are enhanced by its

159   absence, such as denitrification and P release from sediments. The regular daily alternation of contrasting

160   conditions of below- and above-saturation dissolved oxygen concentrations in the water column,

161   particularly in the euphotic zone, promotes changes in the relative abundance of different nutrient forms

162   (Figure 3). This becomes clear when looking, for example, at the nitrogen cycle in the water column and its

163   complex relationship with oxygen availability: the presence of dissolved oxygen speeds up the

164   mineralisation of organic nitrogen to ammonium as well as nitrification, i.e., the microbial oxidation of

165   ammonium into nitrites and then nitrates. The absence of oxygen makes denitrification possible, i.e., the

166   reduction of nitrates into inert gaseous nitrogen is promoted by facultative aerobic bacteria that, in the

167   absence of anoxia, will prefer oxygen to nitrates as an electron acceptor (Palmeri et al., 2013). Ammonium,

168   nitrites and nitrates are important nitrogen forms that are bioavailable to primary producers, and the

169   oscillating oxygen conditions in the water column at the diel scales can promote their removal via the

170   nitrification-denitrification chain. High oxygen concentrations are also associated with high photosynthetic

171   activity (e.g., planktonic) and, therefore, with the fast removal of dissolved inorganic nutrients from water

172   through uptake by primary producers (Caron, 1994). The picture is made more complex by the typically

173   non-linear dependence of biogeochemical reactions on oxygen concentration (e.g., nitrification and

174   denitrification) and on temperature (in the case of most biogeochemical processes), which can both change

175   enormously throughout the day, especially in shallow productive ecosystems, altering reaction rates at sub-

176   daily scales in a way which cannot be appreciated if only the daily mean in dissolved oxygen is considered,

177   but which needs to be quantified if we are to predict future biogeochemical cycling mechanistically under

178   climate change (Caballero-Alfonso et al., 2015). A further source of complexity is given by the feedback

179   between abiotic and biotic components of pelagic ecosystems. The growth of primary producers, both

180   microscopic and macroscopic, is on the one hand affected by the presence of bioavailable nutrient forms,

181   and on the other hand their biomass can reduce light availability by increasing shading or turbidity, limiting

182   light penetration and, so, oxygen production and warming in deeper waters. These examples highlight the

183   importance of higher frequency measurements of oxygen fluctuations, nutrient concentrations, and

184   microbial community abundance, composition and activity in the water column at sub-daily scales to get a

185   better, more quantitative grasp of biogeochemical cycling in coastal water bodies (Meire et al., 2013). A

186   general framework to assess the short-term (hourly) oxygen fluctuations in relation to the movement and

187   related physical properties of water masses, i.e., of processes such as stratification, residence time, and

188   thermohaline flows, in addition to other processes (photosynthesis, respiration, solubility changes, etc.) is

189   important to future oxygen modelling.

190

191   *4.2 Biogeochemical cycles in the benthic compartment in relation to oxygen fluctuation at daily scale*

192   The intertwined oxygen and nutrient dynamics in the water column cannot be understood, at least in

193   relatively shallow aquatic ecosystems, without looking at the interactions between the pelagic and the

194   benthic compartment. This takes place through the vertical transport of matter (settling, resuspension,

195   convection, upwelling currents, etc.) and is also affected by stratification, gradient-driven diffusive fluxes,

196   and organism movements and vertical migrations.

197   When temperature and oxygen concentration in the water column fluctuate at short daily time scale, yet

198   with very large amplitude (from anoxia/hypoxia to hyperoxia), the impact on biogeochemical cycles and

199   chemical transfers is mostly unknown. Based on the trends observed at seasonal "steady-state" conditions,

200   a conceptual model on the location of the major benthic processes in the sediment and the resulting fluxes

201   at the sediment-water interface within the diurnal temporal scale can be drawn (Figure 4).

202   As oxygen penetration depth and concentration in sediment is known to rapidly evolve in response to the

203   oxygen concentration in the overlying water (Glud, 2008), the importance of aerobic process in surface

204   sediment is also expected to fluctuate at the diurnal timescale, with higher contribution during the day than

205   during the night. The fast kinetics of the reductive dissolution/oxidative precipitation of Mn and Fe oxy-

206   hydroxides and the redox cycle of S chemical species (i.e., H_2S/SO_4^{2-}) suggests that those chemical species

207   should evolve with a similar trend over daily timescales, with a reasonable short term (minutes-hours) delay

208   (Rigaud et al., 2018). Consequently, we expect a vertical fluctuation of those biogeochemical redox

209   processes in the sediment and related fluxes under diel oxygen fluctuation (Figure 4). The low oxygen

210   concentration at night should induce a lower oxygen penetration depth and an upward distribution of NO_3^-

211   , Mn and Fe oxyhydroxides and SO_4^{2-} reductions. If the oxygen concentration is low enough, the reductive

212   dissolution of Mn and Fe oxyhydroxides may directly occur at the sediment-water interface, inducing their

213   release to the water column with other chemical species associated with these phases (i.e., PO_4^{3-} and most

214 trace elements). In the specific case of anoxia, the sulfate-reduction process may occur at the sediment

215 surface, releasing H_2S to the water column. It is expected that in such a condition, the release of dissolved

216 metals (Fe, Mn and trace elements), which also present a rapid kinetic for metal sulfide formation in the

217 presence of S(-II), can be reduced and likely reverted (Figure 4). In contrast, the increase of oxygen

218 concentration during the day promotes oxygen penetration in the sediment and the oxidation of reduced

219 species accumulated during the night, such as dissolved Mn, Fe, NH_4^+ and eventually H_2S, preventing their

220 release from the sediment. The reconstitution of the Mn/Fe oxyhydroxide reservoir in surface sediment

221 favours the trapping of PO_4^{3-} and trace elements associated with Fe and Mn cycles. The oxidation of NH_4^+

222 induces the formation of NO_2^- and NO_3^- that may be released from the sediment.

223 In shallow coastal areas, the light radiation may also reach the sediment surface allowing the photosynthetic

224 activity of the microphytobenthos to occur in surface sediment (Figure 4). The local source of oxygen at

225 the sediment surface occurs because photosynthesis strongly enhances the biogeochemical processes

226 described above (Denis et al., 2012; Rigaud et al., 2018). The oxygen released in the water column enhances

227 the water hyperoxia and consumes nutrients and CO_2 during photosynthesis. This creates a very peculiar

228 situation that modifies the direction and intensity of chemical fluxes at the sediment-water interface and

229 the chemical composition of water and surface sediment in coastal areas at the diurnal scale. For those rapid

230 redox-sensitive chemical species, processes and fluxes are thus expected to evolve, between such extreme

231 night/day fluctuations, with a transient response related to the reaction kinetics and transport within the

232 sediment surface.

233 For OM mineralisation processes, the effects of short-term oxygen fluctuation are more challenging to

234 predict. It will also be dependent on the capacity of heterotrophs to react/adapt to the changing oxygen

235 concentrations and eventually shift between different metabolic processes (for microorganisms where

236 variables metabolic pathways coexist) or to activate/cease the process in relation to physicochemical

237 conditions and oxidant availability (for microorganisms with specialised metabolisms). Consequently, the

238 dynamic response of the microbial community to short-term oxygen and chemical fluctuations needs to be

239 investigated in more detail in relation to microbial communities' resilience and adaptation capacity (see

240 section 5).

In productive coastal areas, the benthic organisms, including macro and meiofaunal species, adapt to wide 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 mineralisation 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, 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 wide 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 photosynthesis recovery, re-establishing aerobic respiration as the central metabolism of the microbial communities (Fenchel and Finlay, 2008). For example, in the Bohai Sea (China), under an oxygen concentration lower than 4.2 mg/L, the microbial communities were dominated by bacteria belonging to the group 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.

297   *Bacteroidetes*, SAR11, SAR86 and *Alphaproteobacteria* dominated in waters containing dissolved oxygen

298   concentrations higher than 70 µM. In contrast, taxonomic groups such as Arctic96BD-19, SUP05, SAR324

299   and *Desulfobacterales* were observed at dissolved oxygen concentrations below 70 µM to undetectable levels

300   (Aldunate et al., 2018). The continuous variation of oxygen concentration enhances the diel cycling of

301   nutrients in productive coastal environments, highlighting the importance of assessing the ecologically

302   relevant oxygen fluctuations to determine the effective microbial functionality of the marine coastal

303   ecosystem (Trowbridge et al., 2017).

304   Incorporating methods to assess the ecologically relevant variability of oxygen availability, intensity and

305   synchronicity in future experimental designs will generate a more accurate prediction of the response of

306   bacterial communities and therefore their potential for biogeochemical cycling to climate change, better

307   informing the development of management strategies to mitigate detrimental stressor impact on ecosystems

308   effectively. The current challenge in microbial ecology is to understand the widespread temporal and spatial

309   environmental oxygen variability and switch from the "mean conditions paradigm" often used for

310   investigations of microbial ecological processes to a dynamic model able to capture the microbial changing

311   and functional potential under oxygen fluctuating conditions (Fusi et al., 2022).

312

313   **6. Implications for marine assessment and management**

314   Oxygen production is considered an ecosystem service (https://cices.eu/) because of the benefits humans

315   receive, but, to date, there is limited inclusion of the impacts of deoxygenation or oxygen fluctuation in

316   marine environmental policies. There are only few areas whose oxygen dynamics have been extensively

317   monitored, like in North America (i.e., Chesapeake Bay, Gulf of Mexico, Long Island Sound) and included

318   in   management   plans   for   environmental   protections   (e.g.,

319   https://coastalscience.noaa.gov/project/operational-gulf-of-mexico-hypoxia-monitoring/).   However,

320   globally, there has been a lack of oxygen dynamics' integration into the computation of biodiversity

321   indicators that assess aquatic communities (Breitburg et al., 2019; Chen et al., 2022), and in particular the

322   oxygen dynamic at a daily scale remains largely neglected in marine assessment and management. Policies

323   on pollution or nutrient control had a positive effect on the oxygen level in ocean water, however, there is

324   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 minimum oxygen concentrations in water with the risk of overlooking the effect of the oxygen fluctuation, which is 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 ecologically 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.

Data availability

All the data ae available as supplementary material.

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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Figure captions

598

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 seasons (based on data availability). Data source is specified

for each environment in the Supplementary Dataset for Figures 1 and 2.

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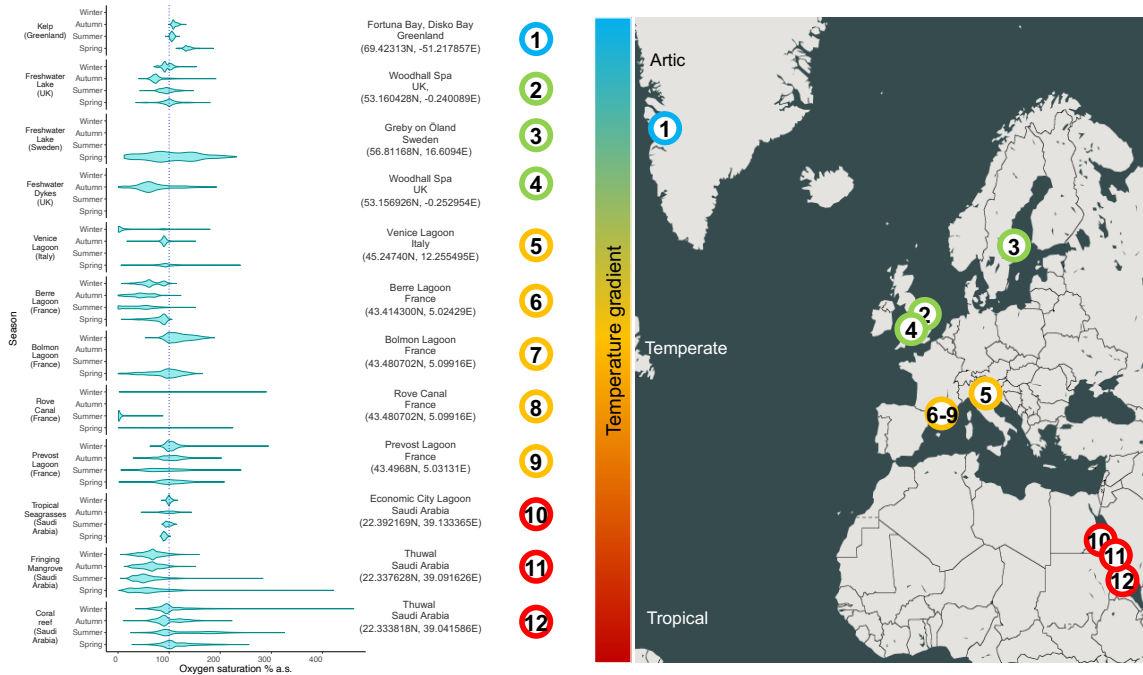
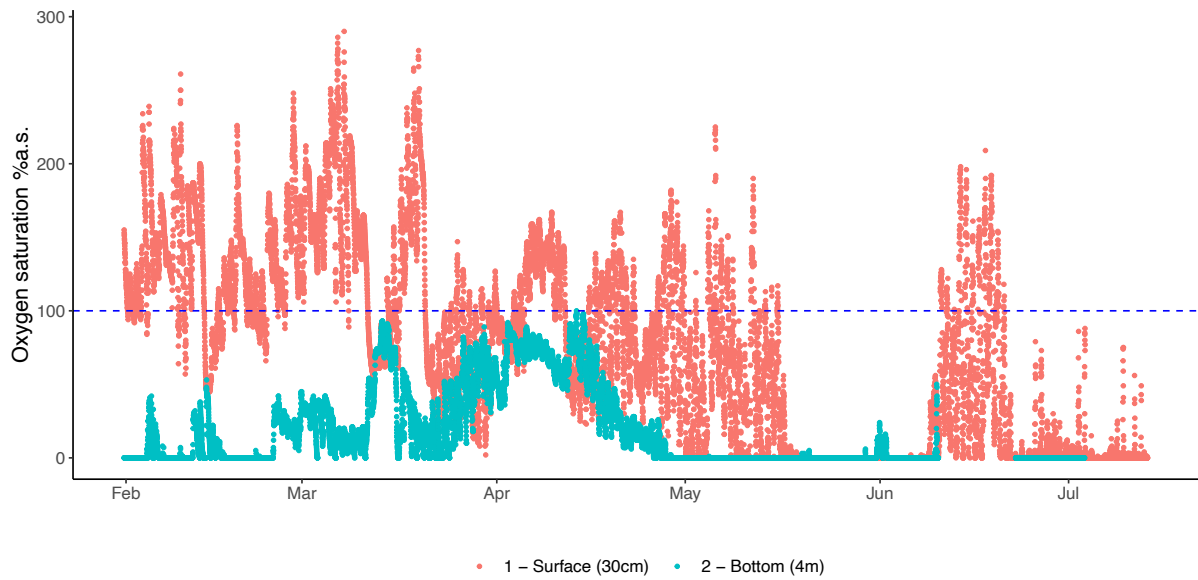


Figure 2. Fluctuations of oxygen saturation measured at the bottom (4 m) and surface (30 cm) oxygen saturation of the Rove canal in France highlight the contrast between the two depths of eutrophicated coastal environment from the winter to summer. The analysis of these case studies revealed different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

611 **Figure 3**. Nutrient concentration, dissolved oxygen and water temperature measurements in the water of

612 a salt marsh of the Northern Venice Lagoon (Italy) on August 13th, 2015. (**A**) The concentration of

613 different nitrogen forms in the marsh water (notice the two different vertical axes) over time in the central

614 part of the day. Measurements are made in the water entering the marsh (flood phase, left of the vertical

615 grey line, which indicates the tidal peak) and quitting from the salt marsh (ebb phase, right of the vertical

616 grey line). After some time spent in the marsh, which is flooded by tide twice per day, water becomes

617 depleted in inorganic nutrients, presumably due to the uptake by primary producers, exchanges with the

618 sediments, and (in the case of ammonium) nitrification. Concurrently, water is enriched with dissolved

619 organic nitrogen related to the intense biological activity within the marsh. (**B**) Dissolved oxygen and

620 temperature of the water entering the marsh (flood phase, left of the vertical grey line, which indicates the

621 tidal peak) and water quitting from the salt marsh (ebb phase, right of the vertical grey line) over time in

622 the central part of the day. Notably, in the biologically productive habitat of the marsh enriches in dissolved

623 oxygen the water,, paralleled by an increase in water temperature.

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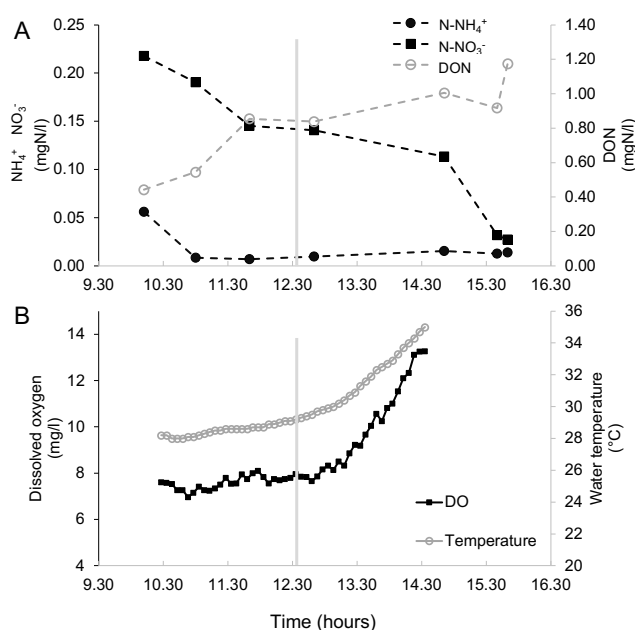
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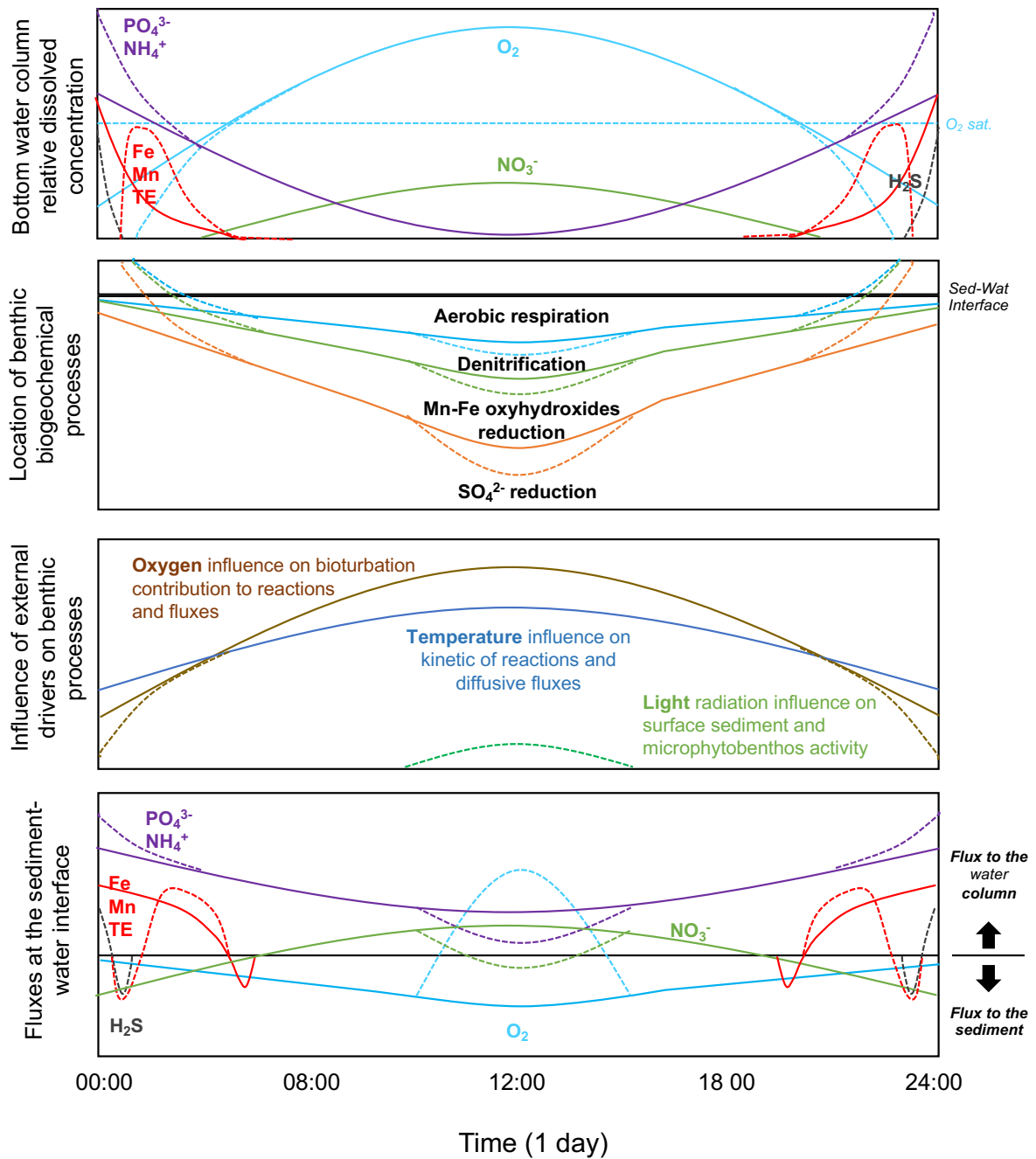
626 **Figure 4.** Scheme of the benthic biogeochemical cycle in relation to diel oxygen fluctuation. Relative
627 evolution of the bottom water chemical composition and evolution of the location of the most important
628 biogeochemical processes in the benthic compartment. Relative influence of external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

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634   **Figure 5.** Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of

635   microbial community controlled by the oxygen availability that controls the ratio between aerobic and

636   anaerobic taxa and their relative function. Oxygen fluctuation is important to determine the diel cycling of

637   the bacterial communities that, in turn, affect the biogeochemistry and the overall functioning of the aquatic

638   ecosystems. Note that the graphs are not drawn to scale.

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640