

Causes and consequences of changing oxygen availability in lakes

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Abstract

Changing oxygen availability in lakes and reservoirs is a fundamental limnological challenge of our time, with massive consequences for freshwater ecosystem functioning and water quality. Cross-lake surveys, paleolimnological studies, and long-term monitoring records indicate that many lakes are exhibiting declines in both surface and bottom-water oxygen availability due to climate and land use change, though a few lakes are exhibiting increases in oxygen. By analyzing time series of oxygen monitoring data from ~400 lakes, I find that some lakes may be experiencing a decoupling of surface and bottom oxygen dynamics: variability in surface oxygen concentrations is decreasing in some lakes while variability in bottom oxygen concentrations is increasing. Changes in both oxygen concentrations and variability have many implications for lake functioning because oxygen concentrations control many ecosystem processes. Consequently, lake ecosystem provisioning and cultural services (e.g., drinking water, fisheries, recreation) will likely be impaired by declining oxygen, whereas the effects of changing oxygen on regulatory and supporting ecosystem services (e.g., nitrate removal through denitrification,

carbon burial, sediment fluxes of phosphorus) may be more equivocal. These challenges motivate a research agenda focused on expanding the geographical range, temporal duration, and spatial extent of lake oxygen monitoring, as well as new approaches for studying and managing lakes (whole-ecosystem experiments, near-term oxygen forecasts). Looking ahead, advances in sensor technology, monitoring networks, data sharing, and forecasting, as well as the demonstrated success of environmental legislation in decreasing hypoxia, provide important opportunities for guiding restoration and science on lake oxygen.

Keywords: Anoxia, Eutrophication, Freshwater ecosystem services, Hypoxia, Oxygen variability, Reservoir

Introduction

Dissolved oxygen (DO) is the most important metric of lake and reservoir water quality (sensu Hutchinson 1957, Wetzel 2001). Oxygen concentrations are an emergent property of a suite of interacting physical, chemical, and biological processes in freshwaters that both increase and decrease oxygen availability (Odum 1956, Langman et al. 2010, Ladwig et al. 2021). Enabled by advances in sensor technology, limnologists are gaining a new perspective on the dynamic nature of lake DO profiles and concentrations, which vary substantially over both space and time (e.g., Crawford et al. 2014, Obertegger et al. 2017, Fernández Castro et al. 2021). This variability has important consequences for the distribution and metabolism of aerobic and anaerobic organisms, biogeochemical processes, and overall ecosystem functioning of freshwaters. Consequently, understanding the availability of – and changes in – oxygen in lakes is critical for understanding lake ecosystems as a whole.

This Kilham Lecture article is divided into five parts, representing a hybrid of a review article, research analysis, and commentary. I first review the evidence on changing oxygen concentrations in lakes and reservoirs (hereafter, lakes) and its causes. Second, I analyze monitoring data from ~400 lakes to explore how variability in lake oxygen concentrations (not just mean oxygen concentrations) may be changing over time. Third, I summarize existing literature to predict how changing oxygen concentrations and variability may affect different lake ecosystem services. Fourth, I present recommendations for lake oxygen research priorities based on the current state of the field. Finally, I provide an outlook for the future of lake oxygen restoration and science, highlighting the promise of near-term oxygen forecasting for lake management.

Oxygen availability in lakes is changing

Oxygen concentrations are changing in many lakes globally, documented by cross-lake surveys, paleolimnological studies, and long-term monitoring time series (e.g., Marcé et al. 2010, Jenny et al. 2016a, Jane et al. 2021). In a synthesis of data from 393 temperate lakes, Jane et al. (2021) observed decreasing DO in both surface waters (by a median of 0.11 mg/L/decade) and in bottom waters (by 0.12 mg/L/decade). Similarly, paleolimnological records from 365 lakes with current hypolimnetic (bottom-water) hypoxia show that 71, or 20%, have begun exhibiting hypoxia since AD 1720 (Jenny et al. 2016a). Changes in oxygen have also been observed in single-lake studies spanning multiple decades, including Blelham Tarn, UK (Foley et al. 2012), Lake Erie, USA (reviewed by Tellier et al. 2022), Sau Reservoir, Spain (Marcé et al. 2010), Lake Tovel, Italy (Flaim et al. 2020), Lake Victoria, Kenya/Tanzania/Uganda (Hecky et al. 1994),

Lake Washington, USA (Edmondson 1966), Lake Zurich, Switzerland (North et al. 2014), and many others.

Decreases in lake oxygen concentrations have been attributed to both land use and climate change, with the relative importance of drivers varying by depth. Jenny et al. (2016a,b) related decreasing hypolimnetic oxygen conditions in primarily European and North American lakes to increased nutrient inputs. In contrast, Jane et al. (2021) found that declines in surface DO were largely due to decreased oxygen solubility as a result of warmer surface waters, which was related to increasing air temperatures and decreasing winds. Jane et al. (2021) related the declines in bottom-water DO to stronger thermal stratification resulting from climate change (following Woolway et al. 2021), which was intensified by greater light attenuation in surface waters due to higher productivity (as also reported by Kumagai et al. 2000, Jones et al. 2005). Altogether, hypoxia may be a synergistic response to the dynamic interplay of climate and land use change (following Rigosi et al. 2014, Shuvo et al. 2021), though the relative importance of these two factors likely varies among lakes.

Despite these large-scale patterns of decreasing oxygen, not all lakes are exhibiting oxygen declines. Jane et al. (2021) observed that DO concentrations in some lakes were increasing in the surface waters, especially those with shallow Secchi depths, high chlorophyll *a*, and warm surface temperatures. These changes were attributed to eutrophication related to land use change, as the lakes with surface DO increases had a significantly higher proportion of agriculture in their catchments than lakes without surface DO increases (Jane et al. 2021). Patterns of increasing oxygen are not restricted to surface waters: some lakes are also exhibiting increases in bottom-water oxygen. For example, deep-water DO availability has increased in Lake Tovel, Italy, over the last eight decades as the decreasing duration of ice cover in the winter

has lengthened mixing periods, thereby resulting in greater oxygen levels at depth (Flaim et al. 2020). These context-dependent effects underscore the need for continued monitoring and comparative studies to better understand the factors governing the effects of global change on lake oxygen.

The variability of oxygen in lakes is also changing

The combination of both decreasing and increasing oxygen availability in lakes suggests that the temporal *variability* of oxygen concentrations may also be changing, which I examined in a new analysis of the oxygen time series data collated for the ~400 temperate lakes in the Jane et al. (2021) study. For this new analysis, I calculated the inter-annual and intra-annual variability in DO concentration separately for the surface (1 m depth) and bottom (the deepest depth available) layers in each lake to examine if variability was increasing or decreasing differently over time between the layers. To estimate inter-annual variability, I first calculated the median annual DO concentration for each year in a lake's time series and then calculated the coefficient of variation (CV) of median annual DO over a rolling window of three years (following Cusser et al. 2021). I then plotted the CV of each three-year rolling window vs. the most recent year in that window and used the slope of that relationship as an estimate of changes in inter-annual variability in DO over time. For intra-annual variability, I calculated the CV of DO within each year in a lake's time series. I then plotted the within-year CV vs. year and used the slope of that relationship as an estimate of intra-annual variability over time.

I restricted this analysis to lakes with at least 10 years of data and 3 sampling days within a year; results were robust to changing this criterion to 5 sampling days within a year (Supplemental Figure 1). Because the inter-annual variability analysis necessitated consecutive

years in a lake's dataset for the rolling window calculation and lakes were more likely to have surface than bottom-water oxygen data available, the number of lakes included in the inter-annual vs. intra-annual variability calculations for surface and bottom layers differed (see Supplemental Material). Following the methods of Jane et al. (2021), and because my objective was to examine if variability was increasing vs. decreasing in the two lake layers, I focused on lakes that exhibited significant ($p < 0.05$) slopes of CV vs. year below; results for all lakes are reported in Supplemental Figure 2. All code for this analysis is archived in the Zenodo repository (Carey 2022); all data analyzed are published in the Environmental Data Initiative repository (Stetler et al. 2021).

In the surface waters of some lakes, inter-annual and intra-annual variability in surface DO concentrations have decreased over time. Of the 76 lakes with significant slopes in the inter-annual analysis of DO variability in surface waters, the majority (64%) had decreasing inter-annual variability (Fig. 1a). Similarly, the intra-annual variability of surface DO also decreased: although only 51% of 36 lakes exhibited significant declines in intra-annual variability, the medians of the intra-annual and inter-annual variability distributions had similar negative values (Fig. 1a).

While it is not possible to determine the exact mechanisms driving lake surface DO variability from this dataset, the patterns observed in Fig. 1a may be related to changes in the lakes' DO concentrations over time. Specifically, the declines in inter- and intra-annual variability in surface DO may be due to increasing surface water temperatures and subsequent decreases in DO solubility (Jane et al. 2021), resulting in overall more homogenized DO dynamics in the surface waters. In contrast, the subset of lakes experiencing increases in surface DO variability may be due to higher productivity related to land use change. Following

Rosenzweig (1971)'s paradox of enrichment, as lakes become more productive, they are likely to experience greater instability, which may be manifested in greater variability in DO: e.g., short-term peaks in surface DO due to algal blooms, then crashes in DO after blooms crash. Overall, the dominant pattern of declining DO concentrations in surface waters due to warming air temperatures could be resulting in more similar surface DO dynamics over time, with coincident declines in surface DO variability, though there are clearly exceptions to this trend.

In contrast to the surface waters, the inter-annual and intra-annual variability in bottom-water DO has increased in some lakes, especially for intra-annual variability, though fewer lakes were included in the analysis. Of the 19 lakes with a significant change in inter-annual DO variability, 53% showed increasing variability, whereas of the 14 lakes that exhibited a significant change in intra-annual DO variability, 100% had increasing variability (Fig. 1b). This greater variability in DO at depth mirrors patterns in lake temperatures over time (Kraemer et al. 2015, Pilla et al. 2020), in which lakes generally exhibit greater variability in hypolimnetic than epilimnetic dynamics. Changes in physical mixing/thermal stratification, water transparency, weather, inflows, and groundwater flux (*sensu* Pilla et al. 2020) may be driving this increasing variability in hypolimnetic DO. Of note is that six of the lakes that exhibited a significant increase in inter-annual or intra-annual DO variability in their bottom waters also exhibited a significant decrease in inter-annual or intra-annual DO variability in their surface waters, but the overall numbers of lakes in this analysis were small so it is challenging to infer broader patterns.

Altogether, this analysis suggests that the inter-annual and intra-annual variability of oxygen – in addition to oxygen concentrations – is changing in some lakes. The divergence between decreasing variability in surface DO and increasing variability in bottom DO suggests that the longer and stronger thermal lake stratification expected in the future (Woolway et al.

2021) will further intensify the decoupling of DO dynamics within lakes. This decoupling is possible even if there is a significant change in DO variability in only one lake layer and not the other, which was exhibited by 41 lakes in the dataset. I note that this analysis provides only one relatively simplistic metric of variability and that additional analyses with more lakes spanning a greater geographic region are needed (nearly all study lakes were located in the USA or Europe; Jane et al. 2021). Despite these limitations, this initial analysis provides an important first step for identifying how lake oxygen variability within lake ecosystems (and conversely, predictability) may be changing over time.

Consequences of changing oxygen dynamics on lake ecosystem services

Changing oxygen concentrations and variability have many implications for lake functioning because oxygen concentrations control many ecosystem and biogeochemical processes. Consequently, we would expect that ecological variables sensitive to oxygen will similarly become more or less variable following the oxygen patterns described above. In this section, I synthesize expected major changes in lake functioning and ecosystem services in response to decreases vs. increases in DO concentrations and variability, following the ecosystem service definitions of Aylward et al. (2005). I conceptualize these changes in the context of a see-saw: as oxygen concentrations fluctuate, so will the resulting ecosystem functioning (Fig. 2).

In general, there is a positive relationship between lake oxygen concentrations and many attributes of water quality that determine the status of several critical lake ecosystem provisioning and cultural services (e.g., drinking water, fisheries, recreation; Fig. 2b). Consequently, low oxygen concentrations are associated with several metrics of impaired water

quality, thereby decreasing those ecosystem services (Fig. 2a). For example, low bottom-water oxygen concentrations result in significantly higher fluxes of dissolved organic carbon (DOC), ammonium (NH_4^+), soluble reactive phosphorus (SRP), dissolved iron (Fe), and dissolved manganese (Mn) from the sediments into the water (Fig. 2a; Mortimer 1941, Davison 1993, Rysgaard et al. 1994, Brothers et al. 2014, Krueger et al. 2020). Increases in these solutes in the water column can in turn decrease light transparency (Sterner et al. 1997, Xiao and Riise 2021), stimulate the growth of algae and cyanobacteria (Elser et al. 2007, Trommer et al. 2020, Yuan et al. 2021), and result in water column concentrations that exceed drinking water safety thresholds (for Fe and Mn; USEPA 2022). Moreover, declining oxygen levels restrict habitat suitability for aerobic organisms, especially fish and benthic macroinvertebrates (Dillon et al. 2003, Jiang and Pu 2009). Thus, declining oxygen availability due to global change will have detrimental effects for many freshwater provisioning and cultural ecosystem services (e.g., Smucker et al. 2021).

The effects of changing oxygen on other freshwater ecosystem services mediated by lake biogeochemical functioning (e.g., nitrate removal, organic carbon storage, greenhouse gas release) are more equivocal (Fig. 2a). While sediment fluxes of DOC, NH_4^+ , and SRP are 2-4× greater in anoxic than oxic lake conditions, denitrification, an important process removing nitrate (NO_3^-) from freshwaters, can be 4× greater in anoxic than oxic conditions (Carey et al. 2022a). Particulate organic carbon (POC) storage in the sediments of lakes and reservoirs, a globally-important POC sink, is also significantly higher in anoxic than oxic conditions (Carey et al. 2018, Carey et al. 2022a). Conversely, anoxia promotes the production of methane (CH_4 ; e.g., (Bastviken et al. 2004, Encinas Fernández et al. 2014, Grasset et al. 2018), a greenhouse gas 34× more potent than carbon dioxide (CO_2 ; Myhre et al. 2013). Subsequently, anoxic waterbodies may have a greater global warming potential than oxic waterbodies (Hounshell et al. 2021). In

sum, anoxia will likely increase *and* decrease lake ecosystem regulatory and supporting services (Fig. 2a).

Because oxygen controls many different components of freshwater ecosystem functioning, it is likely that changes in oxygen concentrations and variability will result in dynamic, complex interactions that play out over different time scales. For example, changes in N:P stoichiometry due to differential NH_4^+ and SRP release from lake sediments into the water column during anoxia at day to week time scales may subsequently alter phytoplankton community structure and organic carbon mineralization at seasonal scales (Carey et al. 2022a). Similarly, increased seasonal anoxia associated with higher DOC sediment release can result in decreased water transparency, shallower oxycline depths, and increased water column stability at decadal time scales (Knoll et al. 2018). These changes to lake food webs, carbon and nutrient cycling, and other ecosystem dynamics stemming from the interacting effects of oxygen underscore the important role of oxygen as a “control point” in lake functioning (Bernhardt et al. 2017).

While less is known about the consequences of changing oxygen variability in lakes than changing oxygen concentrations, it is likely that greater variability in hypolimnetic oxygen (Fig. 1b) will have substantial effects on lake biogeochemical cycles. For example, Bastviken et al. (2004) found that lake organic matter mineralization rates were greater in microcosms that experienced fluctuating anoxic and oxic periods vs. continuous high-oxygen conditions. Similarly, Lewis et al. (2022) observed that lake Fe-DOC complexation rates varied in microcosms experiencing alternating oxic/anoxic conditions in comparison to microcosms with continuous anoxic or continuous oxic conditions. At the ecosystem scale, short-term fluctuations in oxygen availability can have non-linear effects on terminal electron-accepting processes and

the production of CO₂ and CH₄ (McClure et al. 2021), as well as particulate organic C burial (Carey et al. 2018). Bryant et al. (2012) found that short-term changes in the operation of a hypolimnetic oxygenation system were associated with altered sediment microbial community structure, with implications for Fe and Mn oxidation and reduction. Altogether, these examples suggest that increased variability in oxygen availability – as may be occurring in the bottom waters of some lakes (Fig. 1b) – may have a substantial effect on lake ecosystem functioning.

Long-term, lakes exhibit several intensifying ecosystem feedbacks that promote the continuation of low-oxygen concentrations into the future once hypolimnetic anoxia begins to occur. Adapting stable state theory (reviewed by Scheffer and van Nes 2007), once a lake exhibits anoxia, it can take a very long time before it transitions from that stable state back to oxic conditions, a legacy of “the ghost” of anoxia past. Indeed, paleolimnological data collected by Jenny et al. (2016a) show that lakes with hypolimnetic hypoxia do not show recovery even after decades of nutrient abatement. Beyond temporal legacies of anoxia, the consequences of lake anoxia may extend spatially as well: lakes with anoxic hypolimnia can export up to 6× higher loads of DOC, NH₄⁺, and SRP, promoting anoxia in downstream waterbodies (Carey et al. 2022a).

Priorities for future lake oxygen research

Given these major challenges – increasing anoxia in many (but not all) lakes, changing variability in oxygen concentrations in some lakes, altered ecosystem functioning – there are several key knowledge gaps that emerge as priorities for future research addressing the causes and consequences of changing oxygen in lakes. First, our knowledge on oxygen on lakes outside of Europe and North America, especially in the tropics, is sorely lacking. Most of the recent

meta-analyses on oxygen in lakes (e.g., Jenny et al. 2016a, Jane et al. 2021) primarily focused on temperate lakes in the northern hemisphere and thus our understanding on lake oxygen dynamics outside those regions is limited.

Second, recent advances in sensors and monitoring networks reveal substantial spatial variability in within-lake oxygen dynamics. High-resolution (sub-meter) spatial data show that dissolved oxygen saturation can range by 19% within a few meters of a small north temperate lake (Crawford et al. 2014). Deployments of multiple oxygen sensors within a lake at the same depth over a few days (Van de Bogert et al. 2012) to several months (Ward et al. 2022) further suggest that there may be remarkable horizontal variability in oxygen, but the magnitude of these differences, their drivers, and implications for ecosystem functioning remain unknown.

Third, there is much we do not know about the variability and patterns of oxygen under ice (e.g., Obertegger et al. 2017, Brentrup et al. 2021). While some northern temperate lakes exhibit winter oxygen depletion and even anoxia under ice (Prowse and Stephenson 1986, Ellis and Stefan 1989), some of the highest oxygen saturation levels ever observed (>300%) were recorded in amictic lakes in Antarctica (Wharton et al. 1986, Craig et al. 1992). As lake ice cover in many regions is rapidly changing (Sharma et al. 2021), it is vital to quantify the effects of shorter ice duration (Smits et al. 2021), more intermittent ice cover (Sharma et al. 2020), and changing ice quality (Weyhenmeyer et al. 2022) on under-ice depth profiles, especially as shorter durations of ice cover may result in higher oxygen conditions in lake bottom layers (Flaim et al. 2020).

Fourth, there is a pressing need to disentangle the effects of changing DO concentrations on lake ecosystems from water temperature, which is also rapidly changing in many lakes (O'Reilly et al. 2015). Whole-ecosystem experiments in which oxygen is manipulated while

temperature is held constant (and vice versa) hold promise for isolating the effects of changing oxygen on lake ecosystem functioning, but are logistically challenging and still rare (Gerling et al. 2016, Carey et al. 2022a). Long-term lake monitoring programs are critical for examining multi-decadal patterns in oxygen dynamics across changing climatic conditions, and are needed to further examine how variability in oxygen concentrations may be changing (Fig. 1). Oxygen modeling studies also have important utility (e.g., Fang and Stefan 2009, Couture et al. 2015, Bartosiewicz et al. 2019) and will be essential for building upon our accumulated knowledge of historical changes in oxygen in lakes to create near-term forecasts and longer projections of future oxygen dynamics in lakes in response to weather variability, climate change, land use, and management (sensu Carey et al. 2022b), with subsequent effects on lake ecosystem functioning.

Looking ahead

First, the negatives: changing oxygen levels in lakes will likely have decadal to century-long implications. The increasing geographic range, magnitude, and duration of anoxia and hypoxia in many lakes will have long-lasting consequences for ecosystem functioning and services, costing global economies billions to trillions of USD annually. For example, for Lake Erie (USA) alone, impaired water quality due to hypoxia threatens a >50 billion USD annual economy derived from lake ecosystem services of drinking water, fishing, and recreation (Scavia et al. 2014). Moreover, recovering from anoxia, even after decades of reduced external nutrient loads, is extremely challenging and in some cases may be impossible (Jenny et al. 2016a, Watson et al. 2016, van Oosterhout et al. 2022).

However, despite these substantial challenges, there are several positive developments in lake oxygen research and management that provide beneficial opportunities for future restoration

and science and should not be overlooked. First, the 1972 Clean Water Act resulted in the decline of pollution across the USA (Keiser and Shapiro 2019). In tandem with aquatic rehabilitation legislation in Europe (Battarbee et al. 2011), eutrophication and subsequent hypoxia has decreased in these regions in the late 20th century (Jenny et al. 2016a). Second, improved sensor technology, data availability, and monitoring networks have synergistically enabled researchers to observe changing lake oxygen patterns in near-real time, advancing both management and our understanding of ecosystem functioning (Meinson et al. 2015, Marcé et al. 2016). As described above, high-frequency oxygen sensors have revealed that lake oxygen patterns are far more temporally and spatially dynamic than previously thought (e.g., Van de Bogert et al. 2012, Crawford et al. 2014). Third, collaborative monitoring and research networks such as GLEON (Global Lake Ecological Observatory Network; Weathers et al. 2013), NETLAKE (Networking Lake Observatories in Europe; Jennings et al. 2017), and the USA NEON (National Ecological Observatory Network; NRC 2004) have encouraged data sharing, standardization of data and metadata, knowledge transfer, and cross-site syntheses. Continuing to build collaborative communities of limnologists, engineers, computer scientists, modelers, and information managers will be critical for facilitating future lake oxygen research.

Finally, analyzing historical oxygen data and high-frequency monitoring of current oxygen are the first steps towards forecasting future oxygen dynamics, which is necessary for preemptive lake management. As many lakes experience recurring hypoxia on short-term time scales (e.g., seasonally; Bouffard et al. 2013, Biddanda et al. 2018, Ladwig et al. 2021), day to month-ahead forecasts would be most useful for their management. For example, if managers were able to receive notice of impending lake hypoxia in a week's time, with quantified uncertainty, they could potentially implement interventions today to prevent hypoxia from

occurring (e.g., activate oxygenation systems, increase inflows of oxic water) or mitigate its effects on targeted ecosystem services (e.g., alter drinking water treatment processes to better handle higher nutrient and metal concentrations). While the development of aquatic oxygen forecasting systems is still in its infancy (e.g., Peng et al. 2020, Carey et al. 2022b, GLERL 2022), they show great promise for guiding near-term planning. For example, forecasts of dissolved oxygen for a large shallow lake in China had reasonable accuracy up to five days in advance (bias of 0.017 mg/L; Peng et al. 2020). Sixteen day-ahead oxygen forecasts had a root mean square error (RMSE) of 1.74-2.79 mg/L across multiple depths for a small drinking water reservoir in Virginia, USA (Carey et al. 2022b). These shorter-term forecasts set the stage for longer-term seasonal to annual oxygen forecasts that can guide scenario-based planning for water management.

Conclusions

Oxygen concentrations are changing in many lakes globally due to land use and climate change (Jenny et al. 2016a, Jane et al. 2021), necessitating new approaches for studying and managing lake water quality. Importantly, my analysis above suggests that variability in oxygen, not just mean concentrations, may also be changing. The focus on variability, even in the absence of any changes in mean concentrations (following Ruel and Ayres 1999), is critical for identifying the consequences of changing oxygen dynamics because of non-linear relationships between oxygen availability and ecosystem processes (e.g., Michaelis-Menten kinetics, which are commonly used to model lake biogeochemical responses to oxygen availability; Hipsey 2022). For example, increasing fluctuations in bottom-water oxygen concentrations will result in altered rates of sediment fluxes even if the mean oxygen concentration does not change. From a

management perspective, changing oxygen variability also indicates that natural resource decision-makers can no longer rely on historical baselines for predicting next week or next month's oxygen levels, which will have substantial consequences on ecosystem services and lake functioning (Fig. 2). Consequently, in the face of changing ecosystem variability due to global change – for which lake oxygen conditions are no exception (e.g., Fig. 1) – I am excited by advances in collaborative oxygen monitoring and forecasting research to help manage and protect lake and reservoir ecosystems.

Disclosure statement

The author reports there are no competing interests to declare.

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Data availability statement

All code is available in the Zenodo repository (Carey 2022) and all data analyzed are archived in the Environmental Data Initiative repository (Stetler et al. 2021).

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Figure Legends

Figure 1. Inter-annual (red) and intra-annual (blue) variability in dissolved oxygen in the surface waters (a) and bottom waters (b). Inter-annual variability was calculated for each lake as the slope of the relationship between the coefficient of variation (CV) of median annual dissolved oxygen over a three-year rolling window vs. year ($n=76$ surface lakes; $n=19$ bottom lakes). Intra-annual variability was calculated as the slope of the relationship between the CV of dissolved oxygen measured within a year vs. year ($n=37$ surface lakes; $n=14$ bottom lakes). As CV is unitless, the resulting inter- and intra-annual variability metrics are presented in units of year^{-1} .

Figure 2. The effects of oxygen on lake ecosystem functioning and services can be conceptualized as a balance or see-saw between contrasting (a) anoxic (low-oxygen) vs. (b) oxic conditions. Icons represent different lake ecosystem provisioning, regulatory, supporting, and cultural services. In anoxic conditions (a), the rate of particulate organic carbon (POC) burial is higher, as is the removal of nitrate (NO_3^-) to N_2 via denitrification. However, anoxia also promotes the production of methane (CH_4), a potent greenhouse gas, and higher fluxes of dissolved organic carbon (DOC), nitrogen (N), phosphorus (P), iron (Fe), and manganese (Mn) from the sediments to the water column, thereby decreasing water quality. Consequently, there are both positive and negative effects of anoxia on lake ecosystem regulatory and supporting services. In contrast, oxic conditions (b) are associated with higher-quality water for drinking, recreation, habitat for fish and macroinvertebrates, and lake aesthetics, resulting in positive effects of high oxygen on lake ecosystem provisioning and cultural services. When oxygen is high, the rates of POC burial, denitrification, CH_4 production, and sediment fluxes of DOC, N, P, Fe, and Mn are lower (indicated by the smaller size of the icons). All icons used in this figure

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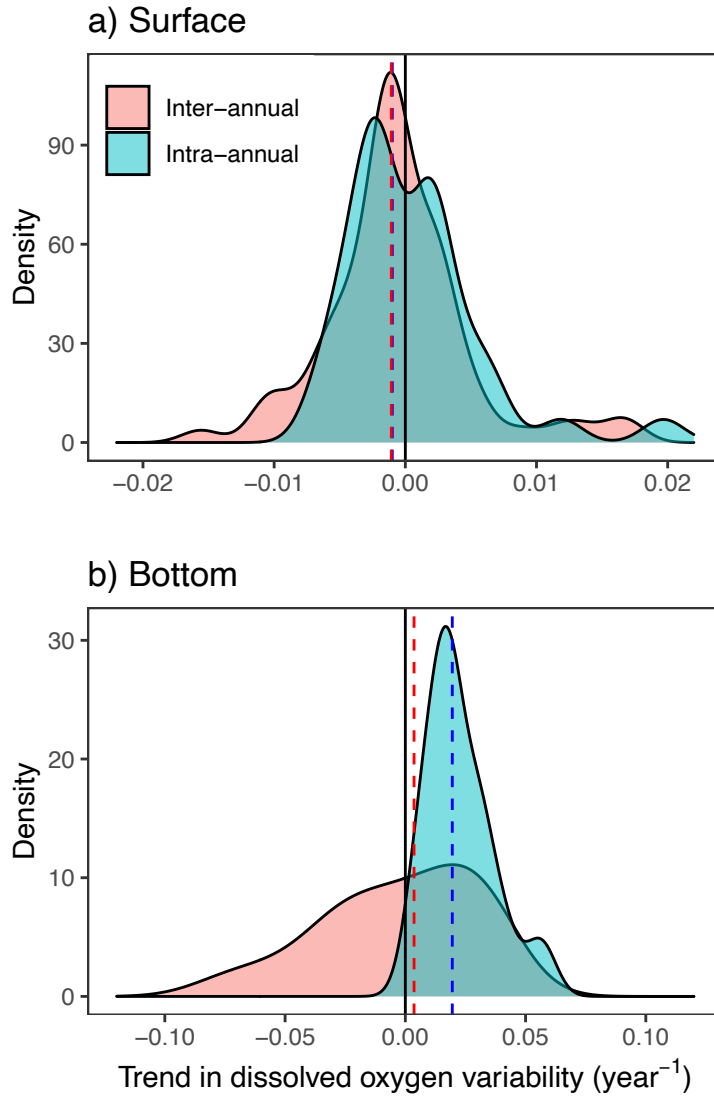


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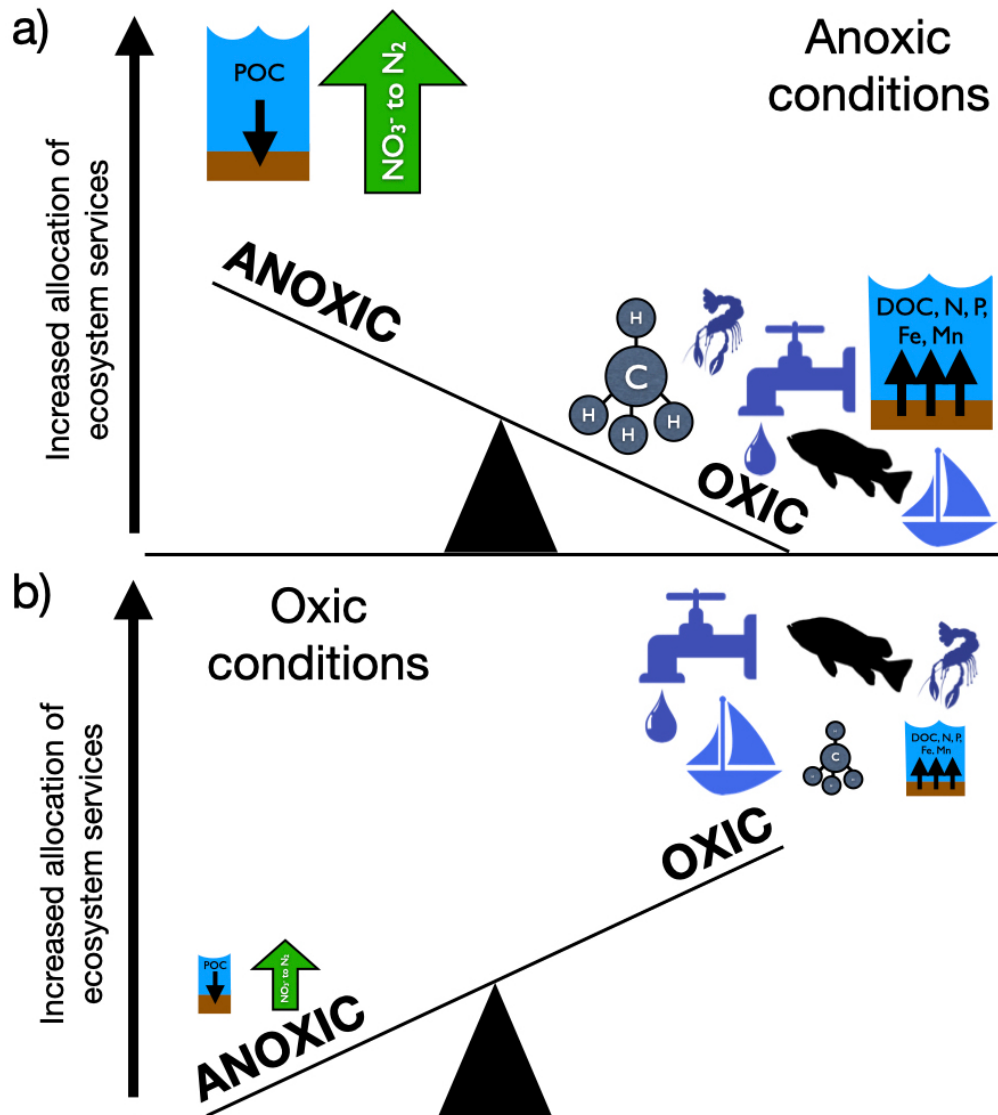


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