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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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**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~~for 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~~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 ~~deep~~ 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). ~~Topography~~The topography of water basins also affects the incidence of

85 hypoxia events influencing the rate of mixing of oxygenated layers and the resident time of water bodies

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

87 geomorphology of the 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 ~~occur~~occurs in a vast range of water bodies

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

100 example, fluctuations of 150% in spring and 30% in winter occur in the Venice lagoon (Figure 1, Location

101 5), and even more pronounced fluctuations occur in mangroves, corals and seagrasses (Figure 1, Locations

102   10-12; Giomi et al., 2019). The magnitude of oxygen fluctuations is site-specific and depends, among other

103   factors, on the solar radiation and water temperature and their effect on primary producers' photosynthetic

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

105   differences in oxygen saturation also occur between surface and bottom water masses because of isolation

106   driven by water stratification, the decrease of light penetration, and the coupling with increased oxygen

107   demand close to the sediments at the bottom of the water column (Figure 2). In summer, enhanced benthic

108   respiration is determined by higher water temperature, which decreases oxygen solubility and enhances

109   oxygen demand. Lower vertical mixing, higher water residence time, and higher turbidity due to higher

110   concentration of organic matter, further decrease oxygen concentrations down to hypoxia in the deep water

111   layers (Figure 2; Talke et al., 2009; Schmidt et al., 2019). Conversely, dissolved oxygen increases in the

112   euphotic part of the water column because of the enrichment of photosynthetic communities (Spietz et al.,

113   2015).

114

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

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

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

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

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

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

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

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

123   2018; Breen and Mann, 1976), and bacterial community dynamics (Guo et al., 2022), govern, at a small

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

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

126   just the meteorological trends.

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

128   1991; Stillman and Somero, 2000). In the design of experiments on the physiology of aquatic animals,

129   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 synchronisation 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

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

159  accelerated by oxygen availability, such as nitrification and mineralis~~z~~ation, while ~~some~~ others are enhanced

160  by its absence, such as denitrification and P release from sediments. The regular daily alternation of

161  contrasting conditions of below- and above-saturation dissolved oxygen concentrations in the water

162  column, particularly in the euphotic zone, promotes changes in the relative abundance of different nutrient

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

164  and its complex relationship with oxygen availability: the presence of dissolved oxygen speeds up the

165  mineralis~~z~~ation of organic nitrogen to ammonium as well as nitrification, i.e., the microbial oxidation of

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

167  reduction of nitrates into inert gaseous nitrogen is promoted by facultative aerobic bacteria ~~which~~that, in

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

169  Ammonium, nitrites and nitrates are important nitrogen forms ~~which~~ that are bioavailable to primary

170  producers, and the oscillating oxygen conditions in the water column at the diel scales can promote their

171  removal via the nitrification-denitrification chain. High oxygen concentrations are also associated with high

172  photosynthetic activity (e.g., planktonic) and, therefore, with the fast removal of dissolved inorganic

173  nutrients from water through uptake by primary producers (Caron, 1994). The picture is made more

174  complex by the typically non-linear dependence of biogeochemical reactions on oxygen concentration (e.g.,

175  nitrification and denitrification) and on temperature (in the case of most biogeochemical processes), which

176  can both change ~~strongly~~enormously throughout the day, especially in shallow productive ecosystems,

177  altering reaction rates at sub-daily scales in a way which cannot be appreciated if only the daily mean in

178  dissolved oxygen is considered, but which needs to be quantified if we are to ~~mechanistically~~ predict future

179  biogeochemical cycling mechanistically under climate change (Caballero-Alfonso et al., 2015). A further

180  source of complexity is given by the ~~feedbacks~~feedback between abiotic and biotic components of pelagic

181  ecosystems. The growth of primary producers, both microscopic and macroscopic, is on the one hand

182  affected by the presence of bioavailable nutrient forms, and on the other hand their biomass can reduce

183  light availability by increasing shading or turbidity, limiting light penetration and, so, oxygen production

184  and warming in deeper waters. These examples highlight the importance of higher frequency measurements

185  of oxygen fluctuations, nutrient concentrations, and microbial community abundance, composition and

186 activity in the water column at sub-daily scales, to get a better, more quantitative grasp of biogeochemical

187 cycling in coastal water bodies (Meire et al., 2013). A general framework to assess the short-term (hourly)

188 oxygen fluctuations in relation to the movement and related physical properties of water masses, i.e., of

189 processes such as stratification, residence time, and thermohaline flows, in addition to other processes

190 (photosynthesis, respiration, solubility changes, etc.) is important to future oxygen modelling.

191

192 *4.2 Biogeochemical cycles in the benthic compartment in relation to oxygen fluctuation at daily scale*

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

194 relatively shallow aquatic ecosystems, without ~~looking also~~looking at the interactions between the pelagic

195 and the benthic compartment. This takes place through the vertical transport of matter (settling,

196 resuspension, convection, upwelling currents, etc.) and is also affected by stratification, gradient-driven

197 diffusive fluxes, and organism movements and vertical migrations.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

233  sediment surface.

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

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

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

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

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

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

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

241  section 5).

242 In productive coastal areas, the benthic organisms, including macro and meiofaunal species, adapt to ~~large~~

243 wide and rapid daily oxygen variation by modifying their behaviour. The bioturbating activity may be

244 favoured during high oxygen concentration and lowered during conditions of low oxygen availability. We

245 expect that, during the night oxygen deficiency, the benthic organism activity is reduced, inducing a decrease

246 in the sediment reworking intensity. This is accompanied by a reduction of the biologically-mediated solute

247 fluxes at the sediment-water interface and oxygen penetration depth in the sediment. In contrast, during

248 oxygen supersaturation occurring in the day, bioturbation is intensified and may induce a short-term change

249 in the contribution of biologically-mediated reactions and transfers. Here also, a delay between the oxygen

250 fluctuation in the water column and the biogeochemical response of the sediment, related to the biological

251 activity, would depend on site characteristics (oxygen concentration and range of fluctuation, bioturbating

252 species). For instance, in areas where anoxia events are recurrent, the absence of macrofauna prevents

253 bioturbation and its influence on the benthic biogeochemistry (Nilsson and Rosenberg, 1997).

254 In response to large amplitude and diel oxygen fluctuations, the sediment' biogeochemical cycles are also

255 expected to fluctuate (Figure 4). However, as the resulting benthic biogeochemistry cycles are associated

256 with the dynamics of three interdependent compartments (i.e., geochemical composition, microbial

257 communities, bioturbating-faunal communities), each presenting its kinetics and responses to oxygen

258 fluctuations, we expect the sediment to be permanently maintained under unsteady-state conditions. This

259 makes it difficult to quantitatively predict the resulting OM ~~mineralization~~mineralisation rates, the

260 proportion of involved processes, and the chemical transfers at the sediment-water interface.

261 The recent development of tools which can measure the chemical composition and sediment-water fluxes

262 over the short-term scale (i.e., microsensors, eddy covariance technic, gradient-flux method), in addition to

263 benthic microbial and macrofaunal activity (*e.g.*, improved sediment profile imaging), may be beneficial to

264 produce experimental data that will help to fill these gaps in understanding. At the same time, specific

265 efforts should be focused on assessing the isolated response to those three different compartments. Those

266 data should then be implemented to appropriately calibrate non-steady-state coupled pelagic-benthic

267 biogeochemical models, which can predict the resulting biogeochemical functioning of productive coastal

268 ecosystems and, thus, ~~to~~ predict their fate under climatic changes.

269

**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~~ 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 ~~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 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

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

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

300  SAR324 and *Desulfobacterales* were observed at dissolved oxygen concentrations below 70 µM to

301  undetectable levels (Aldunate et al., 2018). The continuous variation of oxygen concentration enhances the

302  diel cycling of nutrients in productive coastal environments, highlighting the importance of assessing the

303  ecologically relevant oxygen fluctuations to determine the effective microbial functionality of the marine

304  coastal ecosystem (Trowbridge et al., 2017).

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

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

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

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

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

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

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

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

313

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

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

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

317  marine environmental policies. There are only few areas whose oxygen dynamics hashave been extensively

318  monitored, like in North America (i.e., Cheasapeake Bbay, Gulf of Mexico, Long Island Sound) and

319  included in management plans for environmental protections (e.g.,

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

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

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

323  oxygen dynamic at a daily scale remains largely neglected ins marine assessment and management. Policies

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

325  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~~minimum oxygen concentrations in water ~~and they~~with the risk of overlooking the effect of the oxygen fluctuation, which ~~are~~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 ~~ecological~~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.

**Author contributions**

353 MF and FG conceived the study and wrote sections 1 to 3. AB, GG, SR, FG wrote section 4.1 and 4.2 and

354 provided data for the Mediterranean sites. MF, RM and DD wrote section 5 and provided data for the Red

355 Sea. MF, LP and CVH wrote section 6. All the authors discussed and reviewed the final version.

356

357 **Competing interests**

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

359

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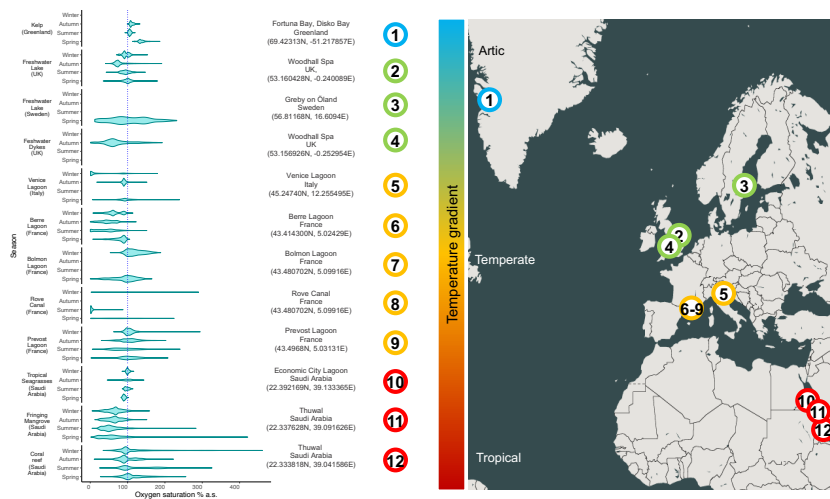
**Figure captions**

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

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

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

610

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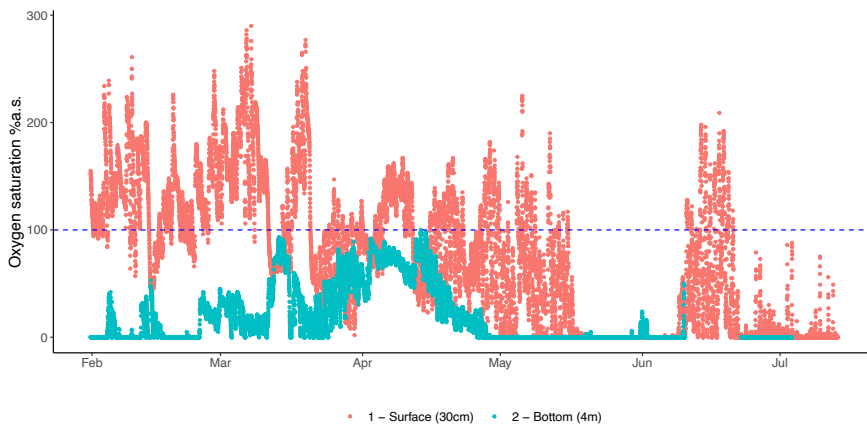
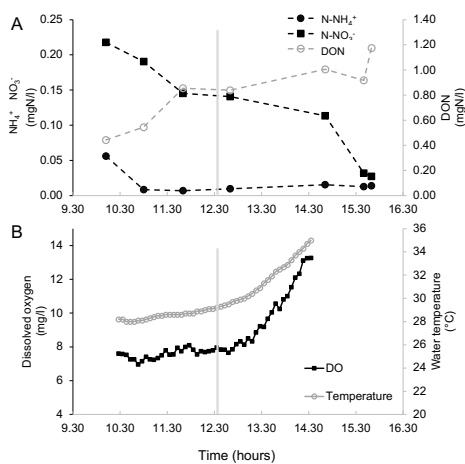


**Figure 3**. Nutrient concentration, dissolved oxygen and water temperature measurements ~~made~~ in the water of a salt marsh of the Northern Venice Lagoon (Italy) on August 13th, 2015. (**A**) ~~Concentration~~The concentration of different nitrogen forms in the marsh water (notice the two different 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~~grey line, which indicates the tidal peak) and quitting from the salt marsh (ebb phase, right of the vertical ~~gray~~grey 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 grey line, which indicates the tidal peak) and water quitting from the salt marsh (ebb phase, right of the vertical grey line) over time in the central part of the day. ~~While~~Notably, in the biologically productive habitat of the marsh ~~(space between water entering and quitting) compared to the surrounding waters, which is a biologically~~ ~~productive habitat compared to the,~~ ~~surrounding waters, the water becomes enriched~~enriches ~~in~~ with dissolved oxygen the water,, paralleled by an increase in water temperature.

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

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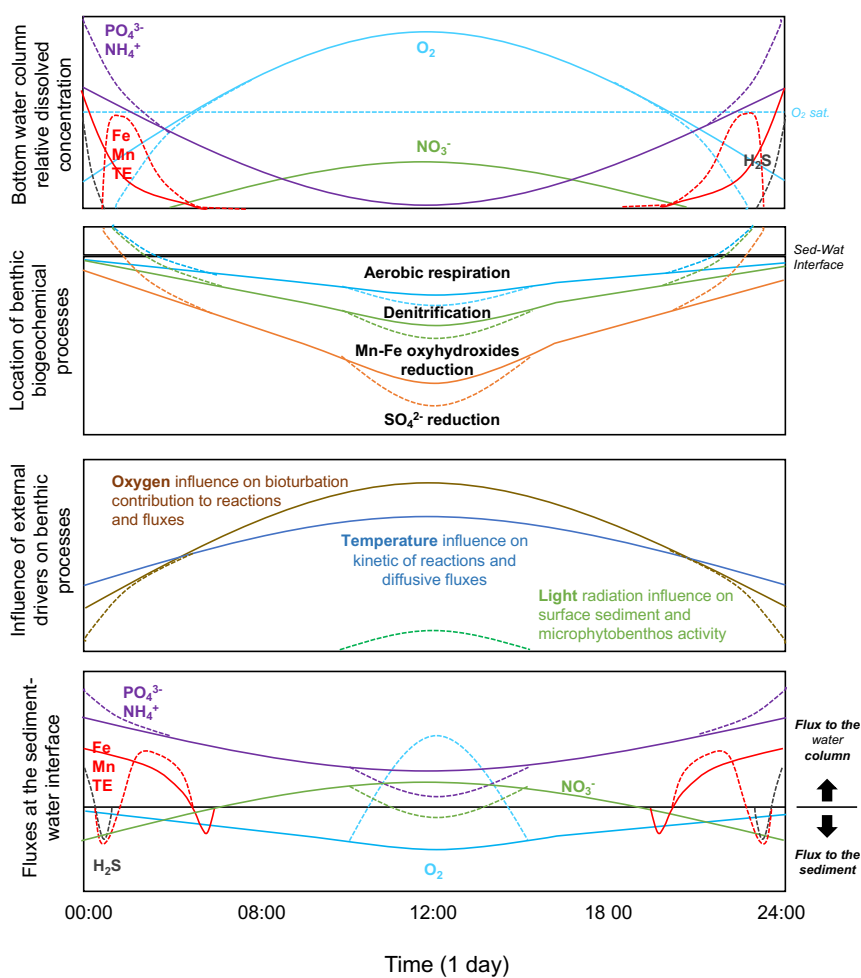
**Figure 5.** Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of microbial community controlled by the oxygen availability that ~~control~~controls the ratio between aerobic and anaerobic taxa and their relative function. Oxygen fluctuation is important to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