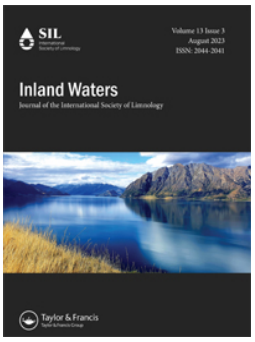

Taylor & Francis
Taylor & Francis Group

Inland Waters

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tinw20

Causes and consequences of changing oxygen availability in lakes

Kilham Plenary Lecture Article

Cayelan C. Carey

To cite this article: Cayelan C. Carey (2023) Causes and consequences of changing oxygen availability in lakes, Inland Waters, 13:3, 316-326, DOI: 10.1080/20442041.2023.2239110

To link to this article: https://doi.org/10.1080/20442041.2023.2239110

INLAND WATERS
2023, VOL. 13, NO. 3, 316–326
https://doi.org/10.1080/20442041.2023.2239110

Causes and consequences of changing oxygen availability in lakes

Kilham Plenary Lecture Article

Cayelan C. Carey

Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia, USA

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, although a few lakes are exhibiting increases in oxygen. By analyzing time series of oxygen monitoring data from ~400 lakes, I found 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.

ARTICLE HISTORY
Received 18 October 2022
Accepted 5 July 2023

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 5 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.

CONTACT Cayelan C. Carey cayelan@vt.edu Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia, USA
Supplemental material for this article can be accessed online here: https://doi.org/10.1080/20442041.2023.2239110.

Oxygen availability in lakes is changing

Oxygen concentrations are changing in many lakes, 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 primarily located in Europe and North America, 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 also primarily located in Europe and North America 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); Douglas Lake, USA (Lind and Dávalos-Lind 1993); 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 availability have been attributed to both land use and climate change, with the relative importance of drivers varying by depth. Jenny et al. (2016a, 2016b) related decreasing hypolimnetic oxygen conditions to increased nutrient inputs in their paleolimnological study. By 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, 2022) 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), although the relative importance of these 2 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 because 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 8 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 interannual and intraannual 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 interannual 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 3 years (following Cusser et al. 2021). I then plotted the CV of each 3-year rolling window versus the most recent year in that window and used the slope of that relationship as an estimate of changes in interannual variability in DO over time. For intraannual variability, I calculated the CV of DO within each year in a lake's time series. I then plotted the within-year CV versus year and used the slope of that relationship as an estimate of intraannual 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 Fig. S1). Because the interannual 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 interannual versus intraannual 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 versus decreasing in the 2 lake layers, I focused on lakes that exhibited significant ($p < 0.05$) slopes of CV versus year (results for all lakes in Supplemental Fig. S2). All code for this analysis is archived in the Zenodo repository (Carey 2023); all data analyzed are published in the Environmental Data Initiative repository (Stetler et al. 2021).

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

While determining the exact mechanisms driving lake surface DO variability from this dataset is not possible, the patterns observed (Fig. 1a) may be related to changes in the lake DO concentrations over time. Specifically, the declines in interannual and intraannual 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 uniform DO dynamics in the surface waters. By contrast, the subset of lakes experiencing increases in surface DO variability may be due to higher productivity related to nutrient-driven responses to land use change. Following the Rosenzweig (1971) paradox of enrichment, as lakes become more productive, they likely experience greater instability, which may be manifested in greater variability in DO: for example, short-term peaks in surface DO due to algal blooms, then decreases 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, although exceptions to this trend clearly exist.

In contrast to the surface waters, the interannual and intraannual variability in bottom-water DO has increased in some lakes, especially for intraannual variability, although fewer lakes were included in the analysis. Of the 19 lakes with a significant change in interannual DO variability, 53% showed increasing variability, whereas of the 14 lakes that exhibited a significant change in intraannual 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 their hypolimnetic DO dynamics than epilimnetic DO 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 6 of the lakes that exhibited a significant increase in interannual or intraannual DO variability in their bottom waters also exhibited a significant decrease in interannual or intraannual DO variability in their surface waters, but the overall number of lakes in this analysis was small and is thus challenging to infer broader patterns.

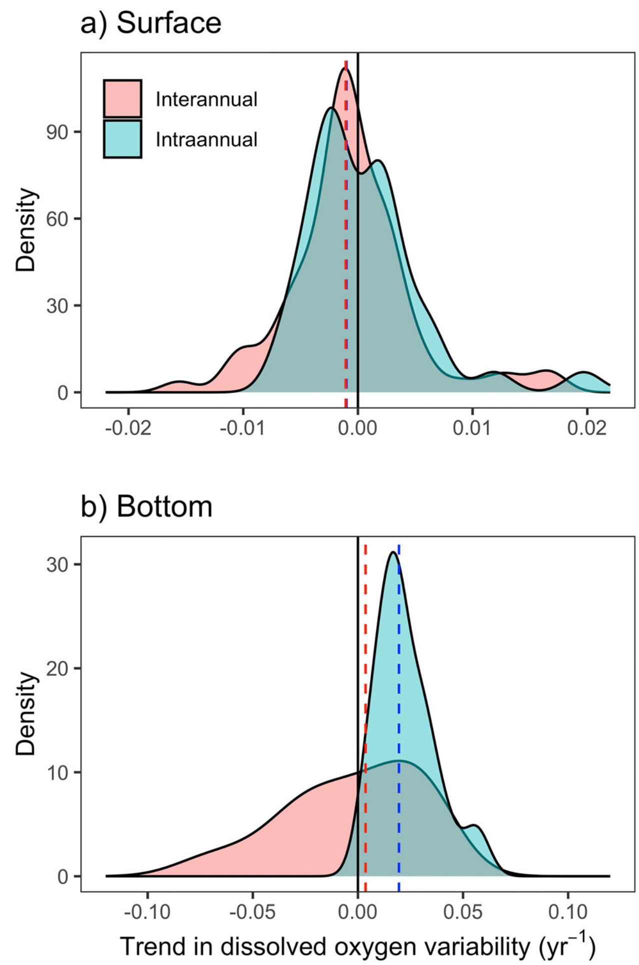

Figure 1. Interannual (red) and intraannual (blue) variability in dissolved oxygen in the (a) surface waters and (b) bottom waters. Interannual variability was calculated for each lake as the slope of the relationship between the coefficient of variation (CV) of median annual dissolved oxygen over a 3-year rolling window vs. year ($n = 76$ surface lakes; $n = 19$ bottom lakes). Intraannual 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). Because CV is unitless, the resulting interannual and intraannual variability metrics are presented in units of yr^{-1}.

Altogether, this analysis suggests that the interannual and intraannual 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 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 a significant change in DO variability occurs in only one lake layer and not the other, which was exhibited by 41 lakes in the dataset. 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 United States 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 important 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 previously described. Here I synthesize expected major changes in lake functioning and ecosystem services in response to decreases versus 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 seesaw; as oxygen concentrations fluctuate, so will the resulting ecosystem functioning (Fig. 2).

In general, a positive relationship exists 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, Molot et al. 2021, 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 times greater in anoxic than oxic lake conditions, denitrification, an important process removing nitrate (NO_3^-) from freshwaters, can be 4 times 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, 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 times 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, changes in oxygen concentrations and variability will likely 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

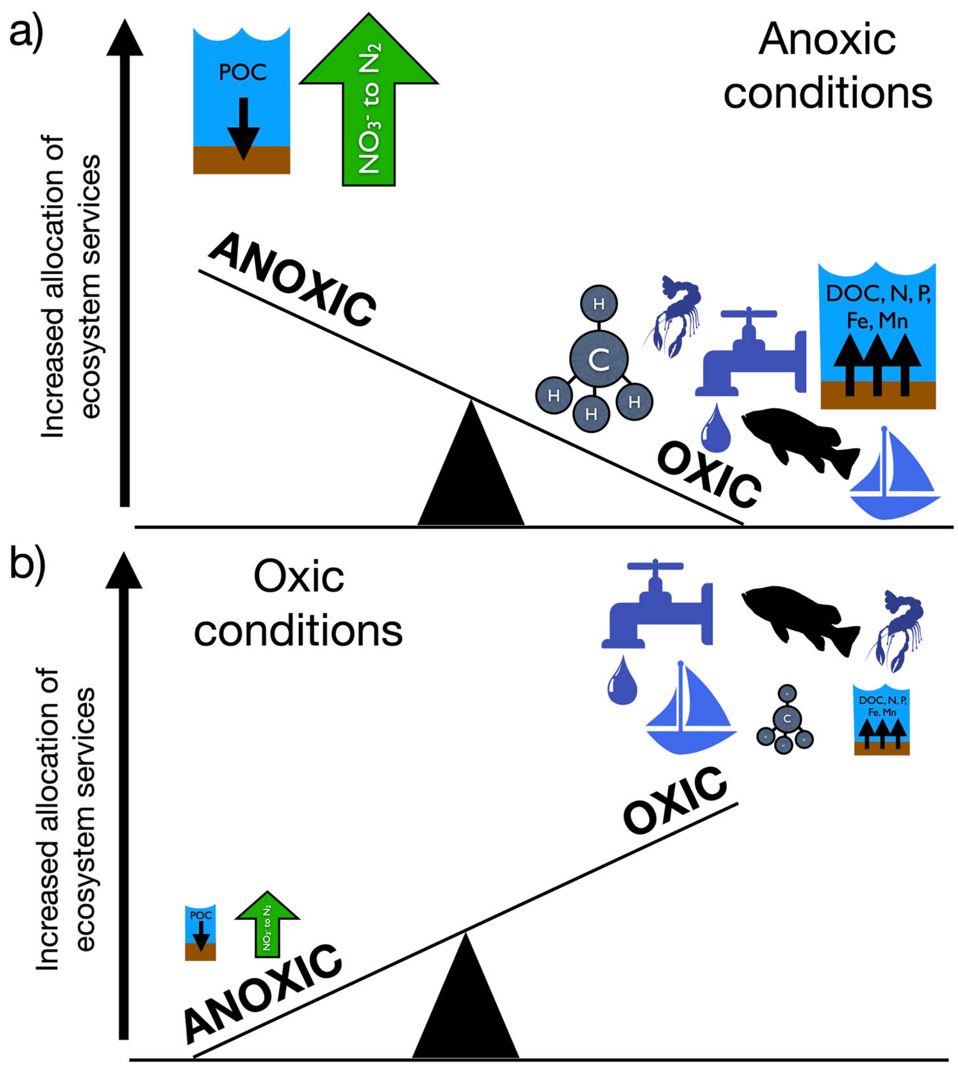

Figure 2. The effects of oxygen on lake ecosystem functioning and services can be conceptualized as a balance or seesaw between contrasting (a) anoxic (low oxygen) vs. (b) oxic conditions. Icons represent different lake ecosystem provisioning, regulatory, supporting, and cultural services. In anoxic 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, both positive and negative effects of anoxia occur on lake ecosystem regulatory and supporting services. By 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 were either created by the author or in the public domain from Creative Commons.

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, greater variability in hypolimnetic oxygen (Fig. 1b) will likely 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 versus continuous high oxygen conditions. Similarly, Lewis et al. (2023) 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 nonlinear effects on terminal electron-accepting processes and the production of CO_2 and CH_4 (McClure et al. 2021), as well as particulate organic C burial (Carey et al. 2018) and coupled sediment–

hypolimnetic redox dynamics (Effler and Matthews 2008, Lau et al. 2016). 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. Adapting stable state theory (reviewed by Scheffer and van Nes 2007), once a lake exhibits anoxia, the transition from that stable state back to oxic conditions can take a long time, 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 times higher loads of DOC, NH_4^+, and SRP, thereby 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—several key knowledge gaps emerge as priorities for future research to address the causes and consequences of changing oxygen in lakes. First, our knowledge on oxygen in 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) focused on temperate lakes in the Northern Hemisphere.

Second, recent advances in sensors and monitoring networks reveal substantial spatial variability in within-lake oxygen dynamics. High-resolution (submeter) 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 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 because 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 multidecadal 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 to build 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 in US dollars annually. For example, for Lake Erie (USA) alone, impaired water quality due to hypoxia threatens a >USD$50 billion 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, several positive developments in lake oxygen research and management 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 United States (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 earlier, 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 the Global Lake Ecological Observatory Network (GLEON; Weathers et al. 2013), Networking Lake Observatories in Europe (NETLAKE; Jennings et al. 2017), and the National Ecological Observatory Network (USA NEON; 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), these systems show great promise for guiding near-term planning (reviewed by Lofton et al. 2023). For example, forecasts of dissolved oxygen for a large shallow lake in China had reasonable accuracy up to 5 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 1.7–2.79 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 because of land use and climate change (Jenny et al. 2016a, Jane et al. 2021), necessitating new approaches for studying and managing lake water quality. Importantly, the analysis described earlier 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 nonlinear relationships between oxygen availability and ecosystem processes (e.g., Michaelis–Menten kinetics, 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. Given that several climate variables that structure lake ecosystems are also exhibiting changes in variability (e.g., altered precipitation patterns; Rodgers et al. 2021), oxygen variability in lakes may further increase in the future.

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.

Acknowledgements

This synthesis was inspired by the legacy of Peter Kilham's pioneering work on lake biogeochemistry and ecosystem science and shared in part during the SIL 2021 Kilham Lecture. I had the honor of meeting Sue Kilham prior to her passing and am grateful to her leadership in limnology and indomitable spirit. I thank members of the Carey Lab and Reservoir Group at Virginia Tech for helpful feedback, as well as many GLEON and limnology colleagues who have shaped my perspectives and research on lake oxygen science, including Nelson Hairston, Jr., David Hamilton, Paul Hanson, Rafa Marcé, and Kak Weathers. Quinn Thomas provided helpful guidance on the mysteries of *ggplot*.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the U.S. National Science Foundation under Grants DEB-1753639, DBI-1933016, and SCC-1737424.

Data availability statement

All code is available in the Zenodo repository (Carey 2023) and all data analyzed are archived in the Environmental Data Initiative repository (Stetler et al. 2021).

ORCID

Cayelan C. Carey http://orcid.org/0000-0001-8835-4476

References

Aylward B, Bandyopadhyay J, Belausteguigota J-C, Borkey P, Cassar A, Meadors L, Saade L, Siebentritt M, Stein R, Tognetti S, et al. 2005. Freshwater ecosystem services. In: Chopra K, Leemans R, Kumar P et al., editors. Ecosystems and human well-being: policy responses. Washington (DC): Island Press; p. 213–255.

Bartosiewicz M, Przytulska A, Lapierre J-F, Laurion I, Lehmann MF, Maranger R. 2019. Hot tops, cold bottoms: Synergistic climate warming and shielding effects increase carbon burial in lakes. Limnol Oceanogr Lett. 4(5):132–144.

Bastviken D, Persson L, Odham G, Tranvik LJ. 2004. Degradation of dissolved organic matter in oxic and anoxic lake water. Limnol Oceanogr. 49:109–116.

Battarbee RW, Morley D, Bennion H, Simpson GL, Hughes M, Bauere V. 2011. A palaeolimnological meta-database for assessing the ecological status of lakes. J Paleolimnol. 45(4):405–414.

Bernhardt ES, Blaszczak JR, Ficken CD, Fork ML, Kaiser KE, Seybold EC. 2017. Control points in ecosystems: moving beyond the hot spot hot moment concept. Ecosystems. 20(4):665–682.

Biddanda BA, Weinke AD, Kendall ST, Gereaux LC, Holcomb TM, Snider MJ, Dila DK, Long SA, VandenBerg C, Knapp K, et al. 2018. Chronicles of hypoxia: Time-series buoy observations reveal annually recurring seasonal basin-wide hypoxia in Muskegon Lake – a Great Lakes estuary. J Great Lakes Res. 44(2):219–229.

Bouffard D, Ackerman JD, Boegman L. 2013. Factors affecting the development and dynamics of hypoxia in a large shallow stratified lake: hourly to seasonal patterns. Water Resour Res. 49:2380–2394.

Brentrup JA, Richardson DC, Carey CC, Ward NK, Bruesewitz DA, Weathers KC. 2021. Under-ice respiration rates shift the annual carbon cycle in the mixed layer of an oligotrophic lake from autotrophy to heterotrophy. Inland Waters. 11(1):114–123.

Brothers SM, Köhler J, Attermeyer K, Grossart HP, Mehner T, Meyer N, Scharnweber K, Hilt S. 2014. A feedback loop links brownification and anoxia in a temperate, shallow lake. Limnol Oceanogr. 59(4):1388–1398.

Bryant LD, Little JC, Bürgmann H. 2012. Response of sediment microbial community structure in a freshwater reservoir to manipulations in oxygen availability. FEMS Microbiol Ecol. 80(1):248–263

Carey CC. 2023. Lake oxygen variability analysis code for Carey Kilham Lecture manuscript, v1.1. Zenodo repository. doi:10.5281/zenodo.8336021

Carey CC, Hanson PC, Doubek JP, McClure RP. 2018. Oxygen dynamics control the burial of organic carbon in a eutrophic reservoir. Limnol Oceanogr Lett. 3:293–301.

Carey CC, Hanson PC, Thomas RQ, Gerling AB, Hounshell AG, Lewis ASL, Lofton ME, McClure RP, Wander HL, Woelmer WM, et al. 2022a. Anoxia decreases the magnitude of the carbon, nitrogen, and phosphorus sink in freshwaters. Glob Chang Biol. 28(16):4861–4881.

Carey CC, Woelmer WM, Lofton ME, Figueiredo RJ, Bookout BJ, Corrigan RS, Daneshmand V, Hounshell AG, Howard DW, Lewis ASL, et al. 2022b. Advancing lake and reservoir water quality management with near-term, iterative ecological forecasting. Inland Waters. 12(1):107–120.

Couture R-M, de Wit HA, Tominaga K, Kiuru P, Markelov I. 2015. Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. J Geophys Res: Biogeosci. 120(11):2441–2456.

Craig H, Wharton RA Jr, McKay CP. 1992. Oxygen supersaturation in ice-covered Antarctic lakes: biological versus physical contributions. Science. 255:318–321.

Crawford JT, Loken LC, Casson NJ, Smith C, Stone AG, Winslow LA. 2014. High-speed limnology: using advanced sensors to investigate spatial variability in biogeochemistry and hydrology. Environ Sci Technol. 49:442–450.

Cusser S, Helms J, Bahlai CA, Haddad NM. 2021. How long do population level field experiments need to be? Utilising data from the 40-year-old LTER network. Ecol Lett. 24:1103–1111.

Davison W. 1993. Iron and manganese in lakes. Earth Sys Rev. 34:119–163.

Dillon PJ, Clark BJ, Molot LA, Evans HE. 2003. Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes. Can J Fish Aquat Sci. 60(8):959–970.

Edmondson WT. 1966. Changes in the oxygen deficit of Lake Washington. SIL Proceedings, 1922–2010. Verh Int Verein Limnol. 16(1):153–158.

Effler SW, Matthews DA. 2008. Implications of redox processes for the rehabilitation of an urban lake, Onondaga Lake, New York. Lake Res Manag. 24(2):122–138.

Ellis CR, Stefan HG. 1989. Oxygen demand in ice covered lakes as it pertains to winter aeration. JAWRA J Am Wat Res Assn. 25(6):1169–1176.

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett. 10(12):1135–1142.

Fang X, Stefan HG. 2009. Simulations of climate effects on water temperature, dissolved oxygen, and ice and snow covers in lakes of the contiguous U.S. under past and future climate scenarios. Limnol Oceanogr. 54(6 part 2):2359–2370.

Fernández JE, Peeters F, Hofmann H. 2014. Importance of the autumn overturn and anoxic conditions in the hypolimnion for the annual methane emissions from a temperate lake. Environ Sci Technol. 48(13):7297–7304.

Fernández Castro B, Chmiel HE, Minaudo C, Krishna S, Perolo P, Rasconi S, Wüest A. 2021. Primary and net ecosystem production in a large lake diagnosed from high-resolution oxygen measurements. Water Resour Res. 57(5):e2020WR029283.

Flaim G, Andreis D, Piccolroaz S, Obertegger U. 2020. Ice cover and extreme events determine dissolved oxygen in a placid mountain lake. Water Resour Res. 56(9): e2020WR027321.

Foley B, Jones ID, Maberly SC, Rippey B. 2012. Long-term changes in oxygen depletion in a small temperate lake: effects of climate change and eutrophication. Freshw Biol. 57(2):278–289.

Gerling AB, Munger ZW, Doubek JP, Hamre KD, Gantzer PA, Little JC, Carey CC. 2016. Whole-catchment manipulations of internal and external loading reveal the sensitivity of a century-old reservoir to hypoxia. Ecosystems. 19:555–571.

[GLERL] Great Lakes Environmental Research Laboratory. 2022. Experimental Lake Erie hypoxia forecast. National Oceanographic and Atmospheric Administration Great Lakes Environmental Research Laboratory. https://www.glerl.noaa.gov/res/HABs_and_Hypoxia/hypoxiaWarningSystem.html

Grasset C, Mendonça R, Villamor Saucedo G, Bastviken D, Roland F, Sobek S. 2018. Large but variable methane production in anoxic freshwater sediment upon addition of allochthonous and autochthonous organic matter. Limnol Oceanogr. 63(4):1488–1501.

Hecky RE, Bugenyi FWB, Ochumba P, Talling JF, Mugidde R, Gophen M, Kaufman L. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnol Oceanogr. 39(6):1476–1481.

Hipsey MR. 2022. Modelling aquatic eco-dynamics: overview of the AED modular simulation platform. Zenodo Repository. doi:10.5281/zenodo.6516222

Hounshell AG, McClure RP, Lofton ME, Carey CC. 2021. Whole-ecosystem oxygenation experiments reveal substantially greater hypolimnetic methane concentrations in reservoirs during anoxia. Limnol Oceanogr Lett. 6(1):33–42.

Hutchinson GE. 1957. A treatise on limnology. I. Geography, physics, and chemistry. New York (NY): Wiley.

Jane SF, Hansen GJA, Kraemer BM, Leavitt PR, Mincer JL, North RL, Pilla RM, Stetler JT, Williamson CE, Woolway RI, et al. 2021. Widespread deoxygenation of temperate lakes. Nature. 594(7861):66–70.

Jane SF, Mincer JL, Lau MP, Lewis ASL, Stetler JT, Rose KC. 2022. Longer duration of seasonal stratification contributes to widespread increases in lake hypoxia and anoxia. Glob Chang Biol. 29(4):1009–1023.

Jennings E, de Eyto E, Laas A, Pierson D, Mircheva G, Naumoski A, Clarke A, Healy M, Šumberová K, Langenhaun D. 2017. The NETLAKE metadatabase—a tool to support automatic monitoring on lakes in Europe and beyond. Limnol Oceanogr Bull. 26(4):95–100.

Jenny J-P, Francus P, Normandeau A, Lapointe F, Perga M-E, Ojala A, Schimmelmann A, Zolitschka B. 2016a. Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. Glob Chang Biol. 22(4):1481–1489.

Jenny J-P, Normandeau A, Francus P, Taranu ZE, Gregory-Eaves I, Lapointe F, Jautzy J, Ojala AEK, Dorioz J-M, Schimmelmann A, et al. 2016b. Urban point sources of nutrients were the leading cause for the historical spread of hypoxia across European lakes. Proc Natl Acad Sci USA. 113(45):12655–12660.

Jiang L, Pu ZC. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. Am Nat. 174:651–659.

Jones I, George G, Reynolds C. 2005. Quantifying effects of phytoplankton on the heat budgets of two large limnetic enclosures. Freshw Biol. 50(7):1239–1247.

Keiser DA, Shapiro JS. 2019. Consequences of the clean water Act and the demand for water quality. Quarter J Econ. 134(1):349–396.

Knoll LB, Williamson CE, Pilla RM, Leach TH, Brentrup JA, Fisher TJ. 2018. Browning-related oxygen depletion in an oligotrophic lake. Inland Waters. 8(3):255–263.

Kraemer BM, Anneville O, Chandra S, Dix M, Kuusisto E, Livingstone DM, Rimmer A, Schladow SG, Silow E, Sitoki LM, et al. 2015. Morphometry and average temperature affect lake stratification responses to climate change. Geophys Res Lett. 42(12):4981–4988.

Krueger KM, Vavrus CE, Lofton ME, McClure RP, Gantzer P, Carey CC, Schreiber ME. 2020. Iron and manganese fluxes across the sediment-water interface in a drinking water reservoir. Wat Res. 182:116003.

Kumagai M, Nakano S-i, Jiao C, Hayakawa K, Tsujimura S, Nakajima T, Frenette J, Quesada A. 2000. Effect of cyanobacterial blooms on thermal stratification. Limnology. 1:191–195.

Ladwig R, Hanson PC, Dugan HA, Carey CC, Zhang Y, Shu L, Duffy CJ, Cobourn KM. 2021. Lake thermal structure drives interannual variability in summer anoxia dynamics in a eutrophic lake over 37 years. Hydrol Earth Syst Sci. 25(2):1009–1032.

Langman OC, Hanson PC, Carpenter SR, Hu YH. 2010. Control of dissolved oxygen in northern temperate lakes over scales ranging from minutes to days. Aquat Biol. 9(2):193–202.

Lau MP, Sander M, Gelbrecht J, Hupfer M. 2016. Spatiotemporal redox dynamics in a freshwater lake sediment under alternating oxygen availabilities: combined analyses of dissolved and particulate electron acceptors. Environ Chem. 13:826–837.

Lewis A, Schreiber M, Niederlehner B, Das A, Hammond N, Lofton M, Wander H, Carey C. 2023. Effects of hypoxia on coupled carbon and iron cycling differ between weekly and multiannual timescales in two freshwater reservoirs. J Geophys Res Biogeosci. 128(1):e2022JG007071.

Lind OT, Dávalos-Lind L. 1993. Detecting the increased eutrophication rate of Douglas Lake, Michigan: the relative areal hypolimnetic oxygen deficit method. Lake Res Manag. 8(1):67–71.

Lofton ME, Howard DW, Thomas RQ, Carey CC. 2023. Progress and opportunities in near-term iterative forecasting of freshwater ecosystems. Glob Chang Biol. 29(7):1691–1714.

Marcé R, George G, Buscarinu P, Deidda M, Dunalska J, de Eyto E, Flaim G, Grossart HP, Istvanovics V, Lenhardt M, et al. 2016. Automatic high frequency monitoring for improved lake and reservoir management. Environ Sci Technol. 50(20):10780–10794.

Marcé R, Rodriguez-Arias MÀ, Garcia JC, Armengol J. 2010. El Niño Southern Oscillation and climate trends impact reservoir water quality. Glob Chang Biol. 16(10):2857–2865.

McClure RP, Schreiber ME, Lofton ME, Chen S, Krueger KM, Carey CC. 2021. Ecosystem-scale oxygen manipulations alter terminal electron acceptor pathways in a eutrophic reservoir. Ecosystems. 24:1281–1298.

Meinson P, Idrizaj A, Nõges P, Nõges T, Laas A. 2015. Continuous and high-frequency measurements in limnology: history, applications, and future challenges. Environ Rev. 24(1):52–62.

Molot LA, Schiff SL, Venkiteswaran JJ, Baulch HM, Higgins SN, Zastepa A, Verschoor MJ, Walters D. 2021. Low sediment redox promotes cyanobacteria blooms across a trophic range. Lake Res Manage. 37(2):120–142.

Mortimer CH. 1941. The exchange of dissolved substances between mud and water in lakes. J Ecol. 29(2):280–329.

Myhre G, Shindell D, Breon F-M, Collins W, Fuglestvedt J, Huang J, Koch D, Lamarque J-F, Lee D, Mendoz B, et al. 2013. Anthropogenic and natural radiative forcing. In: Stocker TF, Qin D, Plattner G-K, et al., editors. Climate change 2013: the physical science basis contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press; p. 659–740.

North RP, North RL, Livingstone DM, Köster O, Kipfer R. 2014. Long-term changes in hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake: consequences of a climate regime shift. Glob Chang Biol. 20(3):811–823.

[NRC] National Research Council. 2004. NEON: addressing the nation's environmental challenges. Washington (DC): National Research Council, National Academies Press.

Obertegger U, Obador B, Flaim G. 2017. Dissolved oxygen dynamics under ice: three winters of high-frequency data from Lake Tovel, Italy. Water Resour Res. 53:7234–7246.

Odum HT. 1956. Primary production in flowing waters. Limnol Oceanogr. 1:102–117.

O'Reilly CM, Sharma S, Gray DK, Hampton SE, Read JS, Rowley RJ, Schneider P, Lenters JD, McIntyre PB, Kraemer BM, et al. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys Res Lett. 42(24):10,773–710,781.

Peng Z, Hu Y, Liu G, Hu W, Zhang H, Gao R. 2020. Calibration and quantifying uncertainty of daily water quality forecasts for large lakes with a Bayesian joint probability modelling approach. Water Res. 185:116162.

Pilla RM, Williamson CE, Adamovich BV, Adrian R, Anneville O, Chandra S, Colom-Montero W, Devlin SP, Dix MA, Dokulil MT, et al. 2020. Deeper waters are changing less consistently than surface waters in a global analysis of 102 lakes. Sci Rep. 10(1):20514.

Prowse TD, Stephenson RL. 1986. The relationship between winter lake cover, radiation receipts and the oxygen deficit in temperate lakes. Atmos Ocean. 24(4):386–403.

Rigosi A, Carey CC, Ibelings BW, Brookes JD. 2014. The interaction between climate warming and eutrophication is dependent on trophic state and varies among taxa. Limnol Oceanogr. 59:99–114.

Rodgers KB, Lee S-S, Rosenbloom N, Timmermann A, Danabasoglu G, Deser C, Edwards J, Kim J-E, Simpson IR, Stein K, et al. 2021. Ubiquity of human-induced changes in climate variability. Earth Syst Dyn. 12(4):1393–1411.

Rosenzweig ML. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science. 171(3969):385–387.

Ruel JJ, Ayres MP. 1999. Jensen's inequality predicts effects of environmental variation. Trends Ecol Evol. 14(9):361–366.

Rysgaard S, Risgaard-Petersen N, Sloth N, Jensen KIM, Nielsen LP. 1994. Oxygen regulation of nitrification and denitrification in sediments. Limnol Oceanogr. 39:1643–1652.

Scavia D, David Allan J, Arend KK, Bartell S, Beletsky D, Bosch NS, Brandt SB, Briland RD, Daloğlu I, DePinto JV, et al. 2014. Assessing and addressing the re-eutrophication of Lake Erie: central basin hypoxia. J Great Lakes Res. 40(2):226–246.

Scheffer M, van Nes EH. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia. 584(1):455–466.

Sharma S, Meyer MF, Culpepper J, Yang X, Hampton S, Berger SA, Brousil MR, Fradkin SC, Higgins SN, Jankowski KJ, et al. 2020. Integrating perspectives to understand lake ice dynamics in a changing world. J Geophys Res Biogeosci. 125(8):e2020JG005799.

Sharma S, Richardson DC, Woolway RI, Imrit MA, Bouffard D, Blagrave K, Daly J, Filazzola A, Granin N, Korhonen J, et al. 2021. Loss of ice cover, shifting phenology, and more extreme events in Northern Hemisphere lakes. J Geophys Res Biogeosci. 126(10):e2021JG006348.

Shuvo A, O'Reilly CM, Blagrave K, Ewins C, Filazzola A, Gray D, Mahdiyan O, Moslenko L, Quinlan R, Sharma S. 2021. Total phosphorus and climate are equally important predictors of water quality in lakes. Aquat Sci. 83(1):16.

Smits AP, Gomez NW, Dozier J, Sadro S. 2021. Winter climate and lake morphology control ice phenology and under-ice temperature and oxygen regimes in mountain lakes. J Geophys Res: Biogeosci. 126(8):e2021JG006277.

Smucker NJ, Beaulieu JJ, Nietch CT, Young JL. 2021. Increasingly severe cyanobacterial blooms and deep water hypoxia coincide with warming water temperatures in reservoirs. Glob Chang Biol. 27(11):2507–2519.

Sterner RW, Elser JJ, Fee EJ, Guildford SJ, Chrzanowski TH. 1997. The light:nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. Am Nat. 150(6):663–684.

Stetler JT, Jane SF, Mincer JL, Sanders MN, Rose KC. 2021. Long-term lake dissolved oxygen and temperature data, 1941–2018 ver. 3. Environ Data Initiative Repository. doi:10.6073/pasta/c45efe4826b5f615023b857dc59856f3

Tellier JM, Kalejs NI, Leonhardt BS, Cannon D, Höök TO, Collingsworth PD. 2022. Widespread prevalence of hypoxia and the classification of hypoxic conditions in the Laurentian Great Lakes. J Great Lakes Res. 48(1):13–23.

Trommer G, Poxleitner M, Stibor H. 2020. Responses of lake phytoplankton communities to changing inorganic nitrogen supply forms. Aquat Sci. 82(2):22.

[USEPA] United States Environmental Protection Agency. 2022. United States Environmental Protection Agency. Secondary drinking water standards: guidance for nuisance chemicals. https://www.epa.gov/sdwa/secondary-drinking-water-standards-guidance-nuisance-chemicals

Van de Bogert MC, Bade DL, Carpenter SR, Cole JJ, Pace ML, Hanson PC, Langman OC. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol Oceanogr. 57(6):1689–1700.

van Oosterhout F, Yasseri S, Noyma N, Huszar V, Manzi Marinho M, Mucci M, Waajen G, Lürling M. 2022. Assessing the long-term efficacy of internal loading management to control eutrophication in Lake Rauwbraken. Inland Waters. 12(1):61–77.

Ward NK, Brentrup JA, Richardson DC, Weathers KC, Hanson PC, Hewett RJ, Carey CC. 2022. Dynamics of the stream–lake transitional zone affect littoral lake metabolism. Aquat Sci. 84(3):31.

Watson SB, Miller C, Arhonditsis G, Boyer GL, Carmichael W, Charlton MN, Confesor R, Depew DC, Höök TO, Ludsin SA, et al. 2016. The re-eutrophication of Lake Erie: harmful algal blooms and hypoxia. Harmful Algae. 56:44–66.

Weathers KC, Hanson PC, Arzberger P, Brentrup J, Brookes JA, Carey CC, Gaiser EE, Hamilton DP, Hong GS, Ibelings B, et al. 2013. The Global Lake Ecological Observatory Network (GLEON): the evolution of grassroots network science. Limnol Oceanogr Bull. 22:71–73.

Wetzel RG. 2001. Limnology: lake and river ecosystems, 3rd ed. New York (NY): Academic Press.

Weyhenmeyer GA, Obertegger U, Rudebeck H, Jakobsson E, Jansen J, Zdorovennova G, Bansal S, Block BD, Carey CC, Doubek JP, et al. 2022. Towards critical white ice conditions in lakes under global warming. Nat Comm. 13(1):4974.

Wharton RA, McKay CP, Simmons GM Jr, Parker BC. 1986. Oxygen budget of a perennially ice-covered Antarctic lake. Limnol Oceanogr. 31(2):437–443.

Woolway RI, Sharma S, Weyhenmeyer GA, Debolskiy A, Golub M, Mercado-Bettín D, Perroud M, Stepanenko V, Tan Z, Grant L, et al. 2021. Phenological shifts in lake stratification under climate change. Nat Comm. 12(1):2318.

Xiao Y, Riise G. 2021. Coupling between increased lake color and iron in boreal lakes. Sci Total Env. 767:145104.

Yuan Y, Jiang M, Zhu X, Yu H, Otte ML. 2021. Interactions between Fe and light strongly affect phytoplankton communities in a eutrophic lake. Ecol Indic. 126:107664.