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PERSPECTIVE

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 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 framework, future analyses, policy-making, and management.

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

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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 et al. 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'Neill et al. 2018), marine plastic pollution (Villarrubia-Gómez 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 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 2023; Rose et al. 2024; Ferrer 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 (Breitburg 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 nor redundant to them, which motivates the case for treating it as a distinct boundary process (Rose et al. 2024; Ferrer 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 and 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. 2023), 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. 2023). 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 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? 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 (Fig. 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.

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) have declined (Oschlies et al. 2018; IPCC 2019). About 50% of contemporary upper-ocean

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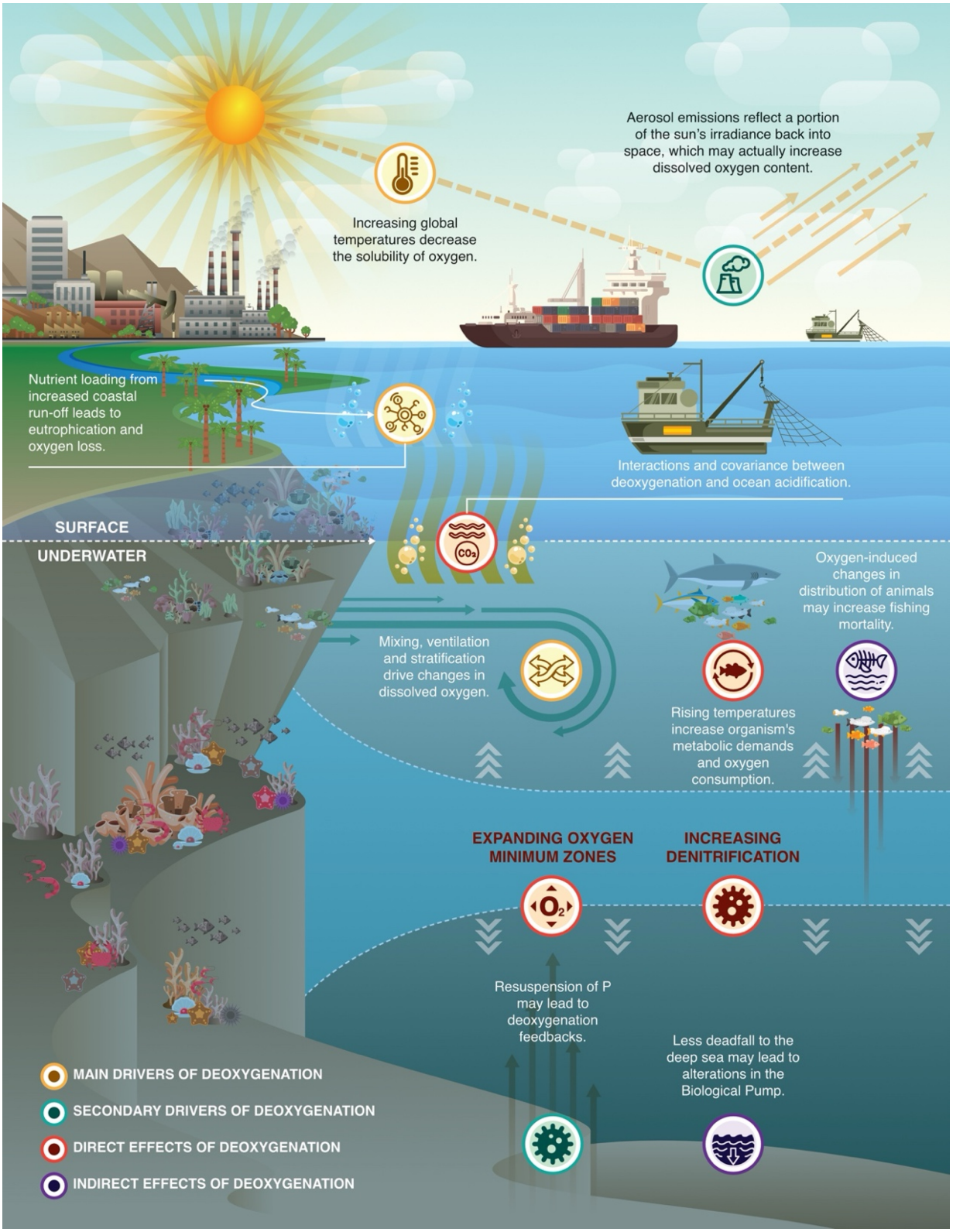


Fig. 1. A diagram showing some of the key interactions that exist between aquatic deoxygenation and the other planetary boundaries, including primary and secondary drivers and effects. Here, emphasis is placed on interactions that occur in the marine environment, however, similar interactions are also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

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Table 1. Summary of key interactions and feedbacks that exist between aquatic deoxygenation and the other planetary boundaries. Several of these are depicted in Fig. 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 associated 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.

(≤ 1000 m) 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 (100–600 m) 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).

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Aquatic deoxygenation may also alter the ability of aquatic habitats to aerobically metabolize organic matter, with secondary 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 2018; Schmidtko et al. 2017)—a potent greenhouse gas and ozone [O_3] depleter. 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 2018; 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 hydrogen sulfide (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) 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 effect 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 we focus on nitrogen (N) and phosphorus (P) here, as these are 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 2018; 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, and 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

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(*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., reductions sediment bioturbation or carbon cycling; Roman et al. 2024).

Even minor decreases in DO can have negative consequences on biodiversity through changes in organisms' 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).

Meanwhile, 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) and that as DO declines, so does organismal diversity and evenness. Paleo evidence suggests a close link between major anoxic events of the past and mass extinction in that 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). To a certain extent, these findings are corroborated by survey data from inside and outside of contemporary OMZ swhich suggest species diversity and evenness are inversely related to DO (e.g., Sperling et al. 2016; Gallo et al. 2020). As DO declines, 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).

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

Land-system change and impacts on climate regulation

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

Within this expanded framing, it is important to consider whether large-scale alterations to ocean oxygen availability may operate in a similar way. Land-system changes that impact climate regulation, including the development of widespread agriculture, clearly interact with oxygen and have effects on aquatic deoxygenation. Simultaneously, given aquatic deoxygenation's potential to impact climate regulation in the long term, we argue that it might be considered a type of land-system change in and of itself.

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

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

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

Aerosol loading, with ties to climate regulation

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

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

In contrast, aerosol-driven biogeochemical feedbacks can *decrease* oxygen and intensify deoxygenation via changes in primary productivity and respiration. Atmospheric deposition of aerosol-bound micronutrients promotes primary productivity at the surface, increased organic carbon export, and enhanced microbial respiration at depth. For instance, accelerated oxygen losses observed in the Pacific Ocean basin since the 1970s have been linked to an increase in iron deposition borne from various anthropogenic aerosol sources (Ito et al. 2016). Similarly, the increasing prevalence of large wildfires may alter DO dynamics in freshwater systems and coastal areas due to increased deposition of iron and ash (e.g., Wall et al. 2024). 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 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 vs. 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

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et al. 2024), which can affect sediment redox chemistry and decrease rates of remineralization (Aller and Cochran 2019). It is therefore easy to imagine how aquatic deoxygenation might induce changes in freshwater quality.

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 toward "safe" vs. "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, although 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 oxygen concentration and the prevalence of anoxia or hypoxia; percent oxygen saturation (% DO); the presence, absence, and change among indicator taxa; and the ratio of oxygen supply-to-demand, known as the Metabolic Index (Φ). We discuss the strengths and limitations of each indicator, including factors that might enable or constrain its application as a control variable within the planetary boundary context (Table 2).

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") vs. 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 and Duarte 2008; Breitburg et al. 2018; IUCN 2019). When systems go suboxic or anoxic, mobile fauna that can escape do, and intolerant species that cannot 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 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. This threshold is largely derived from lethal concentration values of shallow temperate species (e.g., Vaquer-Sunyer and 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 (100–1000 m), 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 and Gillis 2020).

Simultaneously, evidence presented by Vaquer-Sunyer and Duarte (2008) suggests that roughly half of all coastal temperate benthic organisms experience lethal effects at DO

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Table 2. Proposed aquatic deoxygenation indicators describing their strengths, weaknesses, and 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 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	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.
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.

(Continues)

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Table 2. Continued

Indicator	Strengths and weaknesses	Potential use as a control variable
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 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	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 improve.

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, and 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 and 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 (Grégoire et al. 2021). Simultaneously, 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 instance, the ratio of Mn/Mg observed in the otolith "bones" of Baltic cod closely tracks known hypoxic events (Limburg and Casini 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 (e.g., across freshwater tropical and high-latitude locations; 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) modeling 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

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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 criterion for selecting a global control variable, it may carry weight for some.

In general, levels of % DO greater than 60% (at 25°C, 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 and 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 mollusks can tolerate a wide range of oxygen conditions (e.g., Vaquer-Sunyer and 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 is 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 and 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 and 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

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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, or changes in landings (e.g., NCCOS 2019; Cavole et al. 2020; Vedor et al. 2021; Roman et al. 2024). At the same time, 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), which suggests that the presence and abundance of indicator taxa may prove to be a more 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 is 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 1.3–6.5 (Deutsch et al. 2015; Penn and 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.

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

Equipped with information about organisms' metabolic demands and predicted changes in aerobic habitat, we can also estimate the "climate velocity of Φ," known as "CV_Φ" under continued deoxygenation scenarios (Parouffe et al. 2023). This proposed metric applies the well-known idea of "climate velocities" (Loarie et al. 2009; Brito-Morales et al. 2018) to the Metabolic Index (Deutsch et al. 2015) to estimate the change in suitable aerobic habitat over time and at a specific spatial scale given an organism's physiological demands. Traditionally, climate velocity (CV) values are reported in units of space over time, telling us both the direction and speed (i.e., the velocity) that a particular species will need to move to remain within its climatic niche (Loarie et al. 2009). In the case of CV_Φ, the interpretation is as follows: CV_Φ represents the ratio of the temporal trend in Φ (i.e., how the metabolic index changes over time at a given location) relative to the magnitude of spatial gradient of Φ (i.e., how the metabolic index varies over space). Because the magnitude of the spatial gradient of Φ (the denominator of CV_Φ) will always be non-negative, the sign of CV_Φ overall indicates whether Φ is increasing or decreasing over time. A positive CV_Φ indicates that Φ—the ratio of oxygen supply to demand—is growing over time, 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.

CV_Φ values therefore 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.

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At present, critiques of The Metabolic Index (e.g., Seibel 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 exist 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 toward 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 (Rockström 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; Fig. 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 shown, aquatic deoxygenation amplifies other stressors and risks that are associated with other boundary processes like climate regulation, biogeochemical cycling, and biosphere integrity. The feedbacks between aquatic deoxygenation and the other planetary boundaries indicate its importance within the Earth system and suggest we should proceed with a high degree of caution when evaluating what constitutes "unsafe" levels of change.

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

Third, observed rates of marine and freshwater deoxygenation are rapid relative to the limited pathways available for oxygen replenishment. While many factors have contributed to contemporary DO losses, the pathways for production and restoration are constrained by a small number of mechanisms. The vast majority of DO is generated by in situ photosynthesis or supplied from the atmosphere via physical mixing and advection. A third mechanism, dubbed "dark oxygen production," has been proposed following the recent discovery of electrochemical production of O_2 by polymetallic nodules in the deep sea (Sweetman et al. 2024), but this process is likely rare and remains debated. Meanwhile, artificial "reoxygenation" techniques, such as bubbling and artificial downwelling, have been proposed as a means for forcibly 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. 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 and the other planetary boundaries, 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 modeling 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; Grégoire et al. 2021; Rose et al. 2024).

Opportunities for policy and management impact

Incorporating aquatic deoxygenation into the palentary boundary framework and recognizing its progression toward

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and unsafe space is likely to increase public and political awareness of it as a systemic problem and significant hazard, with opportunities for positive 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. Support from managers and policy-makers would help provide a scaffolding for coordinated deoxygenation research, targeted mitigation efforts, and improved adaptive management, as we describe below.

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

Endorsement of aquatic deoxygenation within the planetary boundary framework could strengthen the ability of international policy instruments to address it as a problem. For example, work by Robinson (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 Fig. 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 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. For example, certain types of climate-change interventions may produce unintended negative, or even counterproductive, oxygen outcomes that need to 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 maladaptive outcomes.

Conclusion

In this article, we have provided a novel synthesis of aquatic deoxygenation's interactions with other Earth system

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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 while safegaurding our future.

Author Contributions

Authors Erica M. Ferrer, Véronique Garçon, Kevin C. Rose, and Lisa A. Levin conceived of the initial idea for this study. All authors—Erica M. Ferrer, Yassir A. Eddebbar, Shailja Gangrade, Lillian R. McCormick, Ariel K. Pezner, De'Marcus Robinson, Véronique Garçon, Kevin C. Rose, and Lisa A. Levin—contributed to writing and revisions. Author Erica M. Ferrer led the writing and submission.

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Conflicts of Interest

None declared.

Data Availability Statement

Data sharing is not applicable as no new data sets were generated or analyzed as part of this study.

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