1   **Manuscript type**: *Ideas and perspective*

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

7   **Authors**

8   Marco Fusi[1,*], Sylvain Rigaud[2], Giovanna Guadagnini[3], Alberto Barausse[3], Ramona Marasco[4], Daniele

9   Daffonchio[4], Julie Régis[2], Louison Huchet[2], Capucine Camin[2], Laura Pettit[1], Cristina Vina-Herbon[1], Folco

10   Giomi[5,*]

12   [1]Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY

13   [2]Univ. Nîmes, EA 7352 CHROME, Rue Du Dr Georges Salan, 30021 Nîmes, France

14   [3]Department of Biology, University of Padova, Padova, Italy

15   [4]Biological and Environmental Sciences and Engineering Division (BESE), Red Sea Research Center

16   (RSRC), King Abdullah University of Science and Technology (KAUST), Thuwal, Kingdom of Saudi

17   Arabia

18   [5]Independent Researcher, Padua, Italy

20   *equal contribution and co-corresponding authors:

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

22   Folco Giomi: folcog@gmail.com

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

accelerated by oxygen availability, such as nitrification and mineralisation, while 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 mineralisation 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 that, 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 that are bioavailable to primary producers, and the 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 enormously 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 predict future biogeochemical cycling mechanistically under climate change (Caballero-Alfonso et al., 2015). A further source of complexity is given by the feedback between abiotic and biotic components of pelagic ecosystems. The growth of primary producers, both microscopic and macroscopic, is on the one hand affected by the presence of bioavailable nutrient forms, and on the other hand their biomass can reduce light availability by increasing shading or turbidity, limiting light penetration and, so, oxygen production and warming in deeper waters. These examples highlight the importance of higher frequency measurements of oxygen fluctuations, nutrient concentrations, and microbial community abundance, composition and activity in the water column at sub-daily scales to get a better, more quantitative grasp of biogeochemical cycling in coastal water bodies (Meire et al., 2013). A

general framework to assess the short-term (hourly) oxygen fluctuations in relation to the movement and related physical properties of water masses, i.e., of processes such as stratification, residence time, and thermohaline flows, in addition to other processes (photosynthesis, respiration, solubility changes, etc.) is important to future oxygen modelling.

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

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

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

As oxygen penetration depth and concentration in sediment is known to rapidly evolve in response to the oxygen concentration in the overlying water (Glud, 2008), the importance of aerobic process in surface sediment is also expected to fluctuate at the diurnal timescale, with higher contribution during the day than during the night. The fast kinetics of the reductive dissolution/oxidative precipitation of Mn and Fe oxy-hydroxides and the redox cycle of S chemical species (i.e., H_2S/SO_4^{2-}) suggests that those chemical species should evolve with a similar trend over daily timescales, with a reasonable short term (minutes-hours) delay (Rigaud et al., 2018). Consequently, we expect a vertical fluctuation of those biogeochemical redox processes in the sediment and related fluxes under diel oxygen fluctuation (Figure 4). The low oxygen concentration at night should induce a lower oxygen penetration depth and an upward distribution of NO_3^-, Mn and Fe oxyhydroxides and SO_4^{2-} reductions. If the oxygen concentration is low enough, the reductive dissolution of Mn and Fe oxyhydroxides may directly occur at the sediment-water interface, inducing their release to the water column with other chemical species associated with these phases (i.e., PO_4^{3-} and most

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).

241   In productive coastal areas, the benthic organisms, including macro and meiofaunal species, adapt to wide

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

258   makes it difficult to quantitatively predict the resulting OM mineralisation rates, the proportion of involved

259   processes, and the chemical transfers at the sediment-water interface.

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

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

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

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

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

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

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

267   ecosystems and, thus, predict their fate under climatic changes.

268

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

325 has been given to ocean warming and acidification, daily oxygen dynamics have been overlooked in
326 assessing marine habitat or species' sensitivity to climate changes and anthropogenic disturbances.
327 Including ecologically relevant variations of oxygen availability into aquatic biodiversity indicators, in
328 addition to continuous and high temporal resolution oxygen and chemical concentration measurements in
329 the sediment and water column, offers a great opportunity to refine and produce more robust predictors
330 that will be able to disentangle better the response of aquatic ecosystems to climate change and
331 anthropogenic disturbances (Dafforn et al., 2012).

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

340 In this contribution, based on recent research, we provide evidence that the fluctuating oxygen creates a
341 spatial and temporal heterogeneous aquatic oxygen landscape that we have defined here as "oxyscape". The
342 oxyscape—having an important role for aquatic animal physiology and adaptation and the ecosystem
343 biogeochemistry—should be considered in the modelling and managing policies of aquatic ecosystems to
344 capture the ecologically relevant oxygen fluctuation. Understanding the oxyscape can help to reconsider
345 the dynamics of many productive aquatic ecosystems and we, therefore, call on ecologists to rethink their
346 models and experiments in this light. This would increase understanding of variations and resilience of
347 communities to changes in environmental conditions at the scales of space and time relevant to individual
348 components.

349

350 **Author contributions**

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

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

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

354

355 **Competing interests**

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

357

358 **Financial support**

359 D.D. acknowledge the financial support of King Abdullah University of Science and Technology (KAUST)

360 through the Circular Carbon Economy initiative (grant no. REI/1/4483-01-01). D.D also acknowledge the

361 Competitive Research Grant (CRG-7-3739), "The role of the bacterial symbiome at the gill-water (air)

362 interface in the evolution toward territorialisation (Microlanding)," 1 April 2019 to 31 March 2022. We are

363 very grateful to the LabEx DRIIHM, French Programme "Investissements d'Avenir" (ANR-11-LABX-

364 0010), which is managed by the French ANR, under the Human- Environment Observatory

365 "Mediterranean coast" (OHM Littoral Méditerranéen) for its funding that allowed to collect data from the

366 Prevost lagoon, the Excellence Initiative of Aix-Marseille University - A*MIDEX, a French

367 "Investissements d'Avenir" programme (reference number ANR-11-IDEX-0001- 02), the PACA region

368 and the CNRS-INSU-EC2CO program (PREDHYP- O2 program) for its funding that allowed to collect

369 data from the Berre lagoon, and the Occitanie region and the University of Nîmes for the funding of PhD

370 Thesis of Julie Régis. We also thank all the members who allowed us to collect data from the coastal

371 Mediterranean lagoons in France (syndicat mixte GIPREB, Mairie de Chateauneuf-les-Martigues,

372 Compagnons de Maguelone). The PREDHYPO program has received funding from Excellence Initiative

373 of Aix-Marseille University - A*MIDEX, a French "Investisse- ments d'Avenir" programme (reference

374 number ANR-11-IDEX-0001- 02), the PACA region and the CNRS-INSU-EC2CO program (PREDHYP-

375 O2 program).

376 **References**

377 Aldunate, M., De la Iglesia, R., Bertagnolli, A. D., and Ulloa, O.: Oxygen modulates bacterial community

378 composition in the coastal upwelling waters off central Chile, Deep. Res. Part II Top. Stud. Oceanogr., 156,

379 68–79, https://doi.org/10.1016/j.dsr2.2018.02.001, 2018.

380 Andersen, M. R., Kragh, T., and Sand-Jensen, K.: Extreme diel dissolved oxygen and carbon cycles in

381 shallow vegetated lakes., Proceedings. Biol. Sci., 284, 20171427, https://doi.org/10.1098/rspb.2017.1427,

382 2017.

383 Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., Dornelas, M., and

384 Schipper, A. M.: Temperature-related biodiversity change across temperate marine and terrestrial systems,

385 Nat. Ecol. Evol., 4, 927–933, https://doi.org/10.1038/s41559-020-1185-7, 2020.

386 Bates, A. E., Helmuth, B., Burrows, M. T., Duncan, M. I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros,

387 A. M., Seabra, R., Marsh, R., Belmaker, J., Bensoussan, N., Dong, Y., Mazaris, A. D., Smale, D., Wahl, M.,

388 and Rilov, G.: Biologists ignore ocean weather at their peril, Nature, 560, 299–301, 2018.

389 Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar,

390 A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A.,

391 Morales-Castilla, I., and Olalla-Tárraga, M. Á.: The evolution of critical thermal limits of life on Earth, Nat.

392 Commun., 12, 1–9, https://doi.org/10.1038/s41467-021-21263-8, 2021.

393 Benoiston, A. S., Ibarbalz, F. M., Bittner, L., Guidi, L., Jahn, O., Dutkiewicz, S., and Bowler, C.: The

394 evolution of diatoms and their biogeochemical functions, Philos. Trans. R. Soc. B Biol. Sci., 372,

395 https://doi.org/10.1098/rstb.2016.0397, 2017.

396 Berg, P., Huettel, M., Glud, R. N., Reimers, C. E., and Attard, K. M.: Aquatic Eddy Covariance: The Method

397 and Its Contributions to Defining Oxygen and Carbon Fluxes in Marine Environments, Ann. Rev. Mar.

398 Sci., 14, 431–455, https://doi.org/10.1146/annurev-marine-042121-012329, 2022.

399 Bernhardt, J. R., O'Connor, M. I., Sunday, J. M., and Gonzalez, A.: Life in fluctuating environments, Philos.

400 Trans. R. Soc. Lond. B. Biol. Sci., 375, 20190454, https://doi.org/10.1098/rstb.2019.0454, 2020.

401 Bickler, P. E. and Buck, L. T.: Hypoxia tolerance in reptiles, amphibians, and fishes: Life with variable

402 oxygen availability, Annu. Rev. Physiol., 69, 145–170,

403 https://doi.org/10.1146/annurev.physiol.69.031905.162529, 2007.

404   Bitter, M. C., Wong, J. M., Dam, H. G., Donelan, S. C., Kenkel, C. D., Komoroske, L. M., Nickols, K. J.,

405   Rivest, E. B., Salinas, S., Burgess, S. C., Morash, A. J., Neufeld, C., MacCormack, T. J., and Currie, S.: The

406   importance of incorporating natural thermal variation when evaluating physiological performance in wild

407   species, J. Exp. Biol., 221, https://doi.org/10.1242/JEB.164673, 2018.

408   Bitter, M. C., Wong, J. M., Dam, H. G., Donelan, S. C., Kenkel, C. D., Komoroske, L. M., Nickols, K. J.,

409   Rivest, E. B., Salinas, S., Burgess, S. C., and Lotterhos, K. E.: Fluctuating selection and global change: A

410   synthesis and review on disentangling the roles of climate amplitude, predictability and novelty, Proc. R.

411   Soc. B Biol. Sci., 288, https://doi.org/10.1098/rspb.2021.0727, 2021.

412   Blewett, T. A., Binning, S. A., Weinrauch, A. M., Ivy, C. M., Rossi, G. S., Borowiec, B. G., Lau, G. Y.,

413   Overduin, S. L., Aragao, I., and Norin, T.: Physiological and behavioural strategies of aquatic animals living

414   in fluctuating environments, J. Exp. Biol., 225, jeb242503, https://doi.org/10.1242/jeb.242503, 2022.

415   Booth, J., Fusi, M., Giomi, F., Chapman, E., Diele, K., and McQuaid, C.: Diel oxygen fluctuation drives

416   the thermal response and metabolic performance of coastal marine ectotherms, Proc. R. Soc. B Biol. Sci.,

417   288, 20211141, 2021.

418   Booth, J. M., Fusi, M., Marasco, R., Mbobo, T., and Daffonchio, D.: Fiddler crab bioturbation determines

419   consistent changes in bacterial communities across contrasting environmental conditions, Sci. Rep., 9,

420   https://doi.org/10.1038/s41598-019-40315-0, 2019.

421   Booth, J. M., Giomi, F., Daffonchio, D., Mcquaid, C. D., and Fusi, M.: Disturbance of primary producer

422   communities disrupts the thermal limits of the associated aquatic fauna, Sci. Total Environ., 872, 162135,

423   https://doi.org/10.1016/j.scitotenv.2023.162135, 2023a.

424   Booth, J. M., Fusi, M., Marasco, R., and Daffonchio, D.: The microbial landscape in bioturbated mangrove

425   sediment: A resource for promoting nature-based solutions for mangroves, Microb. Biotechnol., in press,

426   https://doi.org/10.1111/1751-7915.14273, 2023b.

427   Breen, P. A. and Mann, K. H.: Changing lobster abundance and the destruction of kelp beds by sea urchins,

428   Mar. Biol., 34, 137–142, https://doi.org/10.1007/BF00390755, 1976.

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

430   Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert,

431   D., Gutiérrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C.,

432 Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., Telszewski, M., Yasuhara, M., and Zhang, J.:

433 Declining oxygen in the global ocean and coastal waters, Science, 359, eaam7240,

434 https://doi.org/10.1126/science.aam7240, 2018.

435 Breitburg, D. L., Conley, D., Isensee, K., Levin, L. A., Limburg, K. E., and Williamson, P.: What can we

436 do? Adaptation and solutions to declining ocean oxygen, Ocean deoxygenation everyone's Probl. Causes,

437 impacts, consequences Solut., 545–562, 2019.

438 Caballero-Alfonso, A. M., Carstensen, J., and Conley, D. J.: Biogeochemical and environmental drivers of

439 coastal hypoxia, J. Mar. Syst., 141, 190–199, https://doi.org/10.1016/j.jmarsys.2014.04.008, 2015.

440 Caron, D. A.: Inorganic nutrients, bacteria, and the microbial loop, Microb. Ecol. Ecol., 28, 295–298,

441 https://doi.org/10.1007/BF00166820, 1994.

442 Challener, R. C., Robbins, L. L., and Mcclintock, J. B.: Variability of the carbonate chemistry in a shallow,

443 seagrass-dominated ecosystem: Implications for ocean acidification experiments, Mar. Freshw. Res., 67,

444 163–172, https://doi.org/10.1071/MF14219, 2016.

445 Chapman, D.: Water Quality Assessments - A Guide to Use of Biota, Sediments and Water in

446 Environmental Monitoring - Second Edition, E&FN Spon, London, 2021.

447 Chen, H., Costanza, R., and Kubiszewski, I.: Legitimacy and limitations of valuing the oxygen production

448 of ecosystems, Ecosyst. Serv., 58, 101485, https://doi.org/10.1016/j.ecoser.2022.101485, 2022.

449 Craig, H. and Hayward, T.: Oxygen Supersaturation in the Ocean: Biological Versus Physical Contributons,

450 735, 1983–1986, 1983.

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

452 E. L.: The challenge of choosing environmental indicators of anthropogenic impacts in estuaries, Environ.

453 Pollut., 163, 207–217, https://doi.org/10.1016/j.envpol.2011.12.029, 2012.

454 Denis, L., Gevaert, F., and Spilmont, N.: Microphytobenthic production estimated by in situ oxygen

455 microprofiling: Short-term dynamics and carbon budget implications, J. Soils Sediments, 12, 1517–1529,

456 https://doi.org/10.1007/s11368-012-0588-8, 2012.

457 Diaz, R. J. and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science,

458 321, 926–929, https://doi.org/10.1126/science.1156401, 2008.

459 Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., and Marbà, N.: The role of coastal plant

460 communities for climate change mitigation and adaptation, Nat. Clim. Chang., 3, 961–968,

461 https://doi.org/10.1038/nclimate1970, 2013.

462 Fenchel, T. and Finlay, B.: Oxygen and the spatial structure of microbial communities, Biol. Rev., 83, 553–

463 569, https://doi.org/10.1111/j.1469-185X.2008.00054.x, 2008.

464 Fusi, M., Daffonchio, D., Booth, J., and Giomi, F.: Dissolved Oxygen in Heterogeneous Environments

465 Dictates the Metabolic Rate and Thermal Sensitivity of a Tropical Aquatic Crab, Front. Mar. Sci., 8, 1–9,

466 https://doi.org/10.3389/fmars.2021.767471, 2021.

467 Fusi, M., Marasco, R., Ramond, J., Barausse, A., and Baldanzi, S.: Editorial : Fluctuating Habitats :

468 Ecological Relevance of Environmental Variability and Predictability on Species , Communities , and

469 Ecosystems, Front. Ecol. Evol., 10, 1–4, https://doi.org/10.3389/fevo.2022.907622, 2022.

470 Garzke, J., Connor, S. J., Sommer, U., and O'connor, M. I.: Trophic interactions modify the temperature

471 dependence of community biomass and ecosystem function, PLoS Biol., 17, 1–27,

472 https://doi.org/10.1371/journal.pbio.2006806, 2019.

473 Giomi, F., Barausse, A., Duarte, C. M., Booth, J., Agusti, S., Saderne, V., Anton, A., Daffonchio, D., and

474 Fusi, M.: Oxygen supersaturation protects coastal marine fauna from ocean warming, Sci. Adv., 5, 1–8,

475 https://doi.org/10.1126/sciadv.aax1814, 2019.

476 Glud, R. N.: Oxygen dynamics of marine sediments, Mar. Biol. Res., 4, 243–289,

477 https://doi.org/10.1080/17451000801888726, 2008.

478 Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., and MacNeil, M. A.: Seabirds enhance

479 coral reef productivity and functioning in the absence of invasive rats, Nature, 559, 250–253,

480 https://doi.org/10.1038/s41586-018-0202-3, 2018.

481 Guo, X., Song, G., Li, Y., Zhao, L., and Wang, J.: Switch of Bacteria Community Under Oxygen Depletion

482 in Sediment of Bohai Sea, Front. Mar. Sci., 9, 1–13, https://doi.org/10.3389/fmars.2022.833513, 2022.

483 Hochachka, P. W.: Temperature: the ectothermy option, in: Phylogenetic and biochemical perspectives:

484 Biochemistry and molecular biology of fishes, 1, vol. 1, 313–322, https://doi.org/10.1016/B978-0-444-

485 89124-2.50016-6, 1991.

486 Ito, T., Nenes, A., Johnson, M. S., Meskhidze, N., and Deutsch, C.: Acceleration of oxygen decline in the

487 tropical Pacific over the past decades by aerosol pollutants, Nat. Geosci., 9, 443–447,

488 https://doi.org/10.1038/ngeo2717, 2016.

489 Keeling, R. F., Körtzinger, A., and Gruber, N.: Ocean deoxygenation in a warming world, Ann. Rev. Mar.

490 Sci., 2, 199–229, https://doi.org/10.1146/annurev.marine.010908.163855, 2010.

491 Kerrison, P., Hall-Spencer, J. M., Suggett, D. J., Hepburn, L. J., and Steinke, M.: Assessment of pH

492 variability at a coastal CO2 vent for ocean acidification studies, Estuar. Coast. Shelf Sci., 94, 129–137,

493 https://doi.org/10.1016/j.ecss.2011.05.025, 2011.

494 Kinney, E. H. and Roman, C. T.: Response of primary producers to nutrient enrichment in a shallow

495 estuary, Mar. Ecol. Prog. Ser., 163, 89–98, https://doi.org/10.3354/meps163089, 1998.

496 Krause-Jensen, D., Marba, N., Sanz-Martin, M., Hendriks, I. E., Thyrring, J., Carstensen, J., Sejr, M. K.,

497 and Duarte, C. M.: Long photoperiods sustain high pH in Arctic kelp forests, Sci. Adv., 2, e1501938–

498 e1501938, https://doi.org/10.1126/sciadv.1501938, 2016.

499 Laffoley, D. and Baxter, J. M.: Explaining Ocean Warming: Causes, scale, effects and consequences, 458

500 pp., https://doi.org/http://dx.doi.org/10.2305/IUCN.CH.2016.08.en, 2016.

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

502 Consequences and Solutions, 2019.

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

504 2, 24–29, https://doi.org/10.1016/j.oneear.2020.01.001, 2020.

505 Mallin, M. A., Paerl, H. W., Rudek, J., and Bates, P. W.: Regulation of estuarine primary production by

506 watershed   rainfall   and   river   flow,   Mar.   Ecol.   Prog.   Ser.,   93,   199–203,

507 https://doi.org/10.3354/meps093199, 1993.

508 Manzello, D. P.: Ocean acidification hot spots: Spatiotemporal dynamics of the seawater CO2 system of

509 eastern Pacific coral reefs, Limnol. Oceanogr., 55, 239–248, https://doi.org/10.4319/lo.2010.55.1.0239,

510 2010.

511 Marasco, R., Fusi, M., Coscolín, C., Barozzi, A., Almendral, D., Bargiela, R., Gohlke, C., Christopher, P.,

512 Dittrich, J., Gohlke, H., Matesanz, R., Sanchez-carrillo, S., Mapelli, F., Chernikova, T. N., Golyshin, P. N.,

513 Ferrer, M., and Daffonchio, D.: Enzyme adaptation to habitat thermal legacy microbiomes, Nat. Commun.,

514 in press, https://doi.org/10.1038/s41467-023-36610-0, 2023.

515 McArley, T. J., Sandblom, E., and Herbert, N. A.: Fish and hyperoxia—From cardiorespiratory and

biochemical adjustments to aquaculture and ecophysiology implications, Fish Fish., 1–32, https://doi.org/10.1111/faf.12522, 2020.

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

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

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

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

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

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

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

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

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

Rigaud, S., Deflandre, B., Maire, O., Bernard, G., Duchêne, J. C., Poirier, D., and Anschutz, P.: Transient

biogeochemistry in intertidal sediments: New insights from tidal pools in Zostera noltei meadows of

Arcachon Bay (France), Mar. Chem., 200, 1–13, https://doi.org/10.1016/j.marchem.2018.02.002, 2018.

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

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

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

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

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

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

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

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

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

Talke, S. A., De Swart, H. E., and De Jonge, V. N.: An idealized model and systematic process study of oxygen depletion in highly turbid estuaries, Estuaries and Coasts, 32, 602–620,

572   https://doi.org/10.1007/s12237-009-9171-y, 2009.

573   Tomasetti, S. J. and Gobler, C. J.: Dissolved oxygen and pH criteria leave fisheries at risk, Science, 368,

574   372–373, https://doi.org/10.1126/science.aba4896, 2020.

575   Trowbridge, C. D., Davenport, J., Cottrell, D. M., Harman, L., Plowman, C. Q., Little, C., and McAllen, R.:

576   Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough, Reg. Stud. Mar. Sci., 11, 9–16,

577   https://doi.org/10.1016/j.rsma.2017.01.008, 2017.

578   Vargas, C. A., Lagos, N. A., Lardies, M. A., Duarte, C., Manríquez, P. H., Aguilera, V. M., Broitman, B.,

579   Widdicombe, S., and Dupont, S.: Species-specific responses to ocean acidification should account for local

580   adaptation and adaptive plasticity, Nat. Ecol. Evol., 1, 1–7, https://doi.org/10.1038/s41559-017-0084,

581   2017.

582   Vargas, C. A., Cuevas, L. A., Broitman, B. R., San Martin, V. A., Lagos, N. A., Gaitán-Espitia, J. D., and

583   Dupont, S.: Upper environmental pCO2 drives sensitivity to ocean acidification in marine invertebrates,

584   Nat. Clim. Chang., 12, 200–207, https://doi.org/10.1038/s41558-021-01269-2, 2022.

585   Viaroli, P. and Christian, R. R.: Description of trophic status, hyperautotrophy and dystrophy of a coastal

586   lagoon through a potential oxygen production and consumption index - TOSI: Trophic Oxygen Status

587   Index, Ecol. Indic., 3, 237–250, https://doi.org/10.1016/j.ecolind.2003.11.001, 2004.

588   Virtanen, E. A., Norkko, A., Nyström Sandman, A., and Viitasalo, M.: Identifying areas prone to coastal

589   hypoxia - The role of topography, Biogeosciences, 16, 3183–3195, https://doi.org/10.5194/bg-16-3183-

590   2019, 2019.

591   Winter, G., Hetzel, Y., Huang, P., Hipsey, M. R., Mulligan, R. P., and Hansen, J.: Coastal processes, extreme

592   events and forecasting, in: Marine Extreme, Routledge, 17, 2019.

593

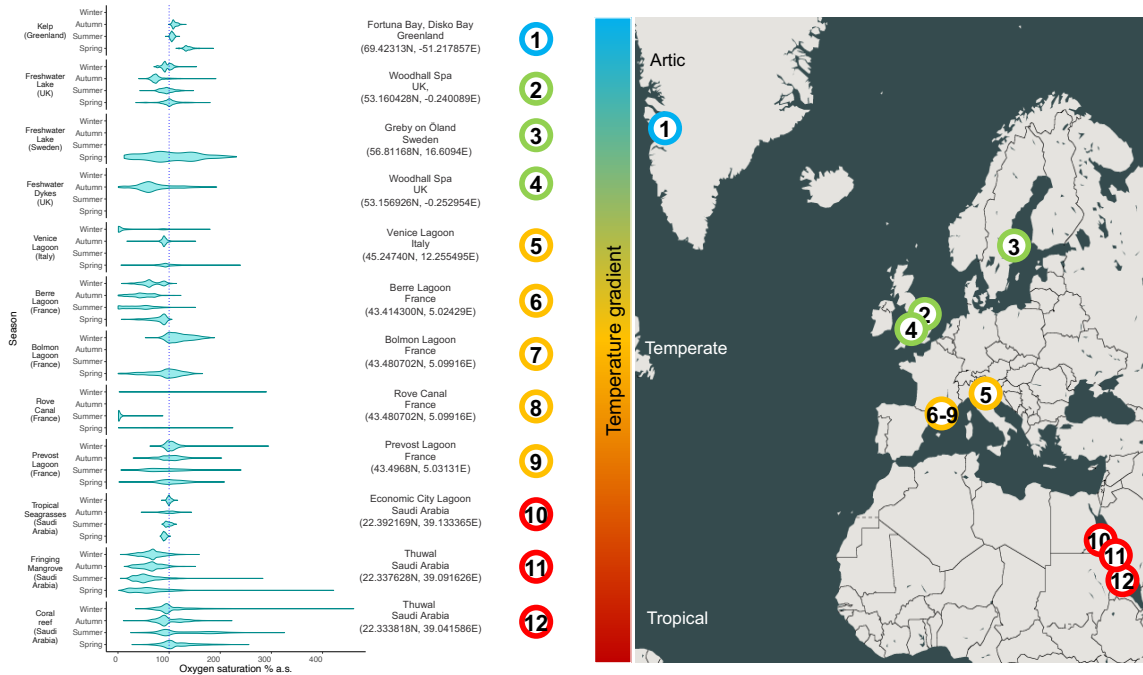
Figure captions

595

596 **Figure 1**. Range of oxygen saturations in several productive aquatic habitats. The dashed line represents

597 100% oxygen saturation. The violin plots report the densities of the frequencies of oxygen saturation

598 measured at each ecosystem across different seasons (based on data availability). Data source is specified

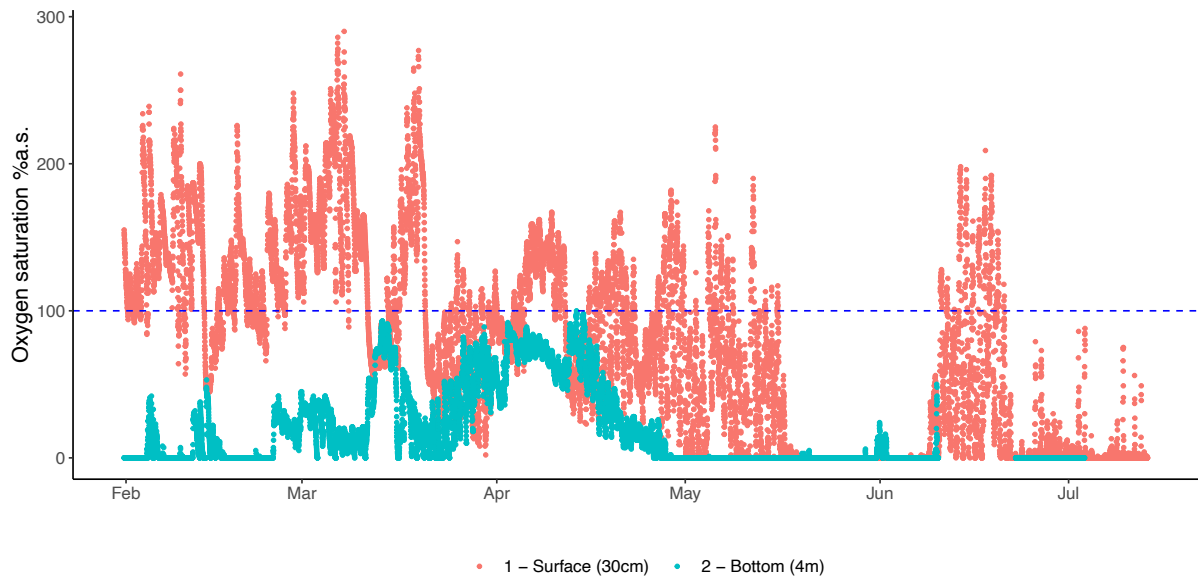
599 for each environment in the Supplementary Dataset for Figures 1 and 2.

600

601

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

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

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

605   to predict oxygen variation.

606

607

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

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

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

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

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

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

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

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

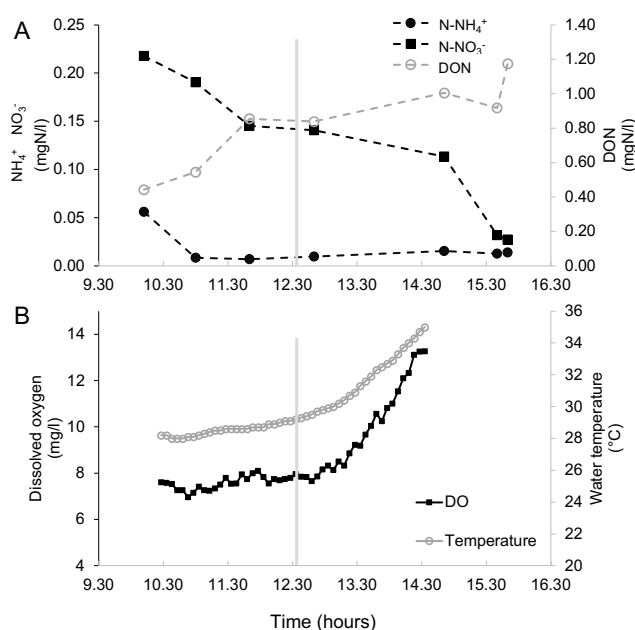
616 organic nitrogen related to the intense biological activity within the marsh. (**B**) Dissolved oxygen and

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

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

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

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

621

622

623 **Figure 4.** Scheme of the benthic biogeochemical cycle in relation to diel oxygen fluctuation. Relative

624 evolution of the bottom water chemical composition and evolution of the location of the most important

625 biogeochemical processes in the benthic compartment. Relative influence of external drivers on benthic

626 processes. Relative evolution of resulting flux direction and intensity. Note that the graphs are not drawn

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

628 represented as similar in this figure for simplification.

629

630

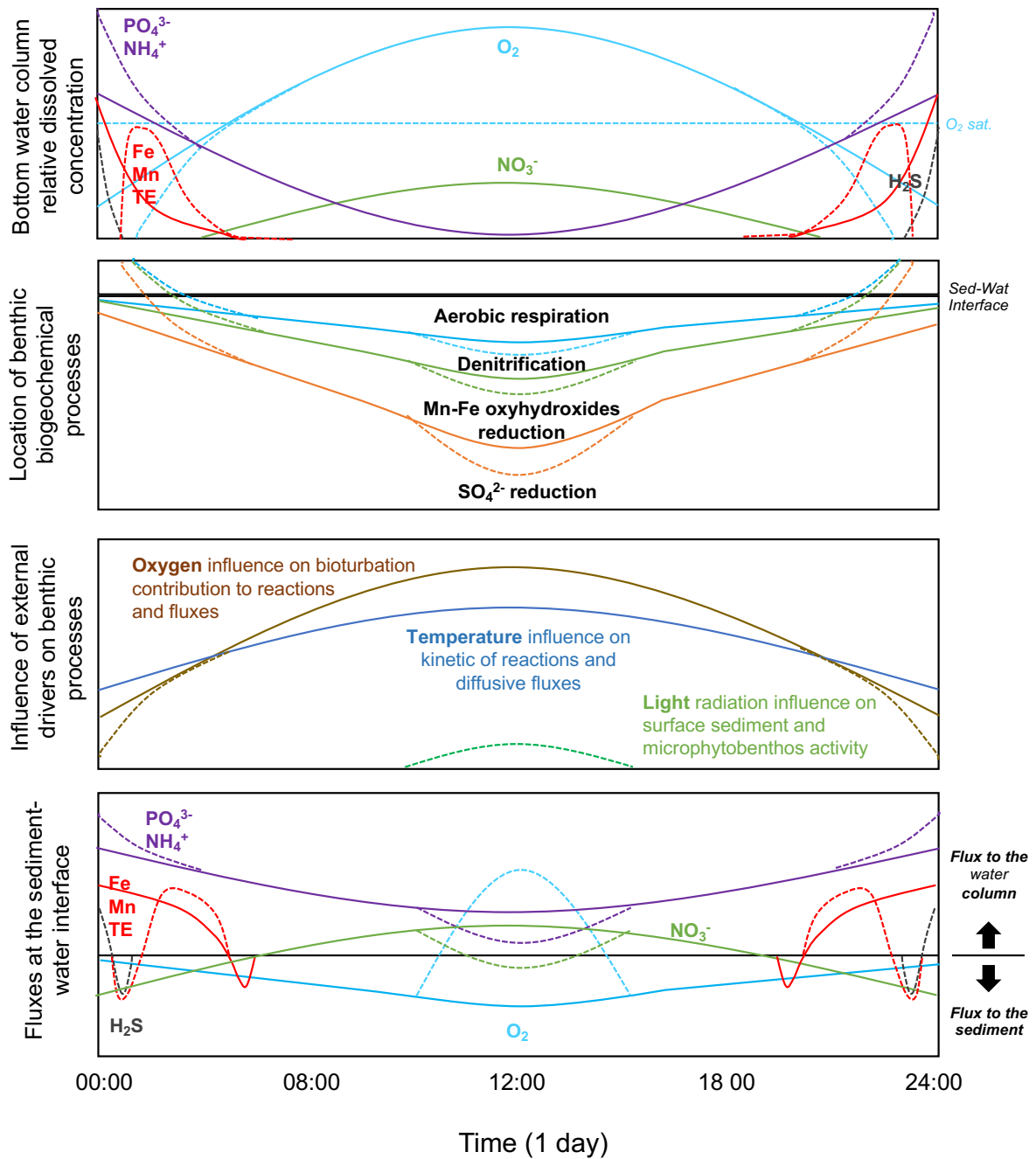



Figure 5. Daily bacterial community cycle scheme in relation to diel oxygen fluctuation. Relative shift of microbial community controlled by the oxygen availability that controls the ratio between aerobic and anaerobic taxa and their relative function. Oxygen fluctuation is important to determine the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