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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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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 of aquatic habitats. Conceptual perspectives on the dynamic nature

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

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

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

33   considers the magnitude of oxygen fluctuation as a key variable that explains adaptation to stress conditions.

34   Oxygen in productive aquatic habitats shows large fluctuations at diel scale, exposing aquatic species from

35   conditions of extreme supersaturation to anoxia. Recent research indicates that such fluctuation tunes the

36   physiological plasticity of the animal in response to thermal stresses. In this contribution, we provide

37   compelling evidence based on current research that the fluctuating oxygen landscape, here defined as

38   "*oxyscape*", has an important role in aquatic animal physiology and adaptation and the ecosystem

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

40   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 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

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 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 occur 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. In highly productive

105   marine environments, increased dissolved oxygen concentration may occur in spring due to the

106   intensification of photosynthetic activity, followed by a decrease of available oxygen during the warmest

107   months and a progressive recovery in autumn and winter (Cowan et al., 1996; Bartoli et al., 2001; Kim et

108   al., 2019). Spatial differences in oxygen saturation occur between surface and bottom water masses because

109   of isolation driven by water stratification, the decrease of light penetration, and the coupling with increased

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

111   benthic respiration is determined by higher water temperature, which decreases oxygen solubility and

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

113   higher concentration of organic matter, further decrease oxygen concentrations down to hypoxia in the

114   deep water layers (Figure 2; Talke et al., 2009; Schmidt et al., 2019). Conversely, dissolved oxygen increases

115   in the euphotic part of the water column because of the enrichment of photosynthetic communities (Spietz

116   et al., 2015).

117

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

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

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

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

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

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

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

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

126   2018; Breen and Mann, 1976), and bacterial community dynamics (Guo et al., 2022), govern, at a small

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

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

129   just the meteorological trends.

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

131 1991; Stillman and Somero, 2000). In the design of experiments on the physiology of aquatic animals,

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

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

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

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

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

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

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

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

140 are largely unknown.

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

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

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

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

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

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

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

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

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

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

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

152 2019; Viaroli and Christian, 2004).

153

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

155 *4.1 Biogeochemical cycles in the pelagic compartment in relation to oxygen fluctuation at daily scale*

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

157 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

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

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

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

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

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

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

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

193   important to future oxygen modelling.

194   Of course, the intertwined oxygen and nutrient dynamics in the water column cannot be understood, at

195   least in relatively shallow aquatic ecosystems, without looking also at the interactions between the pelagic

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

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

198   and organism movements and vertical migrations.

199

200   *4.2 Biogeochemical cycles in the benthic compartment in relation to oxygen fluctuation at daily scale*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

236 sediment surface.

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

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

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

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

241 conditions and oxidant availability (for microorganisms with specialized metabolisms). Consequently, the

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

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

244 section 5).

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

246 and rapid daily oxygen variation by modifying their behaviour. The bioturbating activity may be favoured

247 during high oxygen concentration and lowered during conditions of low oxygen availability. We expect that,

248 during the night oxygen deficiency, the benthic organism activity is reduced, inducing a decrease in the

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

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

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

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

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

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

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

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

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

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

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

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

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

262 makes it difficult to quantitatively predict the resulting OM mineralization rates, the proportion of involved

263 processes, and the chemical transfers at the sediment-water interface. The recent development of tools

264 which can measure the chemical composition and sediment-water fluxes over the short-term scale (i.e.,

265 microsensors, eddy covariance technic, gradient-flux method), in addition to benthic microbial and

266 macrofaunal activity (*e.g.*, improved sediment profile imaging), may be beneficial to produce experimental

267 data that will help to fill these gaps in understanding. At the same time, specific efforts should be focused

268 on assessing the isolated response to those three different compartments. Those data should then be

269 implemented to appropriately calibrate non-steady-state coupled pelagic-benthic biogeochemical models,

270   which can predict the resulting biogeochemical functioning of productive coastal ecosystems and, thus, to

271   predict their fate under climatic changes.

272

273   **5. The interrelationship of oxygen fluctuation and aquatic microbial communities**

274   Oxygen is a two-faced element that acts as the terminal electron acceptor in aerobic respiration (by far the

275   most efficient energy metabolism) and as an element of toxicity because the reduction of O_2 molecules

276   partly results in reactive oxygen species. For this reason, oxygen remains a strong evolutionary force

277   dominating functional interactions and the spatial structure of many microbial communities (Fenchel and

278   Finlay, 2008). Oxygen availability determines microbial metabolism, and many studies have been carried

279   out to elucidate the different kinds of communities and metabolisms occurring under anaerobic or aerobic

280   conditions (Sandrin et al., 2009). Marine microorganisms in productive coastal environments also

281   experience large oxygen diel fluctuations, especially at the boundary layer between sediment/primary

282   producers and water (Pacherres et al., 2022).

283   Assessing the full environmental oxygen variability in aquatic habitats using high-resolution temporal and

284   spatial scales relevant to microorganisms can reveal in detail the complexity of the patterns of community

285   dynamics and diversity in such oxygen-variable environments (Berg et al., 2022). For example, oxygen

286   largely varies during the day in tropical clear shallow waters because of the photosynthetic activity of

287   seagrasses, corals and mangroves (Giomi et al., 2019). Therefore, the microbial communities in these

288   ecosystems can experience environmental conditions ranging from hyperoxia to anoxia (see the oxygen

289   profile in Figure 2). These fluctuations imply that the microbial communities have to shift their composition

290   and function according to the oxygen availability (Fenchel and Finlay, 2008; Booth et al., 2023b, 2019).

291   Microorganisms generally have a short generation time (and high turnover) that favour timely adaptation

292   to new conditions in a changing environment (Steiner et al., 2019). During low oxygen availability at night-

293   time, bacterial communities will shift their composition and function toward anaerobic function (Figure 5).

294   End products of anaerobic metabolisms such as ammonium, sulphur and methane are consumed when

295   oxygen becomes available again during the daylight and the recovery of photosynthesis, re-establishing

296   aerobic respiration as the central metabolism of the microbial communities (Fenchel and Finlay, 2008). For

297   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

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

327 still a clear missing link on specific policies to monitor and manage daily oxygen variability. While attention

328 has been given to ocean warming and acidification, daily oxygen dynamics have been overlooked in

329 assessing marine habitat or species' sensitivity to climate changes and anthropogenic disturbances.

330 Including ecologically relevant variations of oxygen availability into aquatic biodiversity indicators, in

331 addition to continuous and high temporal resolution oxygen and chemical concentration measurements in

332 the sediment and water column, offers a great opportunity to refine and produce more robust predictors

333 that will be able to disentangle better the response of aquatic ecosystems to climate change and

334 anthropogenic disturbances (Dafforn et al., 2012).

335 Current hypoxic thresholds for aquatic ecosystem management are generally calculated on averages and

336 minima oxygen concentrations in water and they risk overlooking the effect of the oxygen fluctuation which

337 are more relevant for communities' physiology (Tomasetti and Gobler, 2020). Enhancing monitoring

338 programs by capturing the daily oxygen fluctuation will allow detection of when night-time low oxygen

339 content is followed by a daytime recovery period, often reaching oxygen supersaturation. This alternation

340 allows the aquatic communities to sustain their homeostasis in a fluctuating environment. Therefore, proper

341 monitoring can inform a correct management to conserve, protect, and restore coastal water mosaic

342 patterns of primary producers to ensure the ecological relevant fluctuations of dissolved oxygen.

343 In this contribution, based on recent research, we provide evidence that the fluctuating oxygen creates a

344 spatial and temporal heterogeneous aquatic oxygen landscape that we have defined here as "oxyscape". The

345 oxyscape—having an important role for aquatic animal physiology and adaptation and the ecosystem

346 biogeochemistry—should be considered in the modelling and managing policies of aquatic ecosystems to

347 capture the ecologically relevant oxygen fluctuation. Understanding the oxyscape can help to reconsider

348 the dynamics of many productive aquatic ecosystems and we, therefore, call on ecologists to rethink their

349 models and experiments in this light. This would increase understanding of variations and resilience of

350 communities to changes in environmental conditions at the scales of space and time relevant to individual

351 components.

352

353 **Author contributions**

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

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

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

357

358   **Competing interests**

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

360

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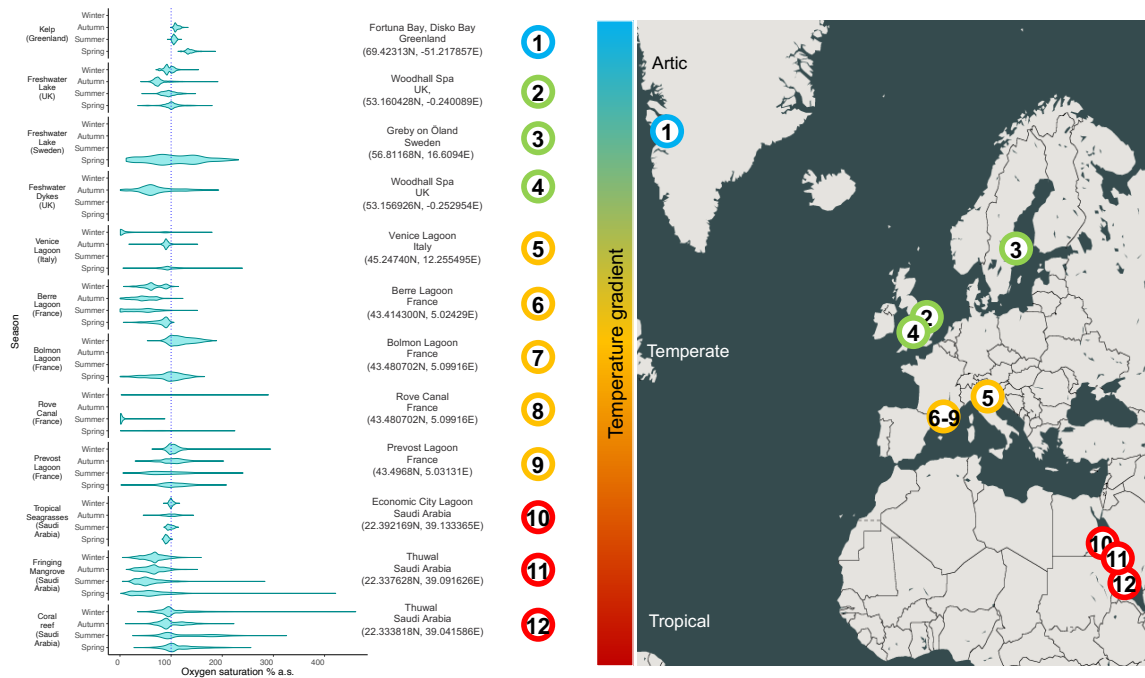
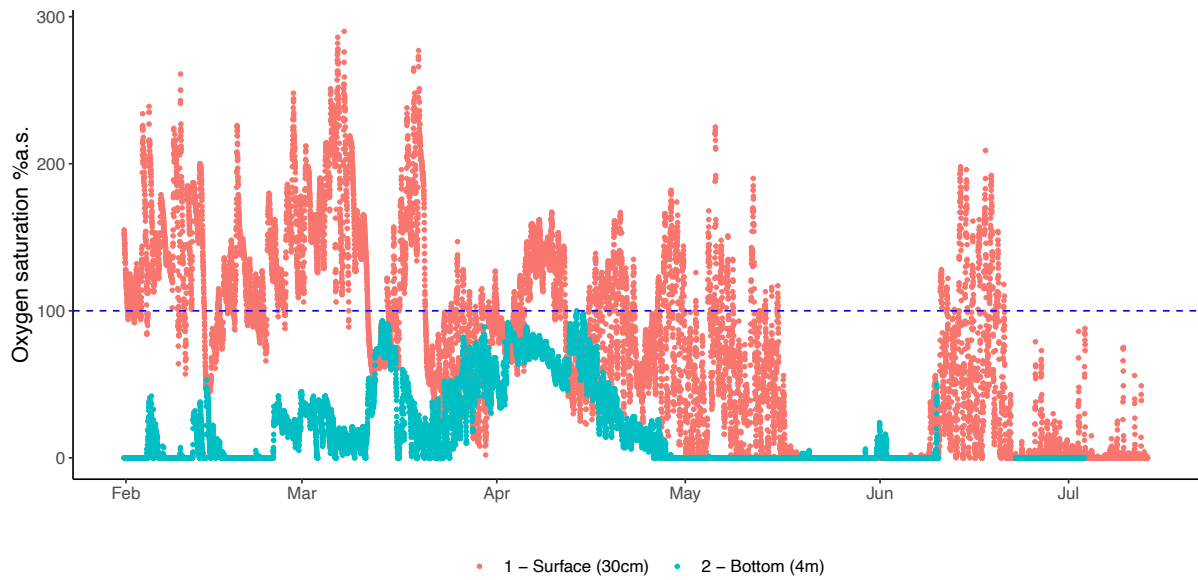
Figure 1. Range of oxygen saturations in several productive aquatic habitats. The dashed line represents 100% oxygen saturation. The violin plots report the densities of the frequencies of oxygen saturation measured at each ecosystem across different season (based on data availability). Data source is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

615 **Figure 2**. Fluctuation of oxygen saturation measured at the bottom (4 m) and surface (30 cm) oxygen

616 saturation of the Rove canal in France that highlight the contrast between the two depths of eutrophicated

617 coastal environment from the winter to summer. The analysis of these case studies revealed different power

618 to predict oxygen variation.

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621 **Figure 3**. Nutrient concentration, dissolved oxygen and water temperature measurements made in the

622 water of a salt marsh of the Northern Venice Lagoon (Italy) on August 13th, 2015. A) Concentration of

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

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

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

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

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

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

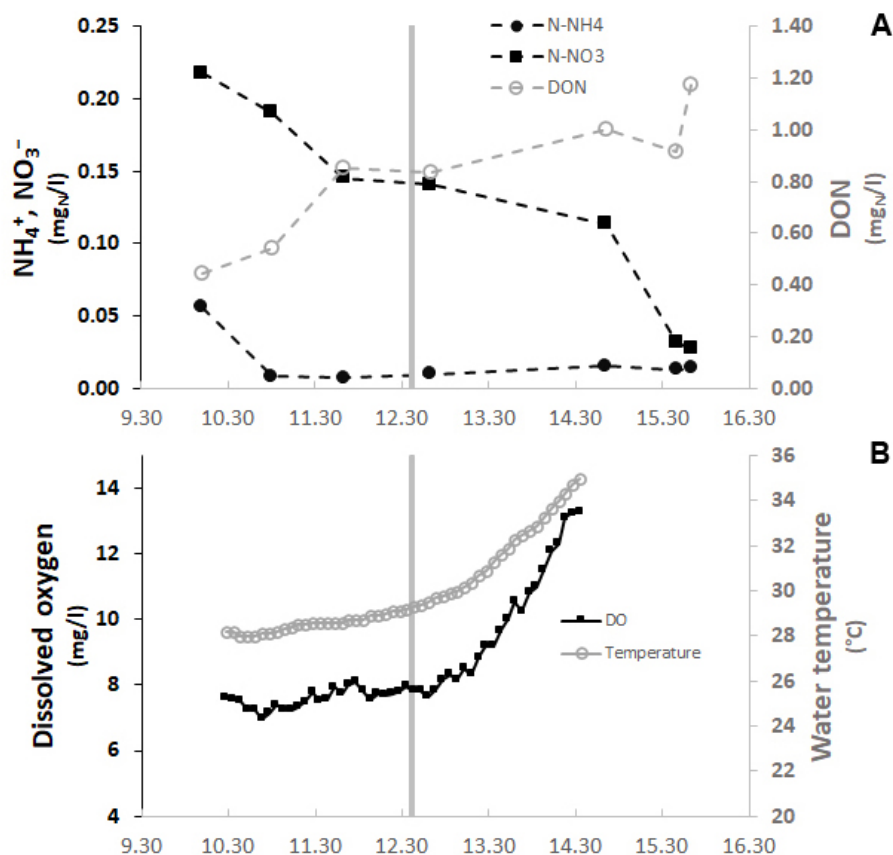
629 organic nitrogen related to the intense biological activity within the marsh. B) Dissolved oxygen and

630 temperature of the water entering the marsh (flood phase, left of the vertical gray line which indicates the

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

632 central part of the day. While in the marsh, which is a biologically productive habitat compared to the

633 surrounding waters, the water becomes enriched with dissolved oxygen paralleled by an increase in water

634 temperature.

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637 **Figure 4.** Scheme of the benthic biogeochemical cycle in relation to diel oxygen fluctuation. (A) The relative

638 evolution of the bottom water chemical composition, (B) evolution of the location of the most important

639 biogeochemical processes in the benthic compartment. (C) Relative influence of external drivers on benthic

640 processes. (D) Relative evolution of resulting flux direction and intensity. Note that the graphs are not

641 drawn to scale. Although concentrations of PO_4^{3-} and NH_4^+ and of Mn and Fe may behave differently,

642 they are represented as similar in this figure for simplification.

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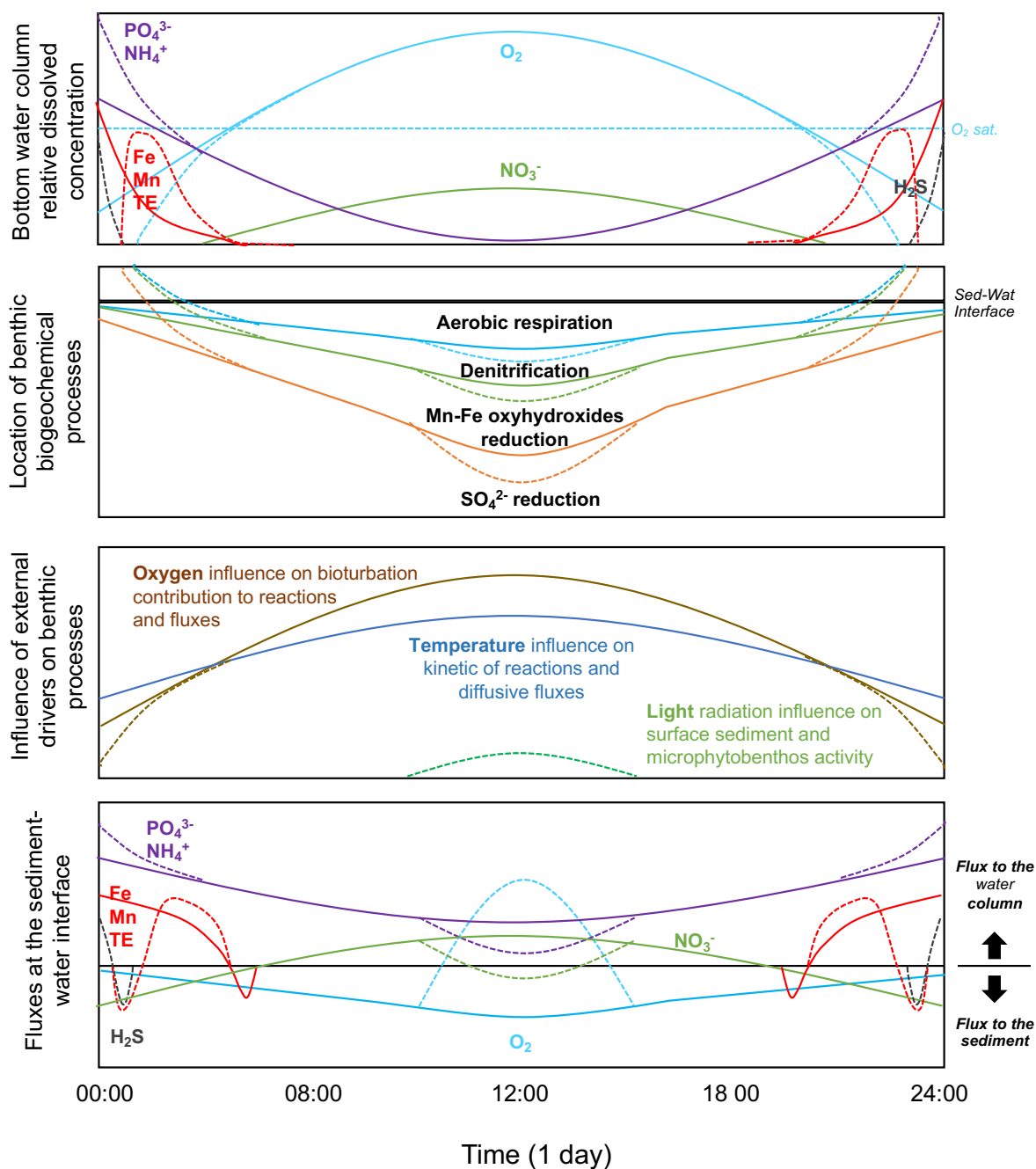
Figure 5. Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of microbial community controlled by the oxygen availability that control the ratio between aerobic and anaerobic taxa and their relative function. Oxygen fluctuation is important to determine the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