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Abstract:	Oxygen is critical for nearly all life on Earth, including aquatic species that breathe dissolved oxygen in both freshwater and marine systems. The rapid, global, and anthropogenic loss of dissolved oxygen known as 'aquatic deoxygenation' threatens life in these environments, the human communities that depend on them, and Earth system stability long-term. Recognizing the important and increasingly widespread effects of aquatic deoxygenation, scientists have proposed that it be added to the planetary boundary framework, which is designed to capture the wider envelope of Earth-system conditions that support a "safe operating space for humanity." Here, we argue that the planetary boundary framework should include maintenance of Earth's aquatic ecosystems and thus dissolved oxygen conditions. We synthesize important, in some cases poorly understood, interactions and feedbacks that exist between deoxygenation and all nine of the already-established planetary boundaries. We find that aquatic deoxygenation interacts with and extensively modulates other boundary processes, including climate change, nutrient loading, biodiversity loss, and aerosol loading. Subsequently, we identify and describe four indicators that can be used

	to assess the status of aquatic deoxygenation and eventually define a global boundary for it within the framework. Given these interactions and current rates of oxygen loss, we argue that aquatic deoxygenation is approaching an "unsafe space", with Earth-system impacts that are likely to be irreversible in our lifetimes. We discuss the wider societal significance of this research, including applications to the planetary boundary framework, future analyses, policy-making, and management.

Scientific Significance Statement Topic

This article is important, extremely timely, and likely to be of high interest to L&O readers. In it, we describe recent developments across the field of aquatic deoxygenation (AD) and expand on the perspective presented by Rose et al. (2024, Nat. Ecol. Evo.), where the authors (some of us included here) call for the addition of AD to the Planetary Boundary framework (Rockstrom et al., 2009; Richardson et al., 2023). The Planetary Boundary framework outlines nine distinct processes that support and exert pressure on Earth system stability, representing the theoretical envelope of â€˜safeâ€™ operating conditions required to maintain a stable, â€˜Holocene-likeâ€™ Earth and has become highly influential in planetary science, policy, and management. At present, AD is not included in the Planetary Boundary framework, but recently there has been interest in updating it to be more inclusive of aquatic processes. We anticipate that this article will be highly influential in guiding those discussions.

Scientific Significance Statement Outlet

L&O is also the best outlet for this publication because of its broad reach, high impact, open-access options, and cross-disciplinary readership. Aquatic Deoxygenation (AD) is global threat that poses serious consequences to life and biogeochemical function in both freshwater and marine systems, thus it is critical that experts from both limnology and oceanography engage with this topic and work to integrate AD into major sustainability frameworks going forward.

Abundant interactions and feedbacks between Aquatic Deoxygenation and the other Planetary Boundaries suggest "unsafe" levels of oxygen loss with far-reaching impacts

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ABSTRACT

Oxygen is critical for nearly all life on Earth, including aquatic species that breathe dissolved oxygen in both freshwater and marine systems. The rapid, global, and anthropogenic loss of dissolved oxygen known as 'aquatic deoxygenation' threatens life in these environments, the human communities that depend on them, and Earth system stability long-term. Recognizing the important and increasingly widespread effects of aquatic deoxygenation, scientists have proposed that it be added to the planetary boundary framework, which is designed to capture the wider envelope of Earth-system conditions that support a "safe operating space for humanity." Here, we argue that the planetary boundary framework should include maintenance of Earth's aquatic ecosystems and thus dissolved oxygen conditions. We synthesize important, in some cases poorly understood, interactions and feedbacks that exist between deoxygenation and all nine of the already-established planetary boundaries. We find that aquatic deoxygenation interacts with and extensively modulates other boundary processes, including climate change, nutrient loading, biodiversity loss, and aerosol loading. Subsequently, we identify and describe four indicators that can be used to assess the status of aquatic deoxygenation and eventually define a global boundary for it within the framework. Given these interactions and current rates of oxygen loss, we argue that aquatic deoxygenation is approaching an "unsafe space", with Earth-system impacts that are likely to be irreversible in our lifetimes. We discuss the wider societal significance of this research, including applications to the planetary boundary framework, future analyses, policy-making, and management.

INTRODUCTION

The planetary boundary framework, proposed by Rockström et al. (2009) and subsequently expanded by others (e.g., Steffen et al., 2015; Nash et al., 2017; Richardson et al., 2023), defines nine Earth-system processes that result from and constrain anthropogenic pressure to our biosphere. These processes – climate change, ocean acidification, land-use change, aerosol loading, stratospheric ozone depletion, disruption of biogeochemical flows, loss of biosphere integrity, freshwater use, and pollution of 'novel entities' – collectively delineate a "safe operating space for humanity," beyond which Earth-system function is at risk of abrupt, irreversible change (Rockström et al., 2009).

While the original framework is not particularly prescriptive about how society should respond to Planetary Boundary changes, subsequent analyses have used it to identify "safe and just corridors" of action (Rockström et al., 2021) and to propose sustainable development pathways (e.g., O'Neill, 2018). Consequently, the planetary boundary framework has become a widely used scientific and policy shorthand for invoking and evaluating multiple anthropogenic stressors at once. References to the framework have become particularly common in global management documents and sustainability objectives (e.g., World Business Council for Sustainable Development – Vision 2050; Pörtner et al., 2021) as well as international laws and treaties (e.g., French and Kotzé, 2021).

At the same time, the value of the planetary boundary framework as an integrative synthesis tool continues to evolve. For example, it has motivated research on diverse topics such as sustainable development (O'Niell et al., 2018), marine plastic pollution (Villarrubia-Gomez et al., 2024), and ocean acidification (Findlay et al., 2025); and efforts to modify the planetary boundary framework and better integrate marine and aquatic ecosystems are ongoing (Nash et al., 2017; S. Mathesius unpubl.). Like other Earth-system frameworks, it serves as a unifying

structure for connecting diverse processes that allows scientists to identify shared drivers, feedbacks, and coupled systemic risks that may not be immediately obvious when stressors are considered in isolation. By summarizing multi-scale observations into a more coherent assessment of Earth-system stability and vulnerability, using 'control variables' as proxies for global, planetary-scale change, the framework helps to support complex inferences about the Earth system as a whole.

In this context, scientists have called for the inclusion of aquatic deoxygenation as a tenth Planetary Boundary (Ferrer et al., 2023; Rose et al., 2024; Ferrer & Pezner et al., 2025). Aquatic deoxygenation refers to the rapid, anthropogenic loss of dissolved oxygen occurring across Earth's lakes (Jane et al., 2021), rivers (Zhi et al., 2023), coastal ecosystems (Brietburg et al., 2018), and open ocean (e.g., Levin, 2018). Aquatic deoxygenation is largely driven by global warming, nutrient loading, reduced physical mixing, and changes in interior ventilation – however, the control variables used to describe these processes within the planetary boundary framework do not entirely explain observed patterns of oxygen loss, nor their effects on Earth System stability. This suggests that while aquatic deoxygenation is not entirely orthogonal to other planetary boundaries, it is also not synonymous with any of them nor redundant within the framework, which motivates the case for treating it as a distinct boundary process (Rose et al., 2024; Ferrer & Pezner et al., 2025).

It is important to distinguish here between low dissolved oxygen (DO) as a potentially natural state and aquatic deoxygenation as an anthropogenically-driven process. Some ecosystems are consistently low in DO and have persisted that way for millennia, while others experience perfectly natural periods of oxygen deprivation (e.g., Levin, 2003; Cox & Gillis, 2020; Gallo et al., 2020). The biogeochemistry of these environments reflects their low-oxygen

legacy, and organisms who live there are typically well-adapted for life under consistent or passing low-DO conditions (see Roman et al., 2024). Thus, we define aquatic deoxygenation as – specifically – the modern-era, anthropogenic *loss* of average dissolved oxygen in both freshwater and marine environments (Keeling et al., 2010).

Across Earth's aquatic systems, DO losses have been substantial over the 20th century (Schmidtko et al., 2017; Breitburg et al., 2018; Levin, 2018; Jane et al., 2021; Zhi et al., 2021), threatening ecosystem stability and, potentially, planetary-scale changes in climate. In the global ocean, DO levels have declined by about 2% on average over the last 50 years (Schmidtko et al., 2017), with pronounced losses in the midwaters, surrounding the poles, the Southeast Atlantic, the Indian Ocean, and parts of the Northern and Equatorial Pacific (Levin, 2018). More than 200 sites now experience persistent hypoxia conditions < 2 mg O_2 / L (Breitburg et al., 2018), while riverine oxygen declines are estimated at a rate of 1–1.5% per decade (Zhi et al., 2021). Oxygen losses have been greatest in lakes, with temperate shallow and deep lakes having exhibited declines upwards of 1.5–5% per decade (estimated from Jane et al., 2021).

In this article, we expand on the points previously presented by Rose et al. (2024), followed by Ferrer & Pezner et al. (2025), to argue that aquatic deoxygenation should be considered within the planetary boundary framework by responding to three major questions that arise from this assertion. First, how does aquatic deoxygenation interact with the other nine Earth system processes (i.e., 'boundaries') articulated by the framework? Second, what metrics can we use to monitor aquatic deoxygenation and eventually define a global boundary? And third, does global DO decline indicate that we are on a trajectory toward "unsafe" levels of change? While developing a fully quantitative global boundary for aquatic deoxygenation will require extensive synthesis of oxygen observations that is beyond the scope of this paper, we detail aquatic

deoxygenation's interactions and feedbacks with other boundary processes (**Figure 1**; **Table 1**) to assert that current rates already exceed levels that most would consider safe. We conclude by outlining how this research can be used to effect positive management and policy outcomes that might mitigate the harmful effects of deoxygenation across scales, including the eventual integration of aquatic deoxygenation into the planetary boundary framework.

DRIVERS, INTERACTIONS, AND FEEDBACKS WITH OTHER PLANETARY BOUNDARIES

Climate change and stratospheric ozone depletion

As a general rule, oxygen solubility in water decreases as temperature rises. Since the Industrial Revolution, the ocean (and other bodies of water) has absorbed over 90% of the total excess heat trapped in our atmosphere by anthropogenic greenhouse gases (IPCC, 2019), while the solubility and partial pressure of elemental oxygen (O_2) has declined (Oschlies et al., 2018; IPCC, 2019). About 50% of contemporary upper-ocean (≤ 1000m) oxygen losses can be attributed to temperature changes in oxygen solubility (Schmidtko et al., 2017). Thus, a well-known feature of climate model projections is that the extent to which aquatic deoxygenation will progress in our lifetimes depends directly on our ability to mitigate greenhouse gas emissions (Keeling et al 2010; Bopp et al., 2013; Kwiatkowski et al 2020).

Under RCP / SSP5–8.5, projected global average air temperatures will warm by an additional 3.7°C by the end of the century, average sea surface temperatures will warm by 2.6°C (IPCC, 2019), and the rate of deoxygenation in the subsurface ocean (100–600m) is projected to triple (-13.3 mmol/m^3; Kwiatkowski et al., 2020). Implementation of stringent climate-change

mitigation strategies would help slow these changes, but we are committed to others. Under RCP / SSP1–2.6, oxygen loss continues at a much slower rate and average subsurface ΔDO would potentially stabilize at -6.4 mmol/m^3, closer to today's rate of -4.5 mmol/m^3 (Kwiatkowski et al., 2020). In the deep ocean, meanwhile, the legacy effects of contemporary emissions, warming, and slow ocean circulation, mean deoxygenation will continue for millennia.

Change in oxygen solubility remains one of the clearest links between climate change and aquatic deoxygenation, however, temperature alone does not perfectly predict the behavior, spatial patterning, nor severity of DO losses. There exists a myriad of physical, biogeochemical, and biological processes that differentially partition heat throughout the world's hydrosphere and give rise to heterogeneous changes in DO, creating surprising deoxygenation hotspots with above-average rates of loss (Breitburg et al., 2018; Levin, 2018; Kwiatkowski et al., 2020). Increased stratification, for instance, is a major driver of DO dynamics in both freshwater and marine systems and is likely to increase under climate change, limiting oxygen exchange between water masses (e.g., Oschlies et al., 2018). Meanwhile, climate-induced changes in upwelling and water transport could lead to the expansion of Oxygen Minimum Zones (OMZs) in some regions, while redistributing oxygen and partially dampening deoxygenation in others (Oschlies et al., 2018; Busecke et al., 2022).

Additionally, aquatic deoxygenation may alter the ability of aquatic habitats to aerobically metabolize organic matter, with knock-on effects to climate regulation and the integrity of Earth's Stratospheric Ozone boundary. Declining O_2 is associated with increased denitrification and the production of nitrous oxide (N_2O) (Battaglia and Joos, 2017; Schmidtko et al., 2017) – a potent greenhouse gas that will deplete ozone [O_3]. The production of N_2O is strongly sensitive to oxygen levels within the OMZ, where low-oxygen regions account for the

large majority of N_2O production from the world's oceans (Bange et al., 2010). Any expansion of OMZs may increase the production of N_2O and emissions into the atmosphere, which in turn would exacerbate both global warming and ozone loss. The magnitude of this feedback and time horizon for resultant changes in N_2O from declining DO is still poorly understood and likely to be long (Bange et al., 2010; Battaglia and Joos, 2017; Busecke et al., 2022). Nevertheless, N_2O production is currently recognized as the top contributor to stratospheric ozone depletion (Portmann et al., 2012), and the interaction between it and aquatic deoxygenation represents a distinct biogeochemical feedback that one need consider when deciding what constitutes "safe" levels of change.

Aquatic deoxygenation can also lead to positive feedback loops that drive the production of other greenhouse gases, like methane (Żygadłowska et al., 2024), aerosols, or aerosol precursors, like hydro sulfuric acid (Slomp, 2013) – all of which bear direct links to climate. In deeper parts of the Baltic and Black Sea, for instance, extremely low oxygen conditions create 'euxinic' waters, characterized by anoxia (no oxygen) and hydrogen sulfide (Slomp, 2013). Anoxia supports microbial production of methane (CH_4) – a potent greenhouse gas – through methanogenesis, while hydrogen sulfide gas (H_2S) is highly toxic to humans and most aerobic aquatic macrofauna. H_2S is oxidized in the atmosphere to form sulfur dioxide (SO_2) and subsequently sulfuric acid and sulfate aerosols that can have a cooling effects on Earth's climate. While euxinia is not common on today's Earth, nor do we expect it to become widespread in our lifetimes, it is worth considering the climate impacts that aquatic deoxygenation might have in systems predisposed to this biogeochemical state.

Biogeochemical flows

Evidently, aquatic deoxygenation is closely tied to several of Earth's biogeochemical cycles and flows, including iron, silicon, and sulfur – but here, we focus on nitrogen (N) and phosphorus (P), the main flows described in the planetary boundary framework. Since the invention and widespread commercial use of synthetic fertilizers over the last century, flows of N and P have been *significantly* altered by human activities, likely surpassing safe levels of change over a decade ago (Rockström et al., 2009; Steffen et al., 2015; Richardson et al., 2023).

In coastal waters, deoxygenation is closely tied to nutrient-loading of N and P via terrestrial runoff through eutrophication, where excess nutrients lead to hyperactive primary production and microbial respiration of organic matter depletes the surrounding waters of oxygen while producing carbon dioxide (CO_2) (as was acknowledged by Rockström et al., 2009). Eutrophication can be episodic, such as when it rains and fertilizers are swept off the land and into the water; seasonal, e.g., due to summer warming; or effectively constant, e.g., due to groundwater seepage (IUCN, 2019). Eutrophic conditions can persist for months to years, particularly in bodies of water with restricted turnover (Carpenter, 2005) or in areas where nutrient injections are effectively constant, as is the case for many freshwater tributaries, wetlands, and river deltas (e.g., Rabalais et al., 2002).

While nutrient loading can lead to aquatic deoxygenation, aquatic deoxygenation affects nutrient cycling by altering the chemical conditions under which fundamental biogeochemical processes play out. These feedbacks are complex, and consequently, it is not entirely clear how the chemical equilibrium of Earth's aquatic habitats will adjust in response to the widespread loss of DO (Battaglia and Joos, 2017; Busecke et al., 2022). This uncertainty arises in part because the remineralization of organic matter into its simplest inorganic forms can take place

through various biogeochemical pathways that are oxygen-, temperature-, salinity-, and pressure-dependent.

One illustration of this complexity lies in how remineralization pathways shift under low-oxygen conditions. When DO is low, the process of remineralization typically occurs through denitrification, representing a loss of fixed nitrogen. This has distinct consequences for the growth and survival of primary producers who use fixed nitrogen to build their amino acids (Bianchi et al., 2012; IUCN, 2019). Simultaneously, excess loading of organic and inorganic P can drive the release of more P from anoxic sediments (Watson et al., 2017), which could actually *stimulate* primary productivity as well as N fixation and bacterial respiration (Niemeyer et al., 2017; Oschlies et al., 2018). On net, this could counteract some of the fixed-N losses borne from elevated rates of denitrification *or* exacerbate eutrophication while driving a reinforcing (positive) feedback loop of declining oxygen (Niemeyer et al., 2017; Oschlies et al., 2018). Continued investigation into these types of biogeochemical feedbacks will be critical for understanding the effects of aquatic deoxygenation on biogeochemical flows and vice versa.

Biodiversity ('Biosphere Integrity')

Aquatic deoxygenation poses severe risks to biodiversity – what the planetary boundary framework refers to as 'Biosphere Integrity'. Severe oxygen depletion poses an acute risk of asphyxiation to most organisms that breathe underwater, and occasionally we are confronted with its lethal effects in the form of mass fish kills and coastal 'dead zones'. A striking example comes from video footage shared by the Oregon Department of Fish and Wildlife (2017), where live Dungeness crabs (*Metacarcinus magister*) caught in a trap go from living and eating normally to deceased in the span of just of few days due to sudden declines in DO. Partial

oxygen losses can also result in physiological stress and important ecological changes, such as reductions in functional integrity (e.g., reducing sediment bioturbation and carbon cycling; Roman et al., 2024).

Even minor decreases in DO can have negative consequences on biodiversity through changes in ecophysiology. To give just a few examples, low oxygen levels have been shown to negatively affect the growth, survival, and abundance of organisms at virtually every level of the food web (Roman et al., 2024). Effects have been documented for zooplankton (e.g., Roman et al., 1993), bivalves (e.g., Gobler et al., 2014), cephalopods (e.g., Navarro et al., 2018), crustaceans (e.g., McCormick et al., 2019), corals (e.g., Pezner et al., 2023), benthic fishes, pelagic fishes (e.g., Stramma et al., 2012; Vedor et al., 2021) and others. Likewise, declines in oxygen have been shown to alter animals' reproductive fitness (Thomas et al., 2007), their susceptibility to disease (Lehmann et al., 2016; Roman et al., 2024), food web dynamics (Roman et al., 2024), ability to orient, and even see (McCormick et al., 2019).

Evidence from the paleo record and modern-day OMZs suggests that the threat of aquatic deoxygenation very likely scales up from individual organisms to entire ecosystems (Roman et al. 2024). Paleo evidence also suggests a close link between major anoxic events of the past and mass extinction: at least two of Earth's previous mass extinction events have been directly linked to periods of low ocean oxygen content or high DO variability (Keeling et al., 2010; Watson et al., 2017; Stockey et al., 2021; Kozik et al., 2022). These findings are, to a certain extent, corroborated by survey data from inside and outside of contemporary OMZs, suggesting that species diversity and evenness are inversely related to DO (e.g., Sperling et al., 2016; Gallo et al., 2020). In other words, as DO declines, so does organismal diversity and evenness, and only a few oxygen-resistant species reign supreme (Levin, 2003; IUCN, 2019; Gallo et al., 2020).

Within the planetary boundary framework, Biosphere Integrity is defined by genetic diversity and functional integrity (Rockström et al., 2009; Steffen et al., 2015; Richardson et al., 2023). Genetic diversity refers to the composition and abundance of genes contained within populations, whereas functional integrity refers to the composition, abundance, and intactness of functional traits represented within an ecosystem. (Examples of functional traits include ability to photosynthesize, calcify, burrow, break down waste, *etc.*) Equipped with various lines of evidence, it is virtually certain that modern-day aquatic deoxygenation will exacerbate our current ecological crisis and interact with the Biosphere Integrity boundary by decreasing both genetic and functional diversity.

Ocean acidification

Ocean acidification (OA) refers to the decline in seawater pH caused by the uptake and dissolution of anthropogenic carbon dioxide (CO_2) emissions at the ocean's surface. Although this phenomenon has been most studied in marine systems, evidence suggests that anthropogenic CO_2-driven acidification also occurs in freshwater systems (e.g., Weiss et al., 2018). Dissolved CO_2 increases the concentration of dissolved hydrogen ions (H^+) which lowers the pH of the surrounding water and alters carbonate chemistry.

Low pH conditions can also be naturally associated with low DO due to the tightly coupled relationship between photosynthesis and respiration. Photosynthesis consumes CO_2 and produces O_2, whereas respiration and microbial remineralization consume O_2 and release CO_2. When nutrients are added – through natural or anthropogenic processes – primary productivity often increases, followed by respiration that reduces oxygen and pH (e.g., during upwelling; Kekuewa et al., 2022; Kroeker et al., 2023).

288 The ecological consequences of low oxygen and low pH appear strongly context-
289 dependent. In areas with coastal upwelling, for instance, where nutrients are typically high, DO
290 and pH are low, and temperatures are cool, we observe non-uniform and occasionally positive
291 physiological outcomes among organisms (e.g., Navarro et al., 2018; Donham et al., 2023).
292 Meanwhile, model evidence suggests that future OA and deoxygenation might decrease primary
293 productivity on net, mediated by an increase in temperature (Kwiatkowski et al., 2020). The
294 long-term biogeochemical and ecological effects of acidification on deoxygenation are not well
295 known, but their interaction is largely predicted to have negative effects at the organismal-level
296 (e.g., Gobler et al., 2014; Gobler & Baumann, 2016), highlighting the importance of studies
297 aimed to disentangle the effects of low pH from low oxygen and / or covarying stressors.

298

299 *Land-system change and impacts on climate regulation*

300 Land-system change is defined by Steffen et al. (2015) as the area of forested land as a
301 percent of original forest cover, where modifications such as agricultural development,
302 desertification, and urbanization are all cited as major contributors to terrestrial land-system
303 change. Nash et al. (2017) later expanded the definition to include changes in the aquatic
304 environment, renaming the boundary 'Earth-surface change' to account for habitat alterations in
305 aquatic ecosystems that affect biodiversity and climate. They cite the deforestation of mangroves
306 and disturbance of seafloor sediments as two notable examples of Earth-surface change.

307 Within this expanded framing, it is important to consider whether large-scale alterations
308 to ocean oxygen availability may operate in a similar way. Land-system changes that impact
309 climate regulation, including the development of widespread agriculture, clearly interact with
310 oxygen and have effects on aquatic deoxygenation. Simultaneously, given ocean

311 deoxygenation's potential to impact climate regulation in the long-term, we argue that aquatic
312 deoxygenation might be considered a type of land-system change in and of itself.

313 Because declining oxygen availability impacts habitat degradation and fragmentation, it
314 is not difficult to imagine potential impacts on carbon cycling and, by extension, climate
315 regulation. For instance, ocean deoxygenation has quickly altered habitat availability for pelagic
316 and semi-pelagic organisms that traverse or spend time near the OMZ (IUCN, 2019). Oxygen
317 limitation of vertical migrations by mesopelagic organisms could reduce vertical carbon transfer
318 into deep water and sequestration through the biological carbon pump (Bianchi et al., 2021).

319 Likewise, animals such as large predatory fishes tend to have high metabolic demands
320 and will typically avoid low-oxygen areas when hunting, which could impact sinking carbon. As
321 aquatic deoxygenation progresses, suitable foraging habitat for these animals is likely to contract,
322 forcing shifts in their distributions and behaviors. Large, commercially-important fish may
323 congregate nearer to the surface of the ocean or closer to shore (e.g., Craig, 2012; Stramma et al.,
324 2012; Vedor et al., 2021), increasing their vulnerability to other anthropogenic stressors, like
325 overfishing (Stramma et al., 2012; Vedor et al., 2021). Meanwhile, a reduction in midwater
326 biomass resulting from changes in behavior and / or fishing mortality may in turn decrease the
327 amount of organic matter flux into the deep sea (Mariani et al., 2020; Bianchi et al., 2021). Thus,
328 as low-oxygen zones expand, overfishing could increase, and carbon sequestration driven by
329 large fish sinking may decrease (Mariani et al., 2020; Bianchi et al., 2021).

330 If these relationships hold true, then aquatic deoxygenation impacts on habitat may be
331 similar to a forest shrinking in terms of degradation and loss of climate-regulating services.
332 Advancing both basic and applied research on the biological carbon pump will be critical for
333 resolving the relationship between it, climate regulation, and aquatic deoxygenation.

334

335 *Aerosol loading, with ties to climate regulation*

336 Atmospheric aerosol loading represents a critical, often underappreciated, link between
337 anthropogenic pollution, climate regulation, and aquatic deoxygenation. Aerosols such as sulfate
338 (SO_4^{2-}) and black carbon directly alter Earth's radiative balance by deflecting, absorbing, and
339 scattering solar energy while modifying biogeochemical pathways (whose full extent we are only
340 beginning to understand).

341 Some aerosols cool land and water through their direct reflection of shortwave irradiance
342 from the Sun, increasing O_2 solubility and modifying stratification in the upper water column
343 (Frölicher et al. 2009; Eddebbar et al., 2019). This is supported by modeling studies that indicate
344 a contemporary slow-down of ocean deoxygenation following major volcanic eruptions
345 (Eddebbar et al., 2019; Fay et al., 2023). These studies also suggest that the external forcing from
346 volcanic aerosols has shielded our atmosphere from additional heating and very likely *added*
347 oxygen into the ocean's interior (Eddebbar et al., 2019; Fay et al., 2023).

348 In contrast, aerosol-driven biogeochemical feedbacks can *decrease* oxygen and intensify
349 deoxygenation via changes in primary productivity and respiration. Atmospheric deposition of
350 aerosol-bound micronutrients promotes primary productivity at the surface, increased organic
351 carbon export, and enhanced microbial respiration at depth. For instance, accelerated oxygen
352 losses observed in the Pacific Ocean basin since the 1970s have been linked to an increase in
353 iron deposition borne from various anthropogenic aerosol sources (Ito et al., 2016). Similarly, the
354 increasing prevalence of large wildfires may alter DO dynamics in freshwater systems and
355 coastal areas due to increased deposition of iron and ash (e.g., Wall et al., 2023), although
356 emerging aerosol-deoxygenation feedbacks like this one remain poorly resolved. Continued

research into these competing effects will be critical as Earth's climate and weather regimes evolve.

Novel entities

Evidence suggests that the pollution by novel entities, particularly plastics, may alter biogeochemistry and biology in that ways that affect DO dynamics through the biological carbon pump (Villarrubia-Gómez et al., 2024).

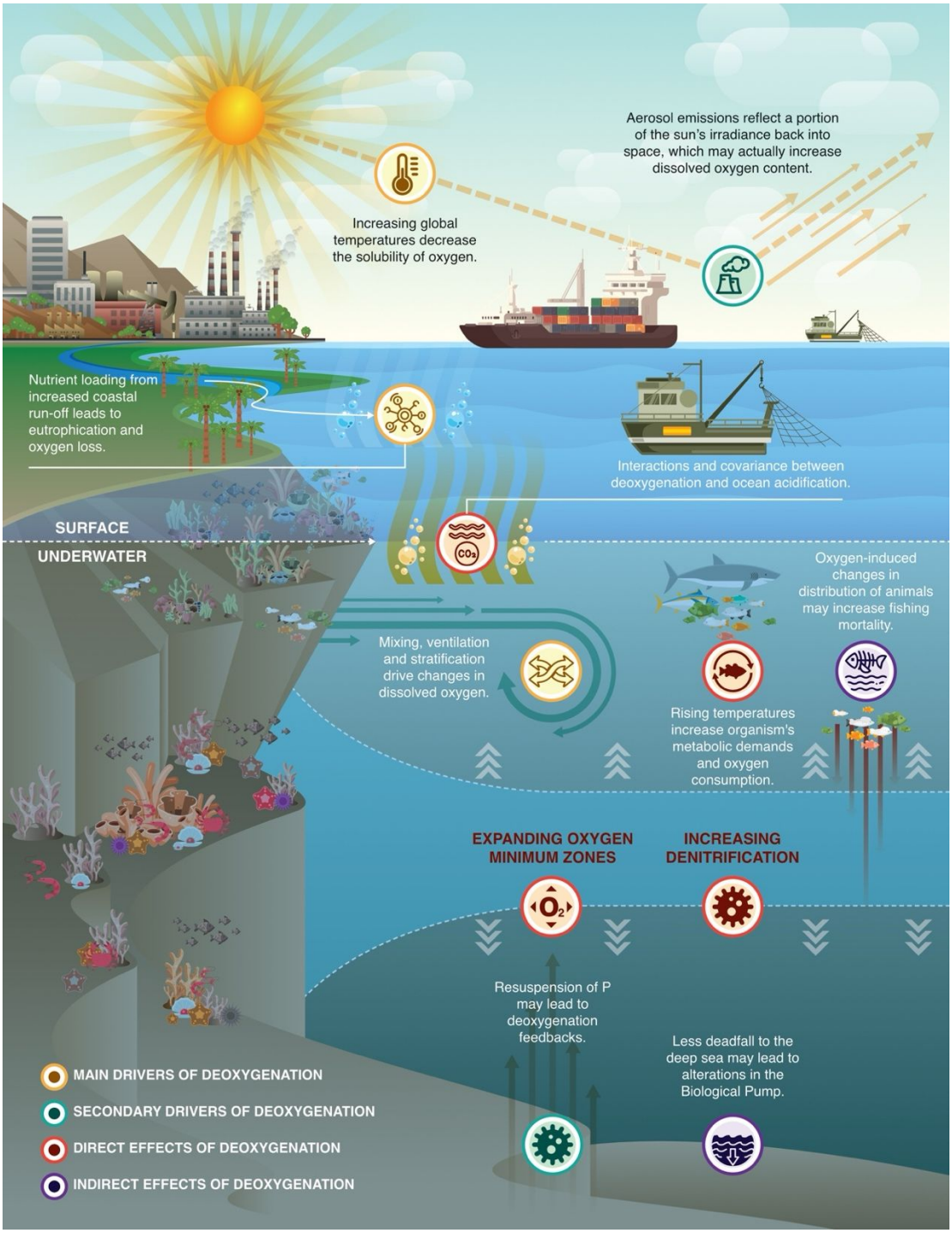
One example comes in the form of microplastic-induced changes to ocean food webs that could draw down oxygen on net (Kvale et al., 2021). Model evidence from Kvale et al. (2021) suggests that in areas where macronutrients do not limit primary productivity, organic particle remineralization may increase due to plastic-mediated shifts in zooplankton versus phytoplankton. Specifically, microplastics may satiate zooplankton and decrease their overall grazing pressure on phytoplankton. Consequently, organic carbon export of phytoplankton out of the euphotic zone and into the deep sea is projected to increase along with rates of remineralization and respiration at-depth.

Further research on nutrient-phytoplankton-zooplankton dynamics and the biological carbon pump in an increasingly plastic-polluted world will help clarify the reality and magnitude of this feedback. Likewise, research into other novel entities may reveal new or additional interactions between aquatic deoxygenation and pollution of other novel entities.

Freshwater change

Aquatic deoxygenation has the potential to interact with the 'freshwater change' boundary by altering the conditions under which ecosystems function. Changes in microbial respiration and remineralization provide one example of this. Many of the aquatic deoxygenation biogeochemical dynamics we have described thus far also apply to sediments and wet or submerged soils, which can be oxic, hypoxic, suboxic, or anoxic. In submerged sediments, anoxia is common, but critically-important ecological processes play out in the first few partially-oxygenated millimeters. As oxygen declines, so does the abundance of multi-cellular life, but aerobic infauna, such as worms and crustaceans typically bioturbate and help to deliver oxygen to microbes. Low oxygen can decrease the rate of bioturbation (Sturdivant et al., 2012; Roman et al., 2024), which can affect sediment redox chemistry and decrease rates of remineralization (Aller & Cochran, 2019). It is therefore easy to imagine how aquatic deoxygenation might induce changes in freshwater quality associated with changes in biology and biogeochemistry.

392 **Figure 1.** A diagram showing some of the key interactions that exist between aquatic
393 deoxygenation and the other planetary boundaries, including primary and secondary drivers and
394 effects. Here, emphasis is placed on interactions that occur in the marine environment, however,
395 similar interactions are also known to take place in freshwater systems. A comprehensive
396 summary of interactions and feedbacks is presented in **Table 1**.


Aerosol emissions reflect a portion of the sun's irradiance back into space, which may actually increase dissolved oxygen content.
Increasing global temperatures decrease the solubility of oxygen.
Nutrient loading from increased coastal run-off leads to eutrophication and oxygen loss.
Interactions and covariance between deoxygenation and ocean acidification.
SURFACE
UNDERWATER
Oxygen-induced changes in distribution of animals may increase fishing mortality.
Mixing, ventilation and stratification drive changes in dissolved oxygen.
Rising temperatures increase organism's metabolic demands and oxygen consumption.
EXPANDING OXYGEN MINIMUM ZONES
INCREASING DENITRIFICATION
Resuspension of P may lead to deoxygenation feedbacks.
Less deadfall to the deep sea may lead to alterations in the Biological Pump.
MAIN DRIVERS OF DEOXYGENATION
SECONDARY DRIVERS OF DEOXYGENATION
DIRECT EFFECTS OF DEOXYGENATION
INDIRECT EFFECTS OF DEOXYGENATION

399 **Table 1.** Summary of key interactions and feedbacks that exist between aquatic deoxygenation
400 and the other planetary boundaries. Several of these are depicted in **Figure 1**.

Other Planetary Boundary	Key Interactions and Feedbacks with Aquatic deoxygenation
Climate Change	Warming reduces oxygen solubility and alters physical mixing, including ventilation and stratification processes, which lead to aquatic deoxygenation. Conversely, aquatic deoxygenation can feedback to climate and stratospheric ozone depletion via changes in biogeochemical cycling and enhanced production of nitrous oxide (N_2O).
Stratospheric Ozone Depletion	aquatic deoxygenation is likely to expand Oxygen Minimum Zones (OMZs), enhancing the microbial production and emissions of nitrous oxide (N_2O), a potent greenhouse gas and ozone depletor.
Biogeochemical Flows	Excess nitrogen (N) and phosphorus (P) loading drives eutrophication and aquatic deoxygenation across aquatic ecosystems. Conversely, aquatic deoxygenation alters N and P cycling in complex ways – for example, aquatic deoxygenation-induced denitrification reduces fixed N, while internal P resuspension can stimulate primary productivity, partially offsetting N losses but depleting oxygen.
Biosphere Integrity	aquatic deoxygenation can lead to biodiversity loss and disruptions in ecosystem function by decreasing genetic and functional diversity. Oxygen losses affect organisms across all trophic levels and pose both lethal and non-lethal risks.
Ocean Acidification	aquatic deoxygenation and ocean acidification often co-occur due to coupled biological and biogeochemical processes, including

	photosynthesis and respiration. Nutrient-driven increases in respiration tend to reduce oxygen and lower pH, and their combined effects can negatively impact organisms.
Land-System Change	Increased nutrient runoff, sediment disturbance, and habitat degradation associate with land-system change in freshwater and coastal systems contribute to aquatic deoxygenation. Conversely, aquatic deoxygenation may itself act as a form of land-system change by reducing aerobically viable habitat and altering carbon sequestration through modifications to the biological carbon pump.
Aerosol Loading	Aerosols have complex, sometimes competing effects on aquatic deoxygenation. Deposition of aerosolized micronutrients can accelerate oxygen loss by stimulating primary productivity and microbial respiration, while aerosol-driven climate cooling can mitigate dissolved oxygen losses.
Pollution of Novel Entities	Interactions between aquatic deoxygenation and pollution of novel entities are understudied but potentially far-reaching. Microplastics and other pollutants may alter food webs and biogeochemical processes, potentially decreasing oxygen availability on net.
Freshwater Change	aquatic deoxygenation may affect freshwater change by altering ecosystem function and biogeochemistry, including changes in sediment bioturbation and remineralization.

401

DEOXYGENATION INDICATORS AND POTENTIAL 'CONTROL VARIABLES'

Integrating aquatic deoxygenation into the planetary boundary framework requires the identification of robust oxygen indicators and, ultimately, what the planetary boundary framework calls 'control variables'. Oxygen indicators are metrics that can be used to track environmental change, evaluate risk, and establish targets for mitigation and adaptation (Roman et al., 2024). They are essential for quantifying trends and enabling consistent assessment across temporal and spatial scales. Meanwhile, control variables represent a specific type of indicator designed to track change at the planetary scale. Their primary purpose is to capture the risk of crossing a planetary boundary by quantifying progress towards "safe" versus "unsafe" levels of global change.

Control variables are used to determine how close an Earth-system process is to triggering an undesirable and potentially irreversible response, though they tend to oversimplify changes at smaller scales by averaging out change across habitat types. In the case of climate change, for example, both the 'atmospheric concentration of carbon dioxide (parts per million)' and the 'amount of energy imbalance present at the top of our atmosphere (Watts / m^2)' are used as control variables because they integrate process-level change at the planetary scale (Rockström et al., 2009; Steffen et al., 2015; Richardson et al., 2023). These proxies are powerful for assessing global change, but tell us relatively little about the extent and effects of climate change locally. In this respect, control variables are often of limited use for regional or local applications, while local indicators can be difficult to scale up.

Below, we present four indicators that can be used to monitor oxygen in the aquatic environment at various geographic scales and which could eventually be used to define a global control variable and boundary for aquatic deoxygenation. These indicators include dissolved

425 oxygen concentration and the prevalence of anoxia or hypoxia; percent oxygen saturation (%
426 DO); the presence, absence, and change among indicator taxa; and the ratio of oxygen supply-to-
427 demand, known as the Metabolic Index (Φ). We discuss the strengths and limitations of each
428 indicator, including factors that might enable or constrain its application as a control variable
429 within the Planetary Boundary context (**Table 2**).

430

431 **Table 2.** Proposed aquatic deoxygenation indicators describing their strengths, weaknesses and
432 potential use as oxygen planetary boundary control variables.

Indicator	Strengths and Weaknesses	Potential Use as a Control Variable
Dissolved oxygen concentration (prevalence of anoxia or hypoxia)	**Strengths:** • Accepted thresholds for hypoxia and anoxia • Extensive observational datasets exist to support this indicator • Captures important changes to biogeochemistry and, to a certain extent, the impacts of low oxygen on organisms • Paleo proxies exist for hypoxia and anoxia **Weaknesses:** • Observational datasets are somewhat biased in their geographic and depth coverage • Does not capture the high spatial and	Could serve as a control variable for aquatic deoxygenation by quantifying areas of hypoxia and anoxia in freshwater and marine systems worldwide. Synthesis and modeling efforts will be required for application.

	temporal variability of oxygen vary by species, ecosystem, and region • Tolerance to low-oxygen conditions varies by species, per ecosystem and region; For example, OMZ species which have evolved under persistent low oxygen are more tolerant than estuarine species which experience seasonal hypoxia	
Percent O_2 Saturation (% DO)	**Strengths:** • Accounts for temperature, salinity, and pressure effects on oxygen 'breathability' – providing important biological context • Can be converted to measure of DO concentration or O_2 partial pressure • Intuitive and easy to interpret compared to O_2 partial pressure **Weaknesses:** • Requires additional measurements of environmental parameters: temperature, salinity, and pressure • Important % DO thresholds vary by species, ecosystem, and region • Does not capture the high spatial and temporal variability of oxygen	Could serve as a control variable for aquatic deoxygenation by integrating oxygen availability with temperature, salinity, and pressure data across freshwater and marine systems. Application would require data synthesis and modeling, as well as additional research to define ecologically meaningful % DO thresholds.

Indicator Taxa	**Strengths:** • Closely reflects the biological responses of oxygen availability • Applicable even when direct measurements of DO are lacking • Can be monitored at low- or no-cost and using a variety of techniques, such as taxonomic sampling, telemetry, acoustics, fisheries-dependent data, or local ecological knowledge **Weaknesses:** • Generally requires some baseline ecological knowledge • Is ecosystem-specific and species-specific, with a few important exceptions • May not capture short-term changes in oxygen	Could serve as a control variable for aquatic deoxygenation by tracking the presence and abundance of an agreed-upon list of oxygen-sensitive taxa. Application would require synthesis of species-specific oxygen tolerances and ecosystem-specific thresholds, and some agreement as to which species are reliable or meaningful indicators.
The Metabolic Index (Φ)	**Strengths:** • Mechanistically links deoxygenation to changes in organisms' aerobic scope; biologically meaningful • Helps to explain the presence and absence of species in certain locations • Can be projected into the future and used to	Could serve as a control variable in the future, when more information is available regarding the metabolic demands and aerobic scope of key taxa, and as global climate (oxygen) models

estimate extinction risk • Climate velocity of Φ ($CV_Φ$) captures changes are across time *and* space **Weaknesses:** • Fairly theoretical and not necessarily intuitive • Requires an abundance of physiological data, which can be difficult and costly to obtain; limited metabolic data currently available across taxa • Assumes limited adaptive capacity of organisms to respond to low oxygen • Accuracy is largely dependent on the accuracy of climate (oxygen) models	improve.

Dissolved Oxygen Concentration: Prevalence of Anoxia or Hypoxia

Dissolved oxygen (DO) concentration refers to the amount of O_2 dissolved in a water sample and can be used to distinguish normal levels of DO ('normoxia') versus low levels of DO ('hypoxia,' 'suboxia,' and 'anoxia') in aquatic systems. This measure can also describe the potential biological and ecological effects of low oxygen as well as the total oxygen inventory for a system.

Hypoxia refers to oxygen levels low enough to cause negative physiological effects, often defined as ≤ 2 mg O_2 / L (~60 µmol / kg, or 1.5 mL / L). Suboxia refers to oxygen levels near zero (commonly defined as < 5 µmol O_2 / kg or ~0.16 mg O_2 / L), and anoxia refers to the complete absence of oxygen (Vaquer-Sunyer & Duarte, 2008; Breitburg et al., 2018; IUCN, 2019). When systems go suboxic or anoxic, mobile fauna that can escape do, and intolerant species that can't usually perish. There tends to be very few plants or algae in shallow suboxic and anoxic areas, and habitat structure is often limited to rocky outcroppings, sandy flats, or muddy plains.

Rose et al. (2024) suggest that, at least preliminarily, the global extent of anoxia can serve as a control variable for aquatic deoxygenation, given its implications for the rate of anaerobic metabolism, biogeochemical cycling, and the production of greenhouse gases. Anoxia is associated with distinct types of biogeochemistry (as we have described above) that make it a useful boundary when attempting to estimate or control for the effects of aquatic deoxygenation on processes that directly affect climate. However, if the planetary boundary framework aims to effectively safeguard humanity and a "Holocene-like" Earth system state, it will be necessary to develop a more complex boundary for aquatic deoxygenation that conserves global Biosphere Integrity by considering oxygen concentrations higher than anoxia.

Hypoxia, for instance, marks the concentration at which many macrofauna begin to show negative symptoms of oxygen deprivation and possibly death. Thus, the spatial extent of hypoxic waters may represent a viable control variable long-term. However, the typical hypoxia threshold of ≤ 2 mg O_2 / L may be more or less relevant for certain taxa and in different locations, as this threshold is largely derived from lethal concentration values of shallow temperate species (e.g., Vaquer-Sunyer & Duarte, 2008) and is lower for organisms in naturally-low O_2 environments.

Some organisms are adapted to survive in low-oxygen conditions far below the conventional hypoxia cut-off. In OMZs (100–1000m), for instance, some fish and macroinvertebrates, meiofauna, and microbes spend their entire lives under low-oxygen conditions near zero (Levin, 2003, Breitburg et al., 2018; Gallo et al., 2019; IUCN, 2019). Cusk eels and cat sharks found in the deep Eastern Pacific have been found in large schools at DO levels circa 0.2 mg O_2 / L (Gallo et al., 2019), and animals living in hypolimnetic-lake, pond, and cave systems are specially adapted to survive periods of complete anoxia (Cox & Gillis, 2020).

Simultaneously, evidence presented by Vaquer-Sunyer & Duarte (2008) suggests that roughly half of all coastal temperate benthic organisms experience lethal effects at DO concentrations greater than 2 mg O_2 / L and propose a more conservative cutoff of 4.6 mg O_2 / L when defining hypoxia in coastal environments. (Specifically, this value corresponds to the 90th percentile of all lethal oxygen measurements produced by their meta-analysis of more than 870 published articles covering 206 animal species.) Most of the species included in their study are benthic fishes and macroinvertebrates found in the shallow parts of the Atlantic ocean, where average DO concentrations tend to be higher than those in the shallow Pacific and many inland waters; it is likely that shelf and slope animals in the Pacific Ocean are better adapted to handle life under low-oxygen conditions than fauna found in the Atlantic (e.g., Chu & Tunnicliffe, 2015). This highlights some of the potential challenges associated with using DO, or a concentration cutoff, as a global indicator for aquatic deoxygenation but does not preclude it.

Despite its limitations, DO concentration remains a valuable indicator for aquatic deoxygenation change across scales because it can be measured extensively and compared across regions over time. Extensive oxygen observational data sets allow us to quantify contemporary DO concentrations and the global extent of hypoxia and anoxia in monitored regions (Gregoire et

al., 2021). Hypoxia and anoxia are also associated with biological and paleo proxies that could be used to construct an ecologically meaningful baseline in the Planetary Boundary context. For example, the ratio of Mn/Mg observed in the otolith 'bones' of Baltic cod closely tracks known hypoxic events (Limburg & Casini et al., 2018), and the fossilized remains of benthic foraminifera, fish bones, and diatoms can be used to infer low O_2 in ecosystems over centuries or thousands of years (e.g., Gutierrez et al., 2009; Kranner et al., 2022).

To enhance the feasibility of using DO concentration as a control variable for aquatic deoxygenation, we recommend: (1) expanded *in situ* monitoring of DO across depths and latitudes (for example, contemporary changes in oxygen across freshwater tropical and high-latitude locations has been poorly investigated; Krause et al., 2026); (2) improved characterization of species-specific oxygen tolerances, their plasticity, and potential for rapid adaptive evolution in the face of chronic oxygen stress; (3) meta-analyses that invoke cross-comparisons of oxygen tolerances across organisms, ecosystems, and time; (4) continued development of paleo proxies to establish ecologically-relevant baselines; and (5) modelling efforts designed to more accurately capture the spatial extent and behavior of hypoxia and anoxia, particularly in areas that are difficult to project. For example, the fate of the tropical OMZs remains highly uncertain, with climate models disagreeing on both the direction and magnitude of projected changes (e.g., Bopp et al 2013; Cabré et al., 2015; Kwiatkowski et al., 2020).

Percent oxygen saturation (% DO)

Another measure used to monitor oxygen and identify important deoxygenation thresholds is percent oxygen saturation (% DO). This metric is calculated as the *in situ* DO

concentration divided by the maximum DO concentration that could exist in solution at that temperature, salinity, and barometric pressure. Percent DO is thus similar to DO concentration but adjusted for context and closely related to the measure of oxygen's partial pressure in water, reported in units of percent.

It is straightforward to convert between units of % DO, DO concentration, and O_2 partial pressure as long as temperature, salinity, and pressure data are available. By accounting for *in situ* pressure, temperature, and salinity, measures of % DO and O_2 partial pressure tell us how 'breathable' water is to organisms who acquire it via diffusion and osmosis. DO values expressed in terms of percent saturation tend to be fairly intuitive for people to understand, especially compared to measures of partial pressure reported in units like Pascals (Pa) or millimeters of mercury (mmHG). While interpretability is not the primary criteria for selecting a global control variable, it may carry weight for some.

In general, levels of % DO greater than 60% (at 25℃, 30 PSU, and pressure at sea-level) can likely be considered safe for most shallow oxygen-breathing organisms (supported by Vaquer-Sunyer & Duarte). However, in areas with naturally high oxygen variability, % DO values can vary substantially throughout the day or by season. For example, in the kelp forests off California, where upwelling is common, lower- and upper-quartile values for % DO range anywhere from ~40–85% DO (Kroeker et al., 2023). At levels below 30%, many shallow-water organisms are threatened with chronic or lethal consequences (estimated from Vaquer-Sunyer & Duarte, 2008). In upper bathyal deep-water environments, % DO is frequently measured at values below 5% (< 20 μmol O_2 / L) (e.g., Breitburg et al., 2018).

Defining a global boundary for aquatic deoxygenation using % DO will require continued monitoring and further research into DO variability. The future directions described for DO concentration (above) also apply to using % DO as a control variable.

The presence, absence, and change among indicator taxa

Certain species, guilds, and functional groups that are consistently associated with high or low levels of oxygen are referred to as 'indicator taxa.' Their presence or absence can help to infer oxygen conditions, while shifts in their abundance and behavior can indicate a loss or increase in DO. In situations where direct measurements of DO are lacking or patchy, these taxa can serve as biological sentinels of oxygen status and change.

High-oxygen indicator taxa often include large-bodied apex predators, macrophyte primary producers, and certain hard-armored invertebrates – whereas low-oxygen indicators include certain smaller or soft-bodied animals and bacterial mats. In general, large-bodied, highly mobile, armored animals or apex predators require more oxygen for survival than small, sessile, and / or soft-bodied organisms that occupy lower trophic levels in food webs. Simultaneously, the presence of large primary producers – macrophytes, such as woody plants, kelps, mangroves, and seagrasses – is typically associated with higher mean DO due to photosynthesis. Some invertebrate taxa, including annelid worms, amphipods, and certain molluscs can tolerate a wide range of oxygen conditions (e.g., Vaquer-Sunyer & Duarte, 2008), while bacterial mats, such as the filamentous carpets formed by *Beggiatoa*, *Thioploca*, and *Thiomargarita* species, are often associated with very low DO (Levin, 2003; IUCN, 2019 – Chapter 8).

These broad, generalized patterns tend to reflect deeper differences in habitat and life history. For instance, shallow benthic species tend to be more tolerant of low DO than shallow pelagic species, likely due their sessile, resident, or slow-moving life styles. By contrast, deep-water pelagic species often live at consistently low-O_2 extremes, and many pelagic freshwater taxa are resilient to temporary DO declines. Adaptations that allow these organisms to survive under low-DO conditions include specialized tissues that help them store oxygen for long periods of time (e.g., some jellies; Purcell et al., 2001) and surface-breathing, as seen in betta fish, tadpoles, and lungfish.

Among vertebrates, mobile predators in particular, the persistence of large fish is often a reliable indicator of high DO. When DO drops below ~5 mg O_2 / L for a protracted period, most species of large-bodied marine fish (e.g., sharks, tunas, billfishes, groupers, and snappers) will either evacuate the area or exhibit abnormal behavior (Stramma et al., 2012; IUCN, 2019; Vedor et al., 2021). Commercially important fishery species, such as Atlantic sturgeon (*Acipenser oxyrhynchus*), Largemouth bass (*Micropterus salmoides*), and Yellow perch (*Perca flavescens*) are especially sensitive to DO declines (Stoklosa et al., 2018). Freshwater and brackish fish are generally more tolerant of short-term fluctuations in DO compared to marine species – a trait believed that's believed to reflect their evolutionary history in turbid rivers, lakes, and streams (Verberk et al., 2022). Still, very few large fish can survive prolonged periods of suboxia or anoxia unless they are capable of surface breathing and / or have proto-lungs.

While generally useful, these patterns have a few important exceptions. Some soft-bodied animals, such as jellies and squid, can grow quite large despite very little DO in the surrounding environment (Purcell et al., 2001; Levin 2003). Gelatinous and soft-bodied animals are typically common in naturally-low oxygen environments, including open-ocean and enclosed seas, deep-

lake environments, and in stagnant ponds, where small-bodied invertebrates and meiofauna (burrowing species) also occur (Levin, 2003; Cox & Gillis, 2020). How these organisms manage to survive and grow large under low-oxygen conditions is still something of an open question, but it helps that many of them have relatively low metabolic demands, efficient oxygen uptake, and specially-adapted cell pathways that conserve against low-oxygen tissue degradation (Levin, 2003; Cox & Gillis, 2020).

Indicator taxa may serve as an especially valuable proxy in contexts where baseline ecological knowledge is high but resources are limited and oxygen sensors cannot be deployed. Changes in the presence, abundance, and behavior of indicator taxa can signal changes in oxygen availability that can be monitored using a variety of techniques, such as biological sampling, telemetry, acoustics, and local knowledge. For instance, fishers, scientists, and managers can sometimes detect when changes in DO are occurring in nearly real-time based on their observations of unusual behavior, mass evacuations, shoaling, increased surface breathing, and / or changes in landings (e.g., NCCOS, 2019; Cavole et al., 2020; Vedor et al., 2021; Roman et al., 2024). At the same time, however, emerging evidence suggests that oxygen-sensitive species can compensate for short periods of low oxygen when previously exposed to high-oxygen or supersaturated conditions (Giomi et al., 2019). Thus, the presence and abundance of indicator taxa may prove to be a meaningful signal of aquatic deoxygenation on longer timescales – weeks to months.

Drawing on the concepts presented above, we offer the following generalized approximation for how indicator taxa could be used as a local proxy for aquatic deoxygenation or, eventually, adapted for use as a global control variable. In shallow aquatic environments, one might refer to the continued presence and steady abundance of medium-sized pelagic and benthic

predators as the "safe" boundary for aquatic deoxygenation. In deeper aquatic environments, the continued presence and abundance of small benthic and meiofauna may serve as a more appropriate benchmark. Synthesis research clarifying the oxygen tolerances of organisms in different ecosystems and under variable oxygen conditions represents an urgent area of need.

The Metabolic Index: the ratio of O_2 supply-to-demand

Finally, a more-theoretical metric by which we can understand the progression of aquatic deoxygenation at the regional and global scale is 'the Metabolic Index' (Φ) (Deutsch et al., 2015), the temperature-dependent ratio of O_2 supply-to-demand at a given partial pressure of O_2. Ultimately, Φ, measures the aerobic scope of an organism (or group of organisms) in an inherently oxygen-limited environment and derived from an equation with component parameters that must be directly measured (e.g., Seibel et al., 2021). Note that these parameter measurements can be difficult and costly to obtain.

The Metabolic Index, Φ, helps to predict many of the physiological dynamics that drive the presence, absence, and behavior of the indicator taxa described above. For an environment to be considered habitable, Φ must exceed a species' critical oxygen threshold known as 'Φ_{crit}'. Φ_{crit} represents the minimum oxygen supply-to-demand ratio required to sustain the aerobic scope of an organism and its population long-term. In general, organisms with low metabolic demands have a Φ_{crit} closer to 1, whereas organisms with high metabolic demands have a Φ_{crit} much greater than 1. While oxygen demands differ across species and ecosystems, reported Φ_{crit} values for marine organisms have been observed to range from approximately 1.3 to 6.5 (Deutsch et al., 2015; Penn & Deutsch, 2022). When Φ falls below Φ_{crit} for organisms in a given environment, they will evacuate, suppress activity, switch to anaerobic metabolism, or perish.

622 At present, models that apply the Metabolic Index to global climate projections suggest
623 that deoxygenation will create physiological stress for most water-breathing animals, including a
624 significant risk of species extinction in or movement out of the tropics due a reduction aerobic
625 scope (Penn & Deutsch, 2022; model results derived from 61 species). Meanwhile, temperature
626 increases associated with anthropogenic climate change may drive the expansion of vertical
627 migrators, whose metabolisms have evolved in fundamentally different ways (Seibel & Birk,
628 2022; results derived from 5 species).

629 Equipped with information about organisms' metabolic demands and predicted changes
630 in aerobic habitat, we can also estimate the 'climate velocity of Φ,' known as 'CV_{Φ}' under
631 continued deoxygenation scenarios (Parouffe et al., 2023). This proposed metric applies the well-
632 known idea of 'climate velocities' (Loarie et al., 2009) to the Metabolic Index (Deutsch et al.,
633 2015) to estimate the change in suitable aerobic habitat over time and at a specific spatial scale
634 given an organism's physiological demands. Traditionally, climate velocity (CV) values
635 are reported in units of space over time, telling us both the direction and speed (i.e., the velocity)
636 that a particular species will need to move to remain within its climatic niche (Loarie et al.,
637 2009). In the case of CV_{Φ}, the interpretation is as follows: CV_{Φ} represents the ratio of the
638 temporal trend in Φ (i.e., how the metabolic index changes over time at a given location) relative
639 to the magnitude of spatial gradient of Φ (i.e., how the metabolic index varies over space).
640 Because the magnitude of the spatial gradient of Φ (the denominator of CV_{Φ}) will always be
641 non-negative, the sign of CV_{Φ} overall indicates whether Φ is increasing or decreasing over time.
642 A positive CV_{Φ} indicates that Φ – the ratio of oxygen supply to demand – is growing over time,
643 whereas a negative CV_{Φ} indicates that Φ is decreasing over time. The magnitude of CV_{Φ} tells us

how Φ shifts across space, i.e., how fast the species will need to move to stay within its current metabolic niche.

Thus, CV_{Φ} values provide us with key insights about the long-term risks of deoxygenation in three-dimensional space that Φ values alone cannot (Parouffe et al., 2023). For example, two populations of the same species – one living nearshore and another living offshore – might have similar Φ values today but could be differentially exposed to the risks of aquatic deoxygenation tomorrow. Parouffe et al. (2023) apply the concept of CV_{Φ} to explore changes in the metabolic habitat of organisms living in the Humboldt Current OMZ and find that organisms with a $CV_{\Phi} < 0$ are at high risk of losing aerobic scope (i.e., loss of habitat suitability), whereas those with a $CV_{\Phi} > 0$ are at a lower risk. Through a series of sensitivity analyses, they demonstrate that, within their model framework, CV_{Φ} is only weakly dependent on the physiological traits of a model organism (Parouffe et al., 2023), which suggests that values for CV_{Φ} could be informative even in the absence of species-specific data.

At present, critiques of The Metabolic Index (e.g., Seibel et al., 2024) and data limitations – including oxygen modeling biases and inter-model disagreement (e.g., Cabré et al., 2015) – introduce uncertainty and limit the application of this indicator at the planetary scale. We currently lack metabolic demand data for most phyla, let alone most species (Deutsch et al., 2020), and the equations behind The Metabolic Index assume very little about animals' physiological plasticity or potential to adapt to lower oxygen levels. It is also possible that in the process of moving, organisms will face new stressors not accounted for by Φ, such as new and altered food sources and food webs that modify their realized metabolic niche. Furthermore, there is little to no consensus (yet) about how to measure the underlying parameters for of Φ,

such as P_{crit} (Seibel et al., 2021), so our empirical data may not be sufficient to support the robust modeling application of Φ as a Planetary Boundary control variable for the time being.

Nevertheless, we anticipate that use of Φ (or CV_{Φ}) as an indicator and global control variable will become more feasible as we continue to make progress in the fields of experimental biology and ecophysiology, improve global climate and oxygen models, and as access to *in situ* oxygen data grows. The Metabolic Index would be most useful as a Planetary Boundary control variable in a future where physiological data are plentiful, observations exists across depths and over time, oxygen observations are accurate, and model projections are reliable.

"UNSAFE" LEVELS OF CHANGE

At present, a precise, quantitative control variable and planetary boundary for aquatic deoxygenation that can be used to define "safe" levels of change across all aquatic systems does not exist. However, the absence of a fully specified global boundary does not preclude us from confidently asserting that aquatic deoxygenation is progressing towards an "unsafe space", referred to within the planetary boundary framework as the "zone of uncertainty" (Rockström et al., 2009). This zone represents a state of increasing risk, beyond safe operating conditions, within which transgression of any one Planetary Boundary threatens to permanently compromise Earth's climate stability and ecological resilience (Rockstrom et al., 2009; Steffen et al., 2015; Richardson et al., 2023). We use three lines of evidence to support this assessment.

First, aquatic deoxygenation is mechanistically linked to all other Planetary Boundary processes (**Table 1**; **Figure 1**) such that even relatively modest declines in DO have the potential to propagate across the Earth system and undermine climate and ecological stability. As we have

688 shown, aquatic deoxygenation amplifies other stressors and risks that are associated with other
689 boundary processes like climate regulation, biogeochemical cycling, and biosphere integrity. The
690 feedbacks between aquatic deoxygenation and the other planetary boundaries indicate its
691 importance within the Earth system and suggest we should proceed with a high degree of caution
692 when evaluating what constitutes "unsafe" levels of change.

693 Second, aquatic systems exhibit strong, long-term 'memory', such that even small
694 declines in present-day DO may signal far larger losses on the horizon. Projections of ocean
695 deoxygenation show that even if we were to stop emitting CO_2 *today*, deoxygenation would
696 continue for centuries due to committed warming and because thermohaline circulation
697 replenishes oxygen on ~1000-year timescales (Keeling et al., 2010; Battaglia and Joos, 2018;
698 Oschlies, 2021). This long-term legacy effect underscores the urgency of recognizing aquatic
699 deoxygenation as a planetary-scale risk with impacts that are likely to be irreversible in our
700 lifetimes.

701 Third, observed rates of marine and freshwater deoxygenation are rapid relative to the
702 limited pathways available for oxygen replenishment. While many factors have contributed to
703 contemporary DO losses, the pathways for production and restoration are constrained by a small
704 number of mechanisms. The vast majority of DO is generated by *in situ* photosynthesis or
705 supplied from the atmosphere via physical mixing and advection. A third mechanism, dubbed
706 'dark oxygen production', has been proposed following the recent discovery of electrochemical
707 production of O_2 by polymetallic nodules in the deep sea (Sweetman et al., 2024), but this
708 process is likely rare and remains debated. Meanwhile, artificial 'reoxygenation' techniques
709 – such as bubbling and artificial downwelling – have been proposed as a means for forcibly
710 restoring oxygen in freshwater and coastal systems, but their implementation has been limited

and their efficacy is highly context-dependent (Slomp et al., 2026). In short, once oxygen is lost from an aquatic environment, recovery pathways are limited.

Taken together, these lines of evidence indicate that aquatic deoxygenation is progressing rapidly toward an unsafe space. And, while additional research will be required to formally demonstrate this according to Planetary Boundary convention using a global control variable, the multiple feedbacks between aquatic deoxygenation the other PBs, long-term memory of aquatic systems, and limited recovery pathways for DO strongly suggest escalating planetary-scale risks.

Priority areas for future research include continued monitoring and synthesis of oxygen observations; expanded Earth system modelling of oxygen dynamics, particularly in the deep ocean, freshwater systems, and difficult-to-predict regions such as the Equatorial Pacific; improved understanding of ecophysiological responses to hypoxia; and targeted paleo-record analyses to establish an ecologically meaningful baseline for contemporary change (Breitburg et al., 2018; IOC, 2018; IUCN, 2019; Gregoire et al., 2022; Rose et al. 2024).

OPPORTUNITIES FOR POLICY AND MANAGEMENT IMPACT

The signal for ocean deoxygenation has been accruing since at least the 1960s (e.g., Sarmiento et al., 1998; Ito et al., 2017), yet only about 25 years have passed since it was first framed as a global threat (e.g., Sarmiento et al., 1998). Since then, scientific attention to deoxygenation in marine and freshwater systems has expanded substantially, but policy and management efforts designed to address aquatic deoxygenation remain largely underdeveloped relative to issues like plastic pollution, ocean acidification, and climate change. Incorporating aquatic deoxygenation into the planetary boundary framework and recognizing its progression

733 towards an unsafe space is likely to increase public and political awareness of aquatic
734 deoxygenation as a systemic problem and significant hazard, supported by a robust community
735 of scientists working on it. Support from managers and policy-makers would help provide a
736 scaffolding for coordinated deoxygenation research, targeted mitigation efforts, and improved
737 adaptive management.

738 At the international level, formal recognition of aquatic deoxygenation could facilitate its
739 integration into policy negotiations and governance instruments that dictate measures such as
740 spatial planning, protected areas, environmental impact assessments, capacity building goals,
741 data practices and technology transfer agreements. At present, references to aquatic
742 deoxygenation or oxygen in international environmental texts are relatively sparse, which likely
743 makes it more difficult for policy-makers and managers to dedicate time, resources, and
744 expertise towards it. Reflecting the era of treaty negotiation, there is no language specific to
745 oxygen, oxygen loss, or even climate change under the United Nations' Convention on the Law
746 of the Sea (UNCLOS, 1992), the legal framework that governs global marine and maritime
747 activities, and oxygen was mentioned only once by countries' initial pledges under the Paris
748 Agreement (as of 2017; Gallo et al., 2017). The new UN agreement on the 'conservation and
749 sustainable use of Marine Biological Diversity of Areas Beyond National Jurisdiction' (The
750 BBNJ Agreement, 2023) is notable, however, in that it mentions deoxygenation twice, once in
751 the Preamble, which recognizes ocean deoxygenation as a stressor adversely affecting
752 biodiversity, and once in Annex II in the context of capacity building and technology transfer.

753 Endorsement of aquatic deoxygenation within the planetary boundary framework could
754 strengthen the ability of international policy instruments to address it as a problem. For example,
755 work by Robinson et al. (2024) demonstrates how deoxygenation could be operationalized under

the BBNJ Treaty using a multi-institutional and multi-scalar framework. They show how recognition could motivate more ambitious action by decision-makers who rely on concise, targeted, and integrative scientific messages to make decisions and apportion resources. In practice, these scientific messages can come in the form of townhalls, international conferences, policy briefs, and popular scientific images like that shown in **Figure 1**.

At the national and regional scale, framing aquatic deoxygenation as a planetary-scale process may give decision-makers the leverage they need to create or expand mandates for action. We can look to the United States as a prime example of this, where current policy and management actions related to aquatic deoxygenation have focused primarily on oxygen losses in the context of nutrient run-off and harmful algal blooms (HABs). Under the 'Harmful Algal Bloom and Hypoxia Research and Control Act' (HABHRCA), the United States' Congress has directed federal agencies such as the National Oceanic and Atmospheric Administration, the Army Corps of Engineers, the Department of Agriculture, the Environmental Protection Agency, and the National Science Foundation to address hypoxia as a HAB-related issue. Activities conducted by these agencies under HABHRCA include the administration of funding for oxygen-related projects within the U.S. Exclusive Economic Zone, such as oxygen observation and monitoring networks, modeling, forecasting, management, and development of mitigation strategies, but language relating to deoxygenation *outside* of HABs is not apparent within HABARCA nor any other U.S. national policy. This means that projects that do not make a clear link between aquatic deoxygenation and harmful algal blooms or coastal ecosystems are likely to be overlooked or underfunded.

By prioritizing aquatic deoxygenation as an environmental issue in its own right, managers may be able to improve water-quality monitoring efforts, protections for biodiversity,

and oxygen mitigation strategies by re-tooling infrastructure that already exists. This might also help to unlock new sources of financial support for deoxygenation mitigation and adaptation, including access to 'green financing' opportunities for related projects. International funds, such as the UNFCCC Green Climate Fund, regional initiatives (e.g., the Europe-organized Blue Action Fund), and national programs (e.g., funds from federal agencies) could enhance support for aquatic deoxygenation-relevant actions, such as expanded DO monitoring networks, protection of vulnerable ecosystems, waterway clean-ups, or improved waste management.

At the same time, incorporating aquatic deoxygenation into the planetary boundary framework may help to identify and ameliorate risks associated with proposed mitigation strategies. Certain types of climate-change interventions, for example, may produce unintended negative – or even counterproductive – oxygen outcomes that need be considered when evaluating total mitigation potential (Levin et al. 2023; Oschlies et al., 2025). Marine carbon dioxide removal technologies that involve nutrient fertilization, algal culture, or biomass sinking could decrease oxygen availability through increased respiration and related processes (Levin et al. 2023; Oschlies et al., 2025). Given the significant funding that has already been pledged globally for research and development of these intervention strategies, investments should include a thorough assessment of deoxygenation risks to avoid supporting maladaptive outcomes.

CONCLUSION

In this article, we have provided a novel synthesis of aquatic deoxygenation's interactions with other Earth system stressors and boundary processes in both marine and freshwater systems, and in so doing have demonstrated its remarkable, complex, and far-reaching importance. We

provide a detailed discussion about indicators that can be used to monitor aquatic deoxygenation progress across scales, including a discussion of how and under what circumstances these indicators could be used as control variables within the planetary boundary framework. Continued quantitative analyses will be required to assign a definitive global boundary or set of boundaries for aquatic deoxygenation, but we argue that current rates of global oxygen loss exceed what most would consider "safe" levels of change. By providing concrete recommendations for aquatic deoxygenation research, adaptation, and mitigation, we hope that this research will help scientists, policy-makers, and managers set realistic priorities and achieve ambitious goals.

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839

840 **DECLARATION OF INTERESTS**

841 The authors declare no competing interests.

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Overview Response:

Thanks very much to the editor and reviewer(s) for your positive review and feedback, we appreciate your time and consideration. We have addressed the Editor's formatting comments in the manuscript and point-by-point below.

Specifically, we spent time standardizing the references, tightening up the abstract, implementing modest edits that improve grammar and flow (see highlighted paragraphs on pages 34, 41, and 43), and responding to all minor revisions. We acknowledge the contributions from the reviewers and editorial team. New changes, including those made in accordance with the requested revisions, are highlighted in yellow.

Please let me / us know if there are any additional formatting issues we should attend to.

Sincerely,

Erica Ferrer, on behalf of the co-author team.

Response to Editor's Comments:

In addition to addressing all reviewer and editor comments in your revision, **please also make sure that your revised manuscript conforms to the style and formatting requirements for *Limnology and Oceanography***, as specified in the online instructions for authors (https://aslopubs.onlinelibrary.wiley.com/hub/journal/19395590/about/author-guidelines).

In particular, please pay attention to guidelines pertaining to use of acronyms and abbreviations (write out AD and PB with text), and use/number of citations.

Regarding use of acronyms and abbreviations, we have now spelled out AD (aquatic deoxygenation) and PB (Planetary Boundary) within the text.

Regarding citations, we have taken great care to standardize all citations and ensure that each one has DOI link or web address associated with it.

We humbly request an exception to the maximum number of citations, n=75. Following major revisions, we were able to remove >30 references, but those remaining seem critical. At present, we cite 102 resources, including >90 peer-reviewed articles, 4 book chapters, 2 theses, and 2 web citations.

Remove shading and vertical lines from tables.

Completed.

Remove in-text footnoting.

Completed. These sources have been moved to the references section.

Finally, web sources are permitted, provided they are cited formally (author or responsible organization, title, publication or last-modified date where available, and URL, with an access date if needed), with author/institution and year cited in the text.

Completed. All web sources are cited formally within the references section and in a standardized format.

Thank you. -kdh

Associate Editor:
Comments to the Author:
Firstly, I would like to thank the authors for their thorough response to the editorial team and the reviewers, you have more than adequately responded to all of our concerns. I look forward to citing this work in the years to come!

Many thanks for this positive and encouraging final feedback. We sincerely appreciate the time you've put towards managing this manuscript.

Reviewer(s):
Reviewer: 2

Comments to the Author
The manuscript has really improved and you have addressed all my comments in an appropriate way. I have no further comments on the manuscript.

Many thanks to the reviewer for your constructive feedback and positive final review. We sincerely appreciate the time you put towards peer-review. The manuscript is much improved as a result.