Title

Aquatic deoxygenation as a planetary boundary and key regulator of Earth system stability

Journal

Nature Ecology & Evolution, 8(8)

ISSN

2397-334X

Authors

Rose, Kevin C

Ferrer, Erica M

Carpenter, Stephen R

et al.

Publication Date

2024-08-01

DOI

10.1038/s41559-024-02448-y

nature ecology & evolution

Perspective

https://doi.org/10.1038/s41559-024-02448-y

Aquatic deoxygenation as a planetary boundary and key regulator of Earth system stability

Received: 2 June 2023

Accepted: 2 May 2024

Published online: 15 July 2024

Check for updates

Kevin C. Rose[1,2] ✉, Erica M. Ferrer[3,4], Stephen R. Carpenter[5], Sean A. Crowe[6], Sarah C. Donelan[7], Véronique C. Garçon[8,9], Marilaure Grégoire[10], Stephen F. Jane[11,12,16], Peter R. Leavitt[13], Lisa A. Levin[4], Andreas Oschlies[14] & Denise Breitburg[15]

Planetary boundaries represent thresholds in major Earth system processes that are sensitive to human activity and control global-scale habitability and stability. These processes are interconnected such that movement of one planetary boundary process can alter the likelihood of crossing other boundaries. Here we argue that the observed deoxygenation of the Earth's freshwater and marine ecosystems represents an additional planetary boundary process that is critical to the integrity of Earth's ecological and social systems, and both regulates and responds to ongoing changes in other planetary boundary processes. Research on the rapid and ongoing deoxygenation of Earth's aquatic habitats indicates that relevant, critical oxygen thresholds are being approached at rates comparable to other planetary boundary processes. Concerted global monitoring, research and policy efforts are needed to address the challenges brought on by rapid deoxygenation, and the expansion of the planetary boundaries framework to include deoxygenation as a boundary helps to focus those efforts.

The concept of planetary boundaries, initially proposed by Rockström et al.[1], describes processes disrupted by human activities that are critical to sustaining Earth's ecological and societal integrity. The designation of nine processes—atmospheric aerosol loading, biogeochemical flows (especially of nitrogen and phosphorus), loss of biosphere integrity, climate change, freshwater use, land system change, introduction of novel entities, ocean acidification and stratospheric ozone depletion—provides a framework to characterize the envelope of safe operating spaces in which ecosystems and society can function sustainably[1–3]. More recently, the inclusion of justice issues that integrate human well-being into the framework[4] and a re-evaluation of the boundaries[3] indicate that most planetary boundary processes have already exceeded safe levels. The nine planetary boundaries are also interconnected, such that shifts in one process can impact many others[3,5]. Since its introduction, the planetary boundaries framework has become an important guiding concept in the natural and social sciences as well as in policy realms. In this Perspective, we describe how the decline in aquatic oxygen, termed 'deoxygenation', warrants consideration as an additional planetary boundary. Like the nine planetary boundary processes originally proposed, aquatic deoxygenation has global ecological importance and substantial relevance to management and policy, and it both regulates and is regulated by other planetary boundary processes[6]. Deoxygenation is occurring rapidly, with many harmful effects.

Oxygen is a fundamental regulator of global biogeochemistry and a requirement for nearly all complex life[7,8]. Over the past several hundred million years, the concentration of O_2 in Earth's atmosphere has fluctuated between about 13% and 35%[9]. These atmospheric O_2 fluctuations have disrupted global biogeochemistry and caused massive shifts in biodiversity over time, which in turn have driven evolutionary events, such as the emergence of placental mammals within the past ~200 million years[10,11]. The concentration of dissolved oxygen (DO) in

A full list of affiliations appears at the end of the paper. ✉e-mail: rosek4@rpi.edu

https://doi.org/10.1038/s41559-024-02448-y

Earth's aquatic ecosystems has also varied enormously over timescales of tens to hundreds of millions of years, and changes in continental configuration, ocean circulation, surface temperature and nutrient loading have driven large fluctuations in aquatic oxygen levels, even when atmospheric oxygen levels have remained stable[12]. Aquatic oxygenation events have led to intense diversification of marine life[13], and the intermittent development of ocean anoxic events has been associated with extreme climate warming, reorganization of biogeochemical cycles, ecological upheaval and extinction.

Oxygen concentrations in aquatic ecosystems are regulated by interconnected processes, including primary production and organic matter inputs, aerobic respiration, exchange fluxes with the atmosphere, circulation and mixing, sediment exchange, and the burial of oxygen-consuming chemical species (for example, carbon burial and pyrite formation). Photosynthesis increases DO concentrations, whereas respiration from both autotrophs and heterotrophs consumes DO. In well-mixed surface waters, where oxygen is plentiful and generally close to equilibrium with the atmosphere, DO levels are high enough to support a wide diversity of aerobic organisms. Below the sunlit euphotic zone, oxygen production is low due to minimal or the complete absence of photosynthesis[14]. Meanwhile, oxygen-consuming respiration often remains substantial at depth. Oxygen-deficient zones (ODZs) are often found below the barriers to circulation (for example, sharp gradients in temperature (thermoclines) and salinity (haloclines)) and are common in both inland waters and throughout the ocean where regular lateral or vertical mixing of DO (ventilation) is slow[15–18]. In freshwaters, estuaries and coastal oceans, ODZs can occur at depths as shallow as several metres below the surface, whereas in the open ocean, they can be hundreds to a few thousand metres deep and spatially extensive. Coastal zones and lake deep-water (hypolimnetic) habitats frequently experience hypoxia (low oxygen) and anoxia (zero oxygen), especially when productivity and the resulting downward flux of organic matter are high[19,20]. In addition, most organic-rich aquatic sediments are naturally anoxic, and the transition depth from oxic to anoxic conditions varies with organic matter sediment content and rate of burial[21].

Recent history of deoxygenation

Although contemporary atmospheric oxygen is relatively stable[22] and sufficient to support an enormous diversity of complex terrestrial life forms, the oxygen supply can be biologically limiting in many of today's aquatic habitats. Hypoxic zones, usually defined as DO levels of <2 mg l^{-1} (or 64 µmol kg^{-1}), and anoxic habitats are commonly observed in aquatic ecosystems. In recent decades, DO concentrations have rapidly and substantially declined across both freshwater and marine habitats, ranging from small ponds to large lakes and reservoirs, rivers, inland seas, estuaries, and areas of the coastal and open ocean[19,20,23–27]. Rates of deoxygenation in lakes and reservoirs since 1980 represent oxygen losses of 5.5% and 18.6% for surface and deep waters, respectively[20]. Meanwhile, average rates of marine deoxygenation have been lower (~2% decrease in DO globally since 1960[24]) but far more geographically and volumetrically extensive. Rates are also highly variable among oceanic basins. For example, some areas of the ocean, such as the midwaters off of Central California, USA, have lost over 40% of baseline DO in only a few decades[28].

Evidence of increasing lake deoxygenation precedes the year 1900[23], whereas data on coastal hypoxia show DO availability declining primarily after around 1950[19] and a broad awareness of open ocean deoxygenation arising only in the twenty-first century[28–30]. Across all types of aquatic ecosystems, the volumes and spatial extents of oxygen-depleted water are expanding substantially[24,31–33]. For example, there has been a fourfold increase in the volume of anoxic ocean water since 1960[24]. The number of hypoxic and anoxic coastal zones is also on the rise, with hundreds of regions recorded across the world[19,25]. In lakes, there has been a more than 50% increase in the volume of anoxic water since 1980, with the amount of low-oxygen lake water increasing by about 1% per decade on average[33]. Deoxygenation thus represents one of the greatest threats to the sustainability of aquatic ecosystems and the stability of the Earth system as a whole.

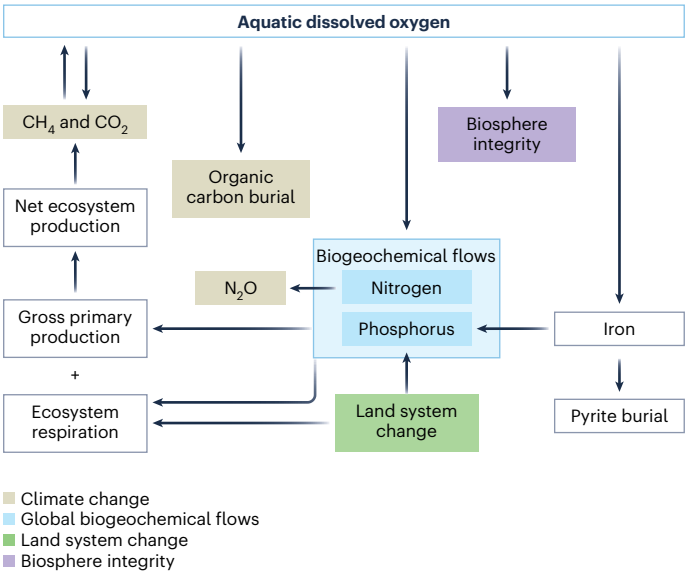

Fig. 1 | How dissolved oxygen interacts with other planetary boundaries and major Earth system elements. The coloured boxes represent planetary boundaries that interact with aquatic deoxygenation, including climate change (brown), global biogeochemical flows (blue), land system change (green) and biosphere integrity (purple). Interactions between other planetary boundary processes that do not include dissolved oxygen are not considered. The specifics of how deoxygenation is affected by other planetary boundaries are described further in Fig. 2.

Deoxygenation control variables and thresholds

Control variables are metrics used to quantify the state of a planetary boundary process[1–3]. In aquatic ecosystems, control variables associated with quantifying the DO concentration and changes through space and time relative to historic norms are essential to determining the impacts of DO loss. The threshold concentrations of DO below which anaerobic metabolisms dominate represent critical control variables to define the impacts of deoxygenation and, when aggregated, the impacts on global biogeochemical processes. The global extent of anoxic waters as a percentage of the total habitat area and volume serves as a suitable control variable that lends itself to empirical determination and to characterizing the effects of deoxygenation on biogeochemical functioning. The engagement of a wide range of anaerobic microbial metabolisms represents a fundamental transition for microbially mediated processes regulating the cycling of many elements, such as nitrogen, phosphorus, sulfur, iron, mercury and carbon (Fig. 1).

A threshold of 2 mg l^{-1} DO is commonly used to define the threshold for hypoxia. Although such an absolute benchmark can be useful for studies of individual species' physiological responses, we note that deoxygenation is often better defined in terms of changes in the area and volume of hypoxic habitat relative to historic norms to characterize the broader biological impacts of oxygen declines. This definition recognizes that sensitivities to low oxygen can differ widely among species and that the biological consequences of deoxygenation vary from lethal to sublethal effects on individual organisms to far-reaching changes in food-web structure. For example, the copepod *Lucicutia hulsemannae*, which is abundant in ODZs, has been found "actively growing and developing" at 0.06 mg l^{-1} (ref. 32). Meanwhile, species

https://doi.org/10.1038/s41559-024-02448-y

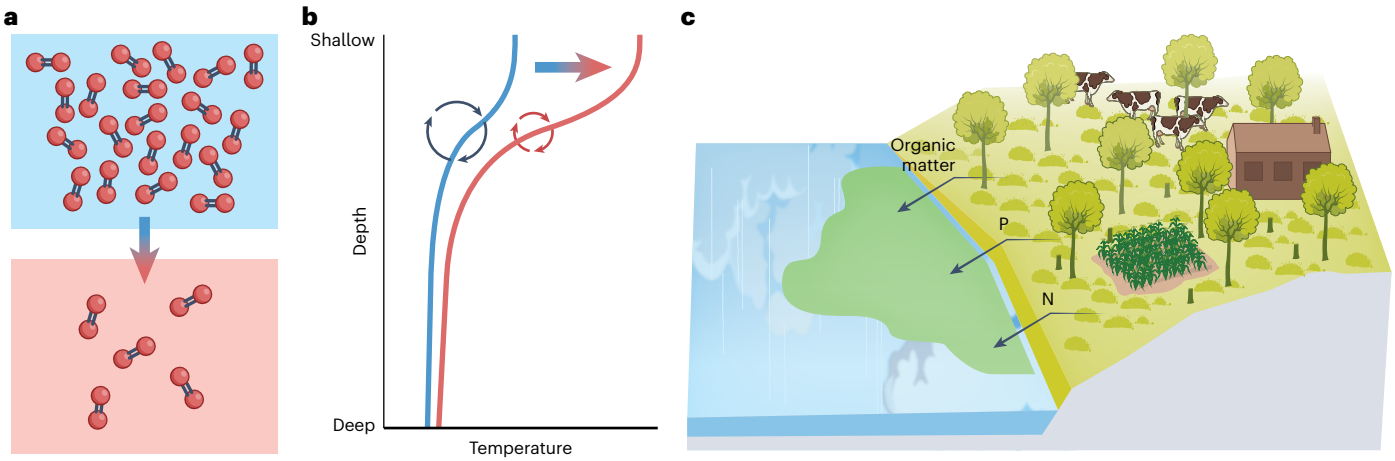

Fig. 2 | Major drivers of deoxygenation in aquatic ecosystems. a–**c**, Many regions have exhibited substantial deoxygenation due to factors including reduced DO solubility at higher temperatures (**a**); increases in density difference between layers in the water column (that is, stratification strength), which reduces the ventilation of deep-water habitats (the blue line indicates an example conceptual historic profile of temperature through the water column, and the red line indicates an example contemporary profile; the circular arrows indicate the relative strength of mixing between depths in the water column in these two profiles) (**b**); and increases in organic matter and nutrient (phosphorous (P) and nitrogen (N)) fluxes that stimulate algal growth, bacterial respiration and overall greater DO consumption (**c**). Blue, cold; red, warm; molecules are O_2.

such as brook trout (*Salvelinus fontinalis*) actively avoid DO concentrations below 5 mg l^{-1} (ref. 33). Sensitivity thresholds are notably much higher for most animals than for microorganisms. However, the overall biological consequences of deoxygenation cannot be predicted using a single DO concentration threshold or partial pressure[34,35]. Rather, the effects of deoxygenation on organisms occur along a continuum dictated by DO supply and demand and ecological and evolutionary exposure history[36]. Determining the biological impacts of deoxygenation thus requires consideration of both DO availability (usually measured as per cent saturation or partial pressure) and organismal requirements. For most organisms, particularly ectotherms, DO demand is physiologically coupled with temperature, with demands increasing as a function of ambient temperature. Biological DO demand can vary among species, populations, life-history stages and individuals, making it difficult to isolate a single threshold even within broadly grouped taxa[35,37]. However, it is well established that as oxygen concentrations decline, an increasing number of species are adversely affected, both through direct physiological effects and via transformations of food-web structure.

There are numerous aquatic habitats where deoxygenation has already contributed to biodiversity loss, from species extirpations to the collapse of entire food webs[25,38]. Deoxygenation can induce state shifts in ecosystems when critical thresholds in control variables are crossed. For example, anthropogenically induced increases in productivity (termed 'cultural eutrophication') also increase the pool of labile carbon entering deep waters, which fuels oxygen-consuming respiration and, consequently, deoxygenation. In turn, increases in anoxia alter chemical reactions, including the release of phosphorus from redox-sensitive iron and manganese in sediments[39], which fuels further productivity. This amplifying feedback can promote a transition to alternative and undesirable ecosystem states, characterized by harmful algal blooms and widespread anoxia[40,41].

The observed, substantial and pervasive ecological consequences of DO losses demonstrate that the global deoxygenation of aquatic systems is approaching critical thresholds, similar to other planetary boundary processes such as climate change and land system change[3]. Crossing the deoxygenation threshold means that DO availability would cause severe and/or nonlinear ecological changes that, in the aggregate, threaten the stability of other Earth system processes. In many freshwater and marine systems, regional thresholds have already been crossed, and severe ecological impairment is pervasive. Continued deoxygenation risks increasing the spatial and temporal extent of DO below levels sufficient to maintain a 'safe operating space', especially when superimposed on natural climate variability and an increasing likelihood of extreme events[42].

Interactions between deoxygenation and other planetary boundaries

Deoxygenation interacts with other planetary boundary processes, including climate change, land system change and biogeochemical flows (Fig. 1). Deoxygenation is caused by three overarching drivers that are components of these other planetary boundary processes (Fig. 2): (1) decreases in the solubility of oxygen in water resulting from increasing temperatures, (2) reduced deep-water ventilation due to stronger stratification and associated reduced water-column mixing and circulation, and (3) increases in oxygen-consuming respiration linked to both elevated temperature and enhanced inputs of nutrients and organic matter. Deoxygenation, in turn, alters global biogeochemical flows and carbon cycling feedbacks to climate change and decreases biodiversity; the aerobic respiration that drives oxygen loss also contributes to acidification, especially at depths below the surface mixed layer.

Climate change is increasing water temperatures globally and thereby decreasing DO solubility[20,43,44]. Indeed, temperature-induced reduction in DO solubility explains the majority of DO losses in the surface waters of both lakes and oceans[20,24]. Climate change is also increasing the frequency and duration of aquatic heatwaves in both oceans and lakes[45,46], which are predicted to increase in severity by the end of the century[46,47]. Although the effects of heatwaves on deoxygenation remain largely unassessed, Henry's law suggests that heatwaves will substantially reduce oxygen solubility and may therefore be a substantial threat exacerbating deoxygenation. Simultaneously, anthropogenic warming is reducing the frequency and intensity of gas exchange between water masses and the atmosphere, reducing ventilation and mixing and thus contributing to deoxygenation in deep waters of both freshwater and marine environments[20,24,25,48]. As surface deoxygenation continues, less DO is delivered to deep-water habitats.

Increases in stratification and associated reductions in ventilation are regulated by several factors. In many lakes, reservoirs and coastal systems, deep waters are often renewed seasonally. By contrast, the deep ocean is supplied with DO through subduction

of oxygen-saturated water at high latitudes, which is subsequently circulated to lower latitudes and bottom waters of coastal systems. Changes in stratification are occurring for several reasons. First, rates of surface-water warming have generally been faster than those in deep waters (for example, see ref. 20). This strengthens density gradients in the water column and thereby reduces vertical mixing. Density gradients can also be strengthened by changes in salinity associated with climate change. Specifically, runoff from the melting continental ice sheets or intense precipitation can reduce surface salinity and enhance stratification in the oceans, particularly in nearshore and high-latitude environments. In lakes and reservoirs, salinity gradients can be induced by subduction of saline water inputs[49]. Additionally, changes in precipitation and evaporation can dramatically alter the salinity balance in both inland and coastal waters. Across many aquatic ecosystems, long-term declines in ice cover also alter stratification and thus gas exchange between water masses and the atmosphere. Ice tends to limit the exchange of oxygen between water and the atmosphere, reducing deep-water ventilation at polar latitudes[50]; hence, in some scenarios, the loss of sea ice may actually enhance deep-sea ventilation[51]. Meanwhile, in lakes and freshwater reservoirs, the widespread loss of ice cover is increasing the duration of seasonal stratification, providing more time for summer deep-water deoxygenation to occur[33,52,53].

Land system change contributes to widespread deoxygenation largely through its controls on biogeochemical flows, including nitrogen, phosphorus and organic matter inputs. Increases in agricultural and urbanized land cover are often the primary driver of deoxygenation in lakes and coastal zones because they are associated with increased mobilization of nitrogen and phosphorus[19,20,23,25]. These two macronutrients tend to increase algal biomass and subsequent photosynthesis, and thus nutrient inputs to surface waters can increase DO concentrations by stimulating primary productivity[20]. However, in deeper waters, increased settling of labile organic matter from this primary production or from watershed inputs can elevate rates of oxygen-consuming bacterial respiration. For example, lakes with high chlorophyll concentrations (an indicator of high primary productivity) are also sites where deep waters are consistently anoxic[20]. Although high primary productivity rates can occur naturally[54], they are frequently amplified by land system change and terrestrial runoff[19,23]. Deoxygenation is not alone in being at least partly caused by other planetary boundary processes, and other planetary boundary processes similarly interact with one another, such as how biogeochemical flows of nitrogen and phosphorus are influenced by land system change and climate change[5].

Impacts of deoxygenation on other planetary boundaries

Because planetary boundary processes are not isolated and independent[5], crossing the deoxygenation boundary threshold would have substantial impacts on other planetary boundary processes, including climate change, biogeochemical flows and biosphere integrity[6] (Fig. 1). DO is a key factor in determining carbon-processing rates and export, and thus affects the exchange of greenhouse gases between aquatic ecosystems and the atmosphere, aquatic biodiversity, and food web functioning[48,55]. However, the effect of deoxygenation on the direction and magnitude of greenhouse gas exchange, and hence climate change, is difficult to predict because deoxygenation increases both aquatic sediment organic carbon sinks[56] and the production of potent greenhouse gases, including nitrous oxide (N_2O) and methane (CH_4)[55], which can exacerbate climate change. It may also decrease carbon dioxide (CO_2) emissions from some aquatic ecosystems[57].

Deoxygenation regulates global biogeochemical flows, including the cycling of nitrogen and phosphorus, sometimes exacerbating eutrophication and initiating an amplifying feedback on deoxygenation[58–60]. By contrast, deoxygenation can reduce bioavailable nitrogen, especially in the oceans. Anaerobic microbial metabolisms, including denitrification and anaerobic ammonium oxidation (anammox), engage under conditions of very low oxygen and result in the loss of fixed nitrogen, and in turn can reduce primary production. Nitrogen fixation by diazotrophs is, on various timescales, also expected to compensate for at least part of any deoxygenation-driven loss of fixed nitrogen, with theoretical potential for an amplifying feedback that may further accelerate deoxygenation[61]. Nitrogen cycling under anaerobic conditions also contributes to N_2O emissions, potentially providing a feedback to climate change. For example, oceanic ODZs generate about half of marine N_2O emissions despite occupying only 0.35% of the ocean's volume[55,62,63]. Aerobic nitrogen metabolisms also represent important oxygen sinks, and these contribute to maintaining marine ODZs[64]. Cumulatively, through its control on the fate of carbon, phosphorus and nitrogen, DO or its absence regulates the role of oceans and inland waters in modulating Earth's climate over geological timescales[58].

Deoxygenation shapes patterns of genetic and functional biodiversity as well as species distributions[36]. At the scale of individual organisms, low oxygen can contribute to reduced sensory abilities, growth, body size and reproduction, as well as high mortality; it can therefore be a strong selective force that shapes evolution[65–68]. Sublethal effects occur at DO levels about 40% higher, on average, than those that cause mortality[34]. These impacts can drive inter-population variation in sensitivities to low DO[69]. Deoxygenation-driven changes in organisms' physiology can also alter species ranges and cause patterns of biodiversity to shift in space and time. For example, as deeper tropical waters become more oxygen depleted, organisms may shift to cooler, higher-latitude shallower waters to find environments that are more suitable to their current physiological demands[25,36]. Moreover, deoxygenation-induced increases in hydrogen sulfide (H_2S) and mixing of this toxic gas into oxygenated habitats can lead to animal kills and gas emissions to the atmosphere[70].

The effects of deoxygenation on individual organisms or populations can aggregate to regulate food-web structure, species extinction rates and carbon processing[71,72]. Indeed, hypoxic and anoxic aquatic habitats, particularly those located in freshwater and coastal areas, are routinely referred to as 'dead zones' due to the substantial loss of eukaryotic life found there. In turn, these compromised habitats threaten the sustainability of critical ecosystem services, including fisheries[48,73], with potential economic and societal consequences[74]. The combined effects of contemporary climate change and deoxygenation are projected to amplify the risks of marine species extinction by >70%, with tropical oceans most likely to exhibit species losses in the coming decades[38]. Equivalent projections for freshwater biodiversity do not exist at this time but may be even more dire given the exceptionally high rates of freshwater deoxygenation to date and the comparatively limited dispersal abilities of freshwater species[20].

Deoxygenation in the future

Maintaining DO above biotic thresholds in the extent, volume and severity of deoxygenation is a paramount research and policy challenge that requires immediate attention. Widespread deoxygenation is likely to continue for decades to centuries as human population growth and intensified, inequitable resource use continue. Reducing greenhouse gas emissions, nutrient runoff and organic carbon inputs (for example, raw sewage loading) would slow or potentially reverse deoxygenation. Avoiding activities that stimulate DO consumption such as CO_2 removal via iron fertilizers or bottom disturbance from trawling and seabed mining may prevent additional deoxygenation. In the absence of major mitigation efforts, ongoing global environmental changes are expected to push deoxygenation—along with several other planetary boundary processes—towards or beyond critical thresholds. Current models predict that ongoing increases in greenhouse gas emissions will continue to increase air and water temperatures, stimulating further deoxygenation in surface waters[75,76]. Continued warming and reduced ventilation will further exacerbate deoxygenation in deeper layers in both lakes and

oceans. Even if climate warming stopped immediately, deep oceans would probably continue to lose DO for centuries, with cumulative losses >10% of pre-industrial levels[77]. However, surface-water deoxygenation would probably respond more quickly than deep waters to a cessation of anthropogenic CO_2 emissions[77].

Future impacts of changes in land use and associated biogeochemical flows on deoxygenation are likewise uncertain. These changes will vary across the globe and are tied to complex socio-ecological feedbacks, including changes in economic activity, population growth and movement, degree of urbanization, water use, agriculture and land management, and regulations[4]. Improved land-use practices can be effective in reducing the flux of macronutrients including nitrogen and phosphorus into aquatic ecosystems. However, challenges wrought by increasing anthropogenic resource consumption, effects of increasing temperatures or precipitation impacts on nutrient mobilization often counteract potential benefits from nutrient management, so more aggressive reductions may be needed to increase lake and coastal DO concentrations. For example, in the Chesapeake Bay, USA, long-term increases in hypoxia have continued due to ongoing warming, despite reductions in nutrient inputs[78]. Increasingly aggressive reductions may thus be required to increase DO concentrations as warming continues, particularly in lake and coastal environments.

Recognition of the importance of aquatic deoxygenation is also growing in many management and policy frameworks. Safe DO levels are essential for maintaining the diverse ecosystem services provided by aquatic ecosystems globally (from fishing and aquaculture to tourism and cultural practices). Oxygen is considered an Essential Ocean Variable by the IOC-UNESCO Global Ocean Observing System, and the World Meteorological Organization considers interior ocean oxygen an Essential Climate Variable. Safe DO levels are also essential for achieving United Nations Sustainable Development Goals (for example, SDG 2, 'End hunger, achieve food security and improved nutrition, and promote sustainable agriculture'; SDG 6, 'Ensure availability and sustainable management of water and sanitation for all'; and SDG 14, 'Conserve and sustainably use the oceans, seas and marine resources for sustainable development'). Notably, several of the ocean-based climate interventions being considered to remove CO_2 from the atmosphere could affect marine DO levels, and some may enhance midwater or seafloor deoxygenation[79]. DO is also a frequently managed water quality criterion. Monitoring networks range from multinational collaborations such as the Baltic Observatory and research networks such as the Global Lake Ecological Observatory Network, to those run by individuals and local organizations. Recognition of deoxygenation as a planetary boundary will increase awareness, mitigation incentives and actionability of this major threat to Earth system stability. Future research on this topic should include quantification of deoxygenation thresholds and assessments of how close we are to surpassing a safe operating space with respect to oxygen loss.

References

1. Rockström, J. et al. A safe operation space for humanity. *Nature* **461**, 472–475 (2009).
2. Steffen, W. et al. Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855 (2015).
3. Richardson, K. et al. Earth beyond six of nine planetary boundaries. *Sci. Adv.* **9**, eadh2458 (2023).
4. Rockström, J. et al. Safe and just Earth system boundaries. *Nature* **619**, 102–111 (2023).
5. Lade, S. J. et al. Human impacts on planetary boundaries amplified by Earth system interactions. *Nat. Sustain.* **3**, 119–128 (2020).
6. Ferrer, E. *Climate–Fishery Interactions in Coastal Ecosystems*. Thesis, Scripps Institute of Oceanography, UC San Diego, 6–47 (2023).
7. Raymond, J. & Segrè, D. The effect of oxygen on biochemical networks and the evolution of complex life. *Science* **311**, 1764–1767 (2006).
8. Fang, J. Animals thrive without oxygen at sea bottom. *Nature* **464**, 825 (2010).
9. Scott, A. C. & Glasspool, I. J. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proc. Natl Acad. Sci. USA* **103**, 10861–10865 (2006).
10. Falkowski, P. G. et al. The rise of oxygen over the past 205 million years and the evolution of large placental mammals. *Science* **309**, 2202–2204 (2005).
11. Poulsen, C. J., Tabor, C. & White, J. D. Long-term climate forcing by atmospheric oxygen concentrations. *Science* **348**, 1238–1242 (2015).
12. Pohl, A. et al. Continental configuration controls ocean oxygenation during the Phanerozoic. *Nature* **608**, 523–527 (2022).
13. He, T. et al. Possible links between extreme oxygen perturbations and the Cambrian radiation of animals. *Nat. Geosci.* **12**, 468–474 (2019).
14. Kraft, B. et al. Oxygen and nitrogen production by an ammonia-oxidizing archaeon. *Science* **375**, 97–100 (2022).
15. Kreling, J. et al. The importance of physical transport and oxygen consumption for the development of a metalimnetic oxygen minimum in a lake. *Limnol. Oceanogr.* **62**, 348–363 (2017).
16. Stramma, L. et al. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* **2**, 33–37 (2012).
17. Mi, C. et al. The formation of a metalimnetic oxygen minimum exemplifies how ecosystem dynamics shape biogeochemical processes: a modelling study. *Water Res.* **175**, 115701 (2020).
18. Smith, K. L., Messié, M., Connolly, T. P. & Huffard, C. L. Decadal time-series depletion of dissolved oxygen at abyssal depths in the northeast Pacific. *Geophys. Res. Lett.* **49**, e2022GL101018 (2022).
19. Diaz, R. J. & Rosenberg, R. Spreading dead zones and consequences for marine ecosystems. *Science* **321**, 926–929 (2008).
20. Jane, S. F. et al. Widespread deoxygenation of temperate lakes. *Nature* **594**, 66–70 (2021).
21. Brune, A., Frenzel, P. & Cypionka, H. Life at the oxic–anoxic interface: microbial activities and adaptations. *FEMS Microbiol. Rev.* **24**, 691–710 (2000).
22. Huang, J. et al. The global oxygen budget and its future projection. *Sci. Bull.* **63**, 1180–1186 (2018).
23. Jenny, J. P. et al. Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. *Glob. Change Biol.* **22**, 1481–1489 (2016).
24. Schmidtko, S., Stramma, L. & Visbeck, M. Decline in global oceanic oxygen content during the past five decades. *Nature* **542**, 335–339 (2017).
25. Breitburg, D. et al. Declining oxygen in the global ocean and coastal waters. *Science* **359**, eaam7240 (2018).
26. Limburg, K. E., Breitburg, D., Swaney, D. P. & Jacinto, G. Ocean deoxygenation: a primer. *One Earth* **2**, 24–29 (2020).
27. Zhi, W., Kligler, C., Liu, J. & Li, L. Widespread deoxygenation in warming rivers. *Nat. Clim. Change* **13**, 1105–1113 (2023).
28. Levin, L. A. Manifestation, drivers, and emergence of open ocean deoxygenation. *Annu. Rev. Mar. Sci.* **10**, 229–260 (2018).
29. Ono, T., Watarlabe, Y. W., Tadokoro, K. & Saino, T. Temporal increases of phosphate and apparent oxygen utilization in the subsurface waters of western subarctic Pacific from 1968 to 1998. *Geophys. Res. Lett.* **28**, 3285–3288 (2001).
30. Keeling, R. F., Körtzinger, A. & Gruber, N. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2**, 199–229 (2010).
31. Stramma, L., Schmidtko, S., Levin, L. A. & Johnson, G. C. Ocean oxygen minima expansions and their biological impacts. *Deep Sea Res. 1 Oceanogr. Res. Pap.* **57**, 587–595 (2010).
32. Grégoire, M. et al. A global ocean oxygen database and atlas for assessing and predicting deoxygenation and ocean health in the open and coastal ocean. *Front. Mar. Sci.* **8**, 724913 (2021).

33. Jane, S. F. et al. Longer duration of seasonal stratification contributes to widespread increases in lake hypoxia and anoxia. *Glob. Change Biol.* https://doi.org/10.1111/gcb.16525 (2022).
34. Vaquer-Sunyer, R. & Duarte, C. M. Thresholds of hypoxia for marine biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 15452–15457 (2008).
35. Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O. & Huey, R. B. Climate change tightens a metabolic constraint on marine habitats. *Science* **348**, 1132–1136 (2015).
36. Deutsch, C., Penn, J. L. & Seibel, B. Metabolic trait diversity shapes marine biogeography. *Nature* **585**, 557–562 (2020).
37. Vaquer-Sunyer, R. & Duarte, C. M. Experimental evaluation of the response of coastal Mediterranean planktonic and benthic metabolism to warming. *Estuaries Coasts* **36**, 697–707 (2013).
38. Penn, J. L. & Deutsch, C. Avoiding ocean mass extinction from climate warming. *Science* **376**, 524–526 (2022).
39. Mortimer, C. H. The exchange of dissolved substances between mud and water in lakes. *Br. Ecol. Soc.* **29**, 280–329 (1941).
40. Wang, S., Jin, X., Bu, Q., Jiao, L. & Wu, F. Effects of dissolved oxygen supply level on phosphorus release from lake sediments. *Colloids Surf. A* **316**, 245–252 (2008).
41. Hilt, S., Brothers, S., Jeppesen, E., Veraart, A. J. & Kosten, S. Translating regime shifts in shallow lakes into changes in ecosystem functions and services. *BioScience* **67**, 928–936 (2017).
42. Harris, R. M. B. et al. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Change* **8**, 579–587 (2018).
43. O'Reilly, C. M. et al. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett*. https://doi.org/10.1002/2015GL066235 (2015).
44. Johnson, G. C. & Lyman, J. M. Warming trends increasingly dominate global ocean. *Nat. Clim. Change* **10**, 757–761 (2020).
45. Frölicher, T. L., Fischer, E. M. & Gruber, N. Marine heatwaves under global warming. *Nature* **560**, 360–364 (2018).
46. Woolway, R. I. et al. Lake heatwaves under climate change. *Nature* **589**, 402–407 (2021).
47. Oliver, E. C. J. et al. Projected marine heatwaves in the 21st century and the potential for ecological impact. *Front. Mar. Sci.* **6**, 734 (2019).
48. Garçon, V. et al. Multidisciplinary observing in the world ocean's oxygen minimum zone regions: from climate to fish—the VOICE Initiative. *Front. Mar. Sci.* **6**, 722 (2019).
49. Wiltse, B., Yerger, E. C. & Laxson, C. L. A reduction in spring mixing due to road salt runoff entering Mirror Lake (Lake Placid, NY). *Lake Reserv. Manage.* **36**, 109–121 (2020).
50. Cliff, E., Khatiwala, S. & Schmittner, A. Glacial deep ocean deoxygenation driven by biologically mediated air–sea disequilibrium. *Nat. Geosci.* **14**, 43–50 (2021).
51. Polyakov, I. V. et al. Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science* **356**, 285–291 (2017).
52. Sharma, S. et al. Widespread loss of lake ice around the Northern Hemisphere in a warming world. *Nat. Clim. Change* **9**, 227–231 (2019).
53. Woolway, R. I. et al. Phenological shifts in lake stratification under climate change. *Nat. Commun.* **12**, 2318 (2021).
54. Zhou, J., Leavitt, P. R., Zhang, Y. & Qin, B. Anthropogenic eutrophication of shallow lakes: is it occasional? *Water Res.* **221**, 118728 (2022).
55. Canadell, J. G. et al. in *Climate Change 2021: The Physical Science Basis* (eds Masson-Delmotte, V. et al.) Ch. 5 (IPCC, Cambridge Univ. Press, 2021).
56. Ruvalcaba Baroni, I., Palastanga, V. & Slomp, C. P. Enhanced organic carbon burial in sediments of oxygen minimum zones upon ocean deoxygenation. *Front. Mar. Sci.* **6**, 839 (2020).
57. Finlay, K. et al. Decrease in CO_2 efflux from northern hardwater lakes with increasing atmospheric warming. *Nature* **519**, 215–218 (2015).
58. Van Cappellen, P. & Ingall, E. D. Redox stabilization of the atmosphere and oceans by phosphorus-limited marine productivity. *Science* **271**, 493–496 (1996).
59. Oschlies, A., Brandt, P., Stramma, L. & Schmidtko, S. Drivers and mechanisms of ocean deoxygenation. *Nat. Geosci.* **11**, 467–473 (2018).
60. Niemeyer, D., Kemena, T. P., Meissner, K. J. & Oschlies, A. A model study of warming-induced phosphorus–oxygen feedbacks in open-ocean oxygen minimum zones on millennial timescales. *Earth Syst. Dyn.* **8**, 357–367 (2017).
61. Landolfi, A., Dietze, H., Koeve, W. & Oschlies, A. Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle. *Biogeosciences* **10**, 1351–1363 (2013).
62. Karstensen, J., Stramma, L. & Visbeck, M. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* **77**, 331–350 (2008).
63. Codispoti, L. A. Interesting times for marine N_2O. *Science* **327**, 1339–1340 (2010).
64. Beman, J. M. et al. Substantial oxygen consumption by aerobic nitrite oxidation in oceanic oxygen minimum zones. *Nat. Commun.* **12**, 7043 (2021).
65. Landry, C. A., Steele, S. L., Manning, S. & Cheek, A. O. Long term hypoxia suppresses reproductive capacity in the estuarine fish, *Fundulus grandis*. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **148**, 317–323 (2007).
66. Brander, K. Reduced growth in Baltic Sea cod may be due to mild hypoxia. *ICES J. Mar. Sci.* **77**, 2003–2005 (2020).
67. Gallo, N. D. & Levin, L. A. Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. *Adv. Mar. Biol.* **74**, 117–198 (2016).
68. Verberk, W. C. E. P. et al. Body mass and cell size shape the tolerance of fishes to low oxygen in a temperature-dependent manner. *Glob. Change Biol.* **28**, 5695–5707 (2022).
69. Chapman, L. J. & Hulen, K. G. Implications of hypoxia for the brain size and gill morphometry of mormyrid fishes. *J. Zool.* **254**, 461–472 (2001).
70. Kump, L. R., Pavlov, A. & Arthur, M. A. Massive release of hydrogen sulfide to the surface ocean and atmosphere during intervals of oceanic anoxia. *Geology* **33**, 397–400 (2005).
71. Stockey, R. G., Pohl, A., Ridgwell, A., Finnegan, S. & Sperling, E. A. Decreasing Phanerozoic extinction intensity as a consequence of Earth surface oxygenation and metazoan ecophysiology. *Proc. Natl Acad. Sci. USA* **118**, e2101900118 (2021).
72. Levin, L. A. & Gallo, N. D. in *Ocean Deoxygenation: Everyone's Problem—Causes, Impacts, Consequences and Solutions* (eds Laffoley, D. & Baxter, J. M.) 341–361 (International Union for Conservation of Nature and Natural Resources, 2019).
73. Breitburg, D. L., Hondorp, D. W., Davias, L. A. & Diaz, R. J. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annu. Rev. Mar. Sci.* **1**, 329–349 (2009).
74. Rose, K. A. et al. in *Ocean Deoxygenation: Everyone's Problem—Causes, Impacts, Consequences and Solutions* (eds Laffoley, D. & Baxter, J. M.) 519–544 (International Union for Conservation of Nature and Natural Resources, 2019).
75. Cabré, A., Marinov, I., Bernardello, R. & Bianchi, D. Oxygen minimum zones in the tropical Pacific across CMIP5 models: mean state differences and climate change trends. *Biogeosciences* **12**, 5429–5454 (2015).
76. Kwiatkowski, L. et al. Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* **17**, 3439–3470 (2020).

77. Oschlies, A. A committed fourfold increase in ocean oxygen loss. *Nat. Commun.* **12**, 8 (2021).
78. Ni, W., Li, M. & Testa, J. M. Discerning effects of warming, sea level rise and nutrient management on long-term hypoxia trends in Chesapeake Bay. *Sci. Total Environ.* **737**, 139717 (2020).
79. Levin, L. et al. Deep-sea impacts of climate interventions. *Science* **379**, 978–981 (2023).

Acknowledgements

K.C.R. acknowledges support from US National Science Foundation (NSF) grant nos 2048031 and 1754265. E.M.F. acknowledges graduate support from the NSF GRFP (UCSD DGE-2038238), UC San Diego (PPPF) and the Aburto Lab at the Scripps Institution of Oceanography, and postdoctoral support from UC Santa Cruz. S.R.C. acknowledges support from the North Temperate Lakes Long-Term Ecological Research programme from the NSF Cooperative Agreement no. DEB-2025982. S.C.D. acknowledges support from NSF grant no. IOS-2345023. V.C.G. and M.G. acknowledge support from the CE2COAST project funded by ANR (FR), BELSPO (BE), FCT (PT), IZM (LV), MI (IE), MIUR (IT), Rannis (IS), IRP MAST (Multiscale Adaptive Strategies) and RCN (NO) through the 2019 'Joint Transnational Call on Next Generation Climate Science in Europe for Oceans' initiated by JPI Climate and JPI Oceans. V.C.G. also acknowledges support from the EU H2020 FutureMares project (Theme LC-CLA-06-2019, grant agreement no. 869300) and the Scientific Committee on Oceanic Research (SCOR) Working Group 155, funded by national SCOR committees and a grant to SCOR from the NSF (grant no. OCE-1840868). P.R.L. acknowledges support from the Canada Research Chairs programme and grants from the Natural Sciences and Engineering Research Council of Canada. M.G. acknowledges support from the EU H2020 BRIDGE-BS project under grant agreement no. 101000240 and the EU HE NECCTON project under grant agreement no. 101081273. S.F.J. was supported by the Cornell Atkinson Center for Sustainability. S.F.J. was also partially supported by a Society of Science Postdoctoral Fellowship from the University of Notre Dame. L.A.L. acknowledges support from an NSF AccelNet Program award no. 2114717 via University of Texas subaward no. 308056-0001A and the National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science Competitive Research Program under award no. NA18NOS4780172. V.C.G., L.A.L., D.B., A.O., S.C. and M.G. acknowledge fruitful discussions around the topic of deoxygenation as a potential planetary boundary, which took place within the Global Ocean Oxygen Network Working Group being supported by IOC UNESCO.

Author contributions

All authors (K.C.R., E.M.F., S.R.C., S.C., S.C.D., V.C.G., M.G., S.F.J., P.R.L., L.A.L., A.O. and D.B.) contributed to the writing and editing of this manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence should be addressed to Kevin C. Rose.

Peer review information *Nature Ecology & Evolution* thanks David Karl, Thorsten Blenckner, Katherine Richardson and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

[1]Department of Biological Sciences, Rensselaer Polytechnic Institute, Troy, NY, USA. [2]Department of Civil and Environmental Engineering, Rensselaer Polytechnic Institute, Troy, NY, USA. [3]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA. [4]Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA, USA. [5]Center for Limnology, University of Wisconsin, Madison, WI, USA. [6]Departments of Microbiology and Immunology and Earth, Ocean, and Atmospheric Sciences, University of British Columbia, Vancouver, British Columbia, Canada. [7]Department of Biology, University of Massachusetts Dartmouth, North Dartmouth, MA, USA. [8]CNRS—Laboratoire d'Etudes en Géophysique et Océanographie Spatiales, Toulouse, France. [9]CNRS - Institut de Physique du Globe de Paris, Paris, France. [10]MAST-FOCUS, Department of Astrophysics, Geophysics and Oceanography, University of Liège, Liège, Belgium. [11]Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, USA. [12]Cornell Atkinson Center for Sustainability, Cornell University, Ithaca, NY, USA. [13]Institute of Environmental Change and Society, University of Regina, Regina, Saskatchewan, Canada. [14]GEOMAR Helmholtz-Centre for Ocean Research Kiel, Kiel, Germany. [15]Smithsonian Environmental Research Center, Edgewater, MD, USA. [16]Present address: Department of Biology, University of Notre Dame, Notre Dame, IN, USA. ✉e-mail: rosek4@rpi.edu