

1 TITLE: Anoxia Begets Anoxia: a positive feedback to the deoxygenation of temperate lakes

2
3 RUNNING HEAD: “Anoxia Begets Anoxia”

4
5 AUTHORS:

6 Abigail S. L. Lewis^{1*}, Maximilian P. Lau², Stephen F. Jane³, Kevin C. Rose⁴, Yaron Be’eri-
7 Shlevin⁵, Sarah H. Burnet⁶, François Clayer⁷, Heidrun Feuchtmayr⁸, Hans-Peter Grossart^{9, 10},
8 Dexter W. Howard¹, Heather Mariash¹¹, Jordi Delgado Martin¹², Rebecca L. North¹³, Isabella
9 Oleksy¹⁴, Rachel M. Pilla¹⁵, Amy P. Smagula¹⁶, Ruben Sommaruga¹⁷, Sara E. Steiner¹⁶, Piet
10 Verburg¹⁸, Danielle Wain¹⁹, Gesa A. Weyhenmeyer²⁰, and Cayelan C. Carey¹

11
12 AFFILIATIONS:

13 ¹ Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA

14 ² Interdisciplinary Environmental Research Centre, Technical University of Mining and
15 Resources Freiberg, 09599 Freiberg, Germany

16 ³ Cornell Atkinson Center for Sustainability, Department of Natural Resources and the
17 Environment, Cornell University, Ithaca, NY 14853, USA

18 ⁴ Department of Biological Sciences, Rensselaer Polytechnic Institute, Troy, NY 12180 USA

19 ⁵ The Kinneret Limnological Laboratory, Israel Oceanographic and Limnological Research,
20 Migdal 14950, Israel

21 ⁶ Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA

22 ⁷ Norwegian Institute of Water Research, Oslo, Norway

23 ⁸ Lake Ecosystems Group, UK Centre for Ecology & Hydrology, Lancaster, UK

24 ⁹ Department of Plankton and Microbial Ecology, Leibniz Institute of Freshwater Ecology and
25 Inland Fisheries (IGB), 16775 Stechlin Germany

26 ¹⁰ Department of Biochemistry and Biology, Potsdam University, 14469 Potsdam, Germany

27 ¹¹ Prince Albert National Park, Parks Canada, SK, Canada

28 ¹² Department of Civil Engineering, Universidade da Coruña, A Coruña, Spain

29 ¹³ School of Natural Resources, University of Missouri-Columbia, Columbia, Missouri, USA

30 ¹⁴ Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA

31 ¹⁵ Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

32 ¹⁶ New Hampshire Department of Environmental Services, Concord, NH, USA

33 ¹⁷ Department of Ecology, Universität Innsbruck, 6020 Innsbruck, Austria

34 ¹⁸ National Institute of Water and Atmospheric Research, Wellington, New Zealand.

35 ¹⁹ 7 Lakes Alliance, Belgrade Lakes, Maine, USA

36 ²⁰ Department of Ecology and Genetics/Limnology, Uppsala University, Norbyvägen 18D, 752
37 36 Uppsala, Sweden

38
39 * Corresponding author. Phone: (262) 565-7269. Email: aslewis@vt.edu.

ABSTRACT

Declining oxygen concentrations in the deep waters of lakes worldwide pose a pressing environmental and societal challenge. Existing theory suggests that low deep-water dissolved oxygen (DO) concentrations could trigger a positive feedback through which anoxia (i.e., very low DO) during a given summer begets increasingly severe occurrences of anoxia in following summers. Specifically, anoxic conditions can promote nutrient release from sediments, thereby stimulating phytoplankton growth, and subsequent phytoplankton decomposition can fuel heterotrophic respiration, resulting in increased spatial extent and duration of anoxia. However, while the individual relationships in this feedback are well established, to our knowledge there has not been a systematic analysis within or across lakes that simultaneously demonstrates all of the mechanisms necessary to produce a positive feedback that reinforces anoxia. Here, we compiled data from 656 widespread temperate lakes and reservoirs to analyze the proposed Anoxia Begets Anoxia (ABA) feedback. Lakes in the dataset span a broad range of surface area (1–126,909 ha), maximum depth (6–370 m), and morphometry, with a median time series duration of 30 years at each lake. Using linear mixed models, we found support for each of the positive feedback relationships between anoxia, phosphorus concentrations, chlorophyll-*a* concentrations, and oxygen demand across the 656-lake dataset. Likewise, we found further support for these relationships by analyzing time series data from individual lakes. Our results indicate that the strength of these feedback relationships may vary with lake-specific characteristics: for example, we found that surface phosphorus concentrations were more positively associated with chlorophyll-*a* in high-phosphorus lakes, and oxygen demand had a stronger influence on the extent of anoxia in deep lakes. Taken together, these results support the

existence of a positive feedback that could magnify the effects of climate change and other anthropogenic pressures driving the development of anoxia in lakes around the world.

KEYWORDS:

Air temperature, anoxia, chlorophyll-a, dissolved oxygen, feedback, hypolimnion, lake, oxygen demand, phosphorus, residence time

Notice: This manuscript has been authored by UT-Battelle, LLC, under contract DE-AC05-00OR22725 with the US Department of Energy (DOE). The US government retains and the publisher, by accepting the article for publication, acknowledges that the US government retains a nonexclusive, paid-up, irrevocable, worldwide license to publish or reproduce the published form of this manuscript, or allow others to do so, for US government purposes. DOE will provide public access to these results of federally sponsored research in accordance with the DOE Public Access Plan (<http://energy.gov/downloads/doe-public-access-plan>).

1. INTRODUCTION

Dissolved oxygen (DO) concentrations are declining in the bottom-waters of many aquatic ecosystems around the world (Jenny et al. 2016a; Schmidtke et al. 2017; Breitburg et al. 2018; Jane et al. 2021; Zhi et al. 2023). These declines pose a significant threat to both marine and freshwater ecosystems, as low DO conditions can decrease habitat suitability for numerous aquatic organisms (e.g., Rosenberg et al. 1991; Vaquer-Sunyer and Duarte 2008; Schindler 2017; Pilla and Williamson 2023), and decrease redox potential, promoting methane production (e.g., Encinas Fernández et al. 2014; Vachon et al. 2017; Hounshell et al. 2021), and altering aquatic nutrient cycling (e.g., Hupfer and Lewandowski 2008; Middelburg and Levin 2009; Carey et al. 2022a). In freshwater lakes, the trend of decreasing DO concentrations may be particularly severe, with rates of decline up to 10 times higher than those observed in marine ecosystems (Jane et al. 2021). As freshwaters are critical ecosystems for drinking water, recreation, irrigation, and biodiversity (Reynaud and Lanzanova 2017; Finlayson et al. 2018; Reid et al. 2019; Lynch et al. 2023), understanding and addressing changes in freshwater DO is essential to ensuring water security and ecosystem functioning in the face of global change.

Declines in bottom-water DO concentrations are often attributed to climate change and/or increased nutrient inputs (Jenny et al. 2016a; Bartosiewicz et al. 2019; Jane et al. 2023). Increased air temperatures have been shown to drive increased duration of thermal stratification (Foley et al. 2012; North et al. 2013; Oleksy and Richardson 2021; Woolway et al. 2021), which reduces or inhibits mixing of oxygen to the bottom waters (hypolimnion). Consequently, increases in stratification duration may provide more time for hypolimnetic DO depletion to occur, resulting in lower late-summer DO concentrations and increased duration of anoxia. Changes in stratification duration appear to be a particularly important driver of DO declines in

recent decades (ca. 1950-2020; Jane et al. 2023). However, historical nutrient inputs have likely also played a role in deoxygenation by increasing phytoplankton biomass and consequently oxygen demand (Jenny et al. 2016a; b). The relative importance of these two pathways to deoxygenation (i.e., greater stratification duration due to climate change and greater oxygen demand due to eutrophication) likely varies both among lakes and within lakes over time. Consequently, understanding interannual DO dynamics across many lakes may be critical to disentangling the independent effects of stratification duration and eutrophication amidst ongoing changes in global climate and land use (e.g., Moss 2011; Parmesan et al. 2022).

Here, we analyze a positive feedback, derived from decades of aquatic research, by which anoxia (i.e., DO at or near 0 mg/L) during a given year begets increasingly frequent and severe occurrences of anoxia in subsequent years. In this “anoxia begets anoxia” (ABA) feedback, anoxic conditions promote internal phosphorus release, thereby stimulating phytoplankton growth and subsequent decomposition, which in turn fuels increased heterotrophic respiration and further accelerates hypolimnetic DO declines over time (Figure 1). As long-term limnological data have become increasingly accessible (e.g., Pilla et al. 2020; Jane et al. 2021), we now have the opportunity to test the strength and ubiquity of this feedback on a multi-continental scale.

While the individual relationships in the ABA feedback cycle (Figure 1) are well-established, these relationships occur over multiple timescales and amidst numerous other interacting factors (e.g., climate variation) that could prevent the detection of the overall feedback. Hypolimnetic anoxia has been shown to enhance internal loading of phosphorus from sediments (e.g., Mortimer 1941; Nürnberg 1984; Orihel et al. 2017; Figure 1A). However, while redox-controlled phosphorus release fluxes have received significant attention, sediment

characteristics, microbial processing, and catchment inputs may also play important roles in phosphorus dynamics (e.g., Hupfer and Lewandowski 2008; Orihel et al. 2017). Increases in hypolimnetic phosphorus are expected to increase surface water (epilimnetic) phosphorus concentrations within a summer stratified period through both biological and physical processes (e.g., organism-mediated transport, diffusion, and internal seiche dynamics; Carpenter et al. 1992; Kamarainen et al. 2009; Haupt et al. 2010; Cottingham et al. 2015) or during autumn mixis when epilimnetic and hypolimnetic waters homogenize (e.g., Nürnberg and Peters 1984, Wetzel 2001; Figure 1B). Higher epilimnetic phosphorus concentrations in turn can stimulate phytoplankton growth in many lakes, thereby increasing chlorophyll-*a* (chl-*a*, Figure 1C; Schindler 1974), though many other important factors, including nitrogen concentrations, climate, and light availability, also contribute to phytoplankton growth (e.g., Paerl and Huisman 2008; Reinl et al. 2023). Increased phytoplankton biomass and subsequent decomposition may fuel increased biological oxygen demand (Figure 1D; Pace and Prairie 2005; Müller et al. 2019; Ladwig et al. 2021) and result in earlier onset of anoxia (Figure 1E), although climate can also play an important role in driving DO dynamics in many lakes, as discussed above. Given the substantial complexity to each of these relationships, all operating on different time scales, it remains unclear the extent to which the full positive feedback plays a role in controlling DO dynamics within lakes around the world.

Lake characteristics including size and residence time could potentially mediate the strength of the ABA feedback across lakes, though these relationships remain largely untested because they can only be characterized with long-term monitoring data across many diverse lakes. Lakes with longer residence time or larger sediment area:volume ratios may have greater sediment-water interactions, increasing the influence of oxygen demand on hypolimnetic DO, as

well as the influence of hypolimnetic DO on hypolimnetic TP (e.g., Jagtman et al. 1992). Likewise, lake size may control the importance of mixing dynamics between the epilimnion and hypolimnion, and residence time may affect the extent to which chl-a and hypolimnetic TP influence biogeochemical dynamics the following year (Wetzel 2001). While many of these expected relationships have not been assessed across lakes, an empirical analysis of data from 2849 lakes suggests that the impact of phosphorus concentrations on chlorophyll-a may be stronger in shallow lakes relative to deep lakes, potentially due to differences in light availability and macrophyte cover (Zhao et al. 2023). Characterizing the effect of lake characteristics on the ABA feedback relationships is needed to identify which lakes are most susceptible to the feedback, enabling managers to prioritize conservation efforts across lakes.

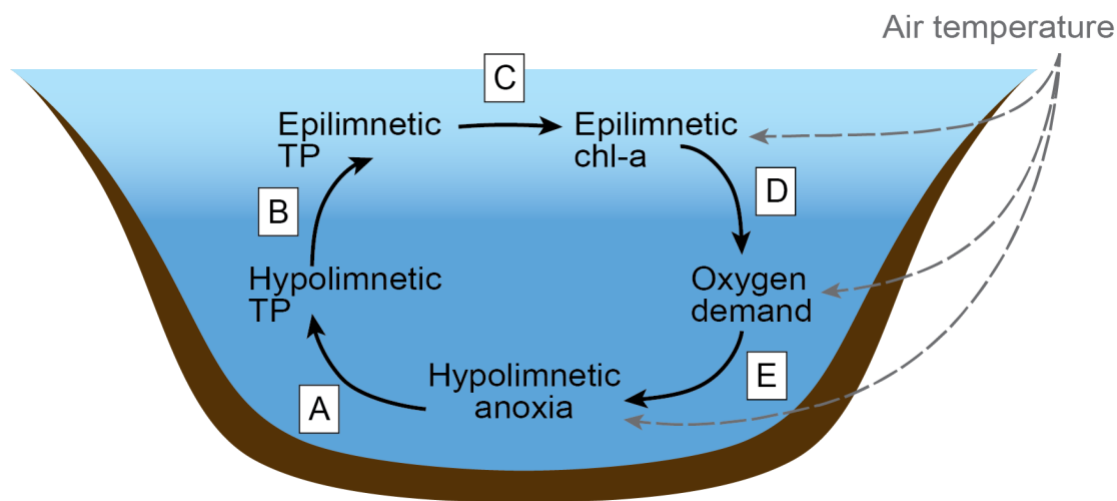


Figure 1: The proposed positive feedback through which “anoxia begets anoxia” (ABA). Hypolimnetic anoxia results in internal hypolimnetic phosphorus (TP) loading (A), which in turn increases epilimnetic TP (B) and stimulates phytoplankton growth, resulting in increased chlorophyll-*a* (chl-*a*; C). Phytoplankton decomposition fuels increased oxygen demand rates (D), which further drive hypolimnetic oxygen declines (E). This feedback can be externally influenced by increased air temperatures (gray dashed lines), among other factors.

In this study, we analyzed data from 656 widespread temperate lakes to study the drivers and consequences of interannual changes in hypolimnetic DO. Our research had three primary goals: first, we assessed the extent of support for each of the hypothesized relationships between anoxia, hypolimnetic phosphorus concentrations, epilimnetic phosphorus concentrations, epilimnetic chl-a, and oxygen demand across and within lakes (Figure 1). Second, we analyzed records of air temperature at each lake to assess how the ABA feedback may interact with changes in climate (Figure 1). We focused on climate as an external driver of the ABA feedback in lieu of accessible nutrient loading records for the study lakes. Third, we analyzed whether the strength of ABA relationships may vary with lake characteristics including lake depth and residence time. While our multi-lake approach precluded detailed consideration of external nutrient inputs and use of causal inference methods within a lake over time, analyzing data from many lakes was essential to testing the proposed relationships in this study and disentangling lake-specific effects amidst substantial heterogeneity.

2. METHODS

2.1 Overview of data compilation and analysis

Analyzing the ABA feedback required time series data for hypolimnetic DO, hypolimnetic total phosphorus (TP), epilimnetic TP, epilimnetic chlorophyll-*a* (chl-*a*), hypolimnetic oxygen demand, and climate records across numerous lakes (Figure 1). We compiled in-lake data from 656 geographically widespread stratified lakes to enable these analyses (2.2 *Dataset compilation*). We used linear mixed models, including relevant lags and climatic data when appropriate (2.3.2 *Mixed effects modeling*) to assess support for the ABA feedback relationships across all lakes. We then ran the same linear models within individual

lakes when sufficient data were available to assess whether the strength of ABA relationships may vary with lake characteristics (2.3.3 *Within-lake regressions*). All data compilation and analyses are described in detail below.

2.2 Dataset compilation

2.2.1 In-lake data

We synthesized data from a total of 656 temperate, seasonally-stratified lakes (Figure 2; Appendix S1: Text S1.1). Data were collated from Jane et al. (2021; $n = 316$ unique lakes not also available in the other datasets described here), the U.S. Wisconsin Department of Natural Resources (DNR; $n = 163$), the U.S. New Hampshire Volunteer Lake Assessment Program (VLAP; $n = 93$), the U.S. Lake Stewards of Maine (LSM) Volunteer Lake Monitoring Program ($n = 48$), the U.S. Adirondack lakes database (Winslow et al. 2018; Leach et al. 2018; $n = 17$), and members of the Global Lake Ecological Observatory Network (GLEON; $n = 29$). Chlorophyll-*a* data from Filazzola et al. (2020) were added for $n = 15$ lakes for which we did not have any other chl-*a* data.

Data availability and collection methods differed substantially among sites (documented in Lewis et al. 2023). For each site, we collated available data for DO, water temperature, TP, and chl-*a*, as well as lake metadata including geographic coordinates, depth (mean and maximum), surface area, and elevation (Lewis et al. 2023). Total nitrogen (TN) and dissolved organic carbon (DOC) were also compiled, but were more limited in availability ($n = 111$ lakes for DOC and $n = 119$ lakes for TN), motivating us to primarily focus on TP in our analyses below. To harmonize multiple datasets, quality control was performed on all data, as described in the data publication (Lewis et al. 2023).

In sum, the complete dataset consisted of 108,736 distinct water temperature and DO profiles across 656 lakes during 1938-2022 (Appendix S2: Figure S2.1). The median data duration was 30 years at each lake (range: 3–81 years). Lakes in the dataset had a median depth of 14 m (Z_{\max} ; range: 6–370 m), median surface area of 100 ha (range: 1–126,909 ha), and median elevation of 264 m (range: -215–2804 m). The lakes were located in 18 countries across 5 continents, with latitudes ranging from -42.6 to 68.3 (Lewis et al. 2023).

2.2.1.1 HydroLAKES

We collated additional metadata for each lake using HydroLAKES, a global database of 1.4 million lakes (with surface area ≥ 10 ha; Messenger et al. 2016). For lakes with missing mean or maximum depth (i.e., the depths were not reported with the data; $n = 43$), we used HydroLAKES data to fill in these values (Lewis et al. 2023). We also compiled residence time estimates from HydroLAKES to assess whether the strength of ABA feedback relationships may vary with differences in residence time across lakes.

2.2.2 Epilimnetic and hypolimnetic concentrations

2.2.2.1 Profile interpolation

We interpolated all temperature and DO profiles to a 1-m resolution following Jane et al. (2021). Briefly, we selected all profiles with at least three depths, then used the *pchip()* function of the *pracma* R package (Borchers 2022) to interpolate measurements from the surface to the deepest sampled depth.

To account for variation and error in sampling procedures, we implemented a standardized screening protocol to remove temperature and DO profiles that were substantially shallower or deeper than the reported maximum depth of the lake (Appendix S3).

2.2.2.2 Mean concentrations

We averaged data for all focal variables to an annual timestep using data from the entire stratified period and, separately, the late-summer period at each lake (Appendix S1: Text S1.2). The late summer (i.e., mid-July through August in the northern hemisphere, following Jane et al. 2021) is when DO concentrations are likely to approach their lowest value (Wetzel 2001), and may consequently be a critical time period for some processes in the ABA feedback. Conversely, other processes occurring throughout the entire summer stratified period (e.g., oxygen demand, hypolimnetic temperature) can also be critical to the ABA feedback, motivating the study of both periods within a year.

For each profile during either the entire summer stratified period or the late-summer period, we calculated the depths of the top and bottom of the metalimnion (the middle thermal layer of the lake) using the *rLakeAnalyzer* R package (Winslow et al. 2019). We used mean metalimnion depths to estimate the bottom of the epilimnion and top of the hypolimnion for each lake-year. We then averaged all hypolimnetic and epilimnetic water quality measurements throughout the time-period of analysis, using interpolated profiles for temperature and DO and all measurements for TP, chl-a, TN, and DOC. To estimate the strength of stratification at the thermocline, we calculated maximum buoyancy frequency using *rLakeAnalyzer* (Read et al., 2011; Winslow et al. 2019) for each temperature profile. Maximum buoyancy frequency was averaged throughout the stratified period for each lake-year (Table 1).

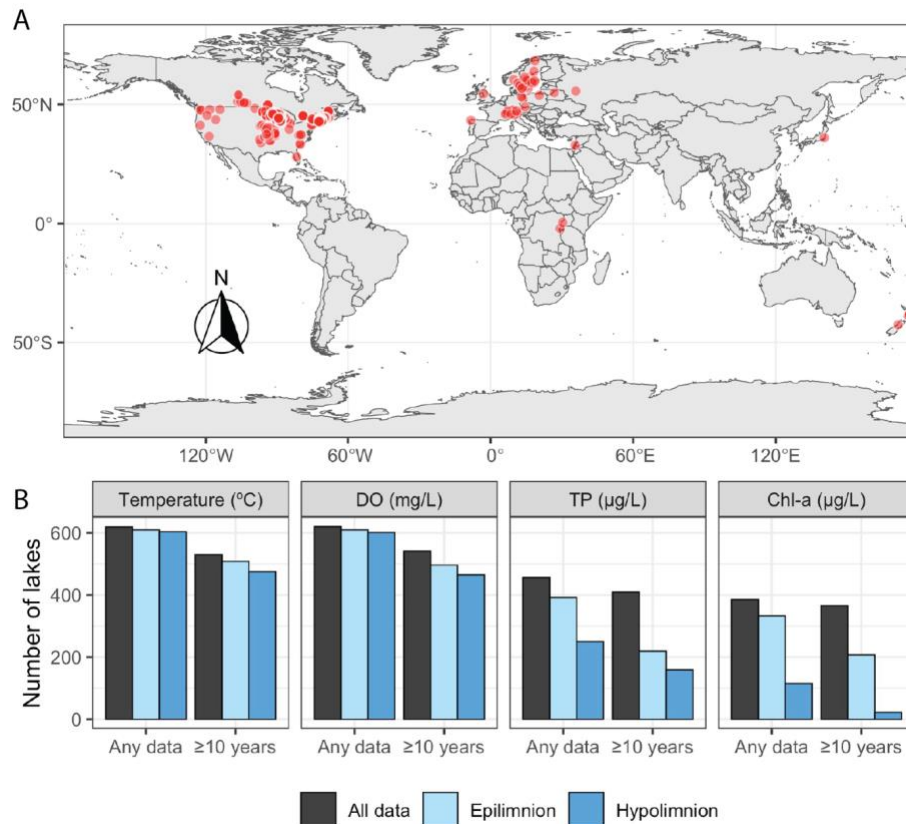


Figure 2: Data were compiled from a total of 656 widespread temperate lakes, with data availability differing across sites. A: map of all sites included in this dataset. Note that due to overlapping data points, many sites are not visible. More detailed maps of the United States and Europe are provided in Appendix S2: Figures S2 and S3. B: Summary of data availability for water temperature, dissolved oxygen (DO), total phosphorus (TP), and chlorophyll-*a* (chl-*a*) in the epilimnion (epi.) and hypolimnion (hypo.) of lakes in this study.

2.2.3 Volume-weighted hypolimnetic oxygen demand

We calculated volume-weighted hypolimnetic oxygen demand (VHOD; hereafter oxygen demand) within each lake-year, following Wetzel and Likens (2000). Briefly, we used measured or modeled bathymetric contours and interpolated DO profiles to calculate the volume-weighted

hypolimnetic DO concentration for each sampling date, then used linear regression models to calculate the rate of decline in volume-weighted hypolimnetic DO concentrations within the summer stratified period. We calculated an oxygen demand rate based on the raw data, as well as a temperature-corrected oxygen demand rate following Pace & Prairie (2005). Detailed methods for both calculations are provided in Appendix S4.

2.2.4 Anoxic Factor

Anoxic factor (AF) describes the spatial and temporal extent of anoxia within a lake, and is therefore a useful metric of deoxygenation in lakes that experience hypolimnetic anoxia (Nürnberg 1995; Nürnberg 2019). AF is expected to increase with increased oxygen demand, and can predict internal TP loading in lakes that experience hypolimnetic anoxia (Nürnberg 1995; Nürnberg 2019; Figure 1). Here, we calculated AF within each lake-year following Nürnberg (1988) and Nürnberg (2019), modified to address limited data availability across and within lakes (Appendix S5). Briefly, we estimated the duration of anoxia using oxygen profiles, oxygen demand, and modeled turnover dates, and we used modeled or measured bathymetry to quantify the spatial extent of anoxia within each lake-year. The DO threshold for anoxia was defined operationally, as described below (*2.3.3 Operational definition of anoxia*), with detailed methods provided in Appendix S5.

2.2.5 Climate data

To disentangle the roles of changing climate and in-lake processes on DO dynamics in stratified lakes, we collated monthly air temperature and precipitation data for every lake in our dataset from the ERA5 climate reanalysis. ERA5 is a fifth-generation product from the European

Centre for Medium-Range Weather Forecasts (ECMWF), and provides meteorological data from 1959–2022 on a 0.25-degree global grid (Hersbach et al. 2019). For our analysis, we used the monthly 2-m air temperature and total precipitation ERA5 data products, and found the closest gridded values for every lake in our dataset. We summarized “seasonal” air temperature and precipitation values by averaging across multiple months for each lake-year, with southern hemisphere data offset by six months. Spring values were calculated as the average of March and April air temperature or precipitation (following, e.g., Williamson et al. 2015). While stratification onset varies across latitudes and lakes, these spring months are the most likely to correspond to ice melt and spring mixing across the temperate lakes in this study (Woolway et al. 2021; Appendix S1: Figure S1.2). Summer values were calculated as the average of July and August air temperature or precipitation, as these summer months most closely correspond with our late-summer in-lake data and were the warmest two months on average across the dataset (Appendix S2: Figure S2.4). Winter temperature and precipitation were calculated as the average of January and February air temperature and precipitation. These winter months were, on average, the coldest months in our dataset (Appendix S2: Figure S2.4), and likely constituted a significant portion of the ice-covered period in lakes that experience seasonal ice cover (Magnuson et al. 2000).

2.3 Data analysis

To analyze the proposed ABA relationships, we used lag analysis (*Section 2.3.1*), mixed effects modeling (*Section 2.3.2*), and within-lake regressions (*Section 2.3.3*). All data analyses were performed in R, version 4.2.1 (R Core Team, 2021). Analysis code is archived as a Zenodo repository for reproducibility (Lewis and Lau, 2023).

2.3.1 Lag analysis

Several of the relationships in the proposed ABA feedback may operate across years, rather than within one year. To assess the appropriate lag for each step, we calculated the Spearman correlation between each variable of analysis and the preceding variable in the feedback cycle (e.g., between oxygen demand and chl-a; Figure 1) with 0, 1, and 2-year lags. These correlations were calculated separately for each lake with at least 10 years of paired data for the target parameters. Across all lakes, we calculated whether the mean of the resulting distribution of correlations was significantly different than zero using Wilcox tests with $\alpha = 0.05$.

2.3.2 Mixed effects modeling

To assess the proposed mechanisms by which anoxia could create a positive feedback that promotes subsequent anoxia (Figure 1), we used linear mixed models to estimate the magnitude and direction of effect for drivers of AF, epilimnetic and hypolimnetic TP, epilimnetic chl-a, and oxygen demand among lake-years. To assess the relationship between oxygen demand and hypolimnetic DO concentrations in lakes that did not experience anoxia (i.e., AF = 0 days throughout the entire time series), we conducted an additional regression analysis for oxygen demand and late-summer hypolimnetic DO concentrations, rather than AF (Appendix S6). Lake ID was included as a random effect on the intercept in all models. Mixed effect models were run using the package *lme4* in R (Bates et al. 2023).

For each response variable, we filtered all data to only include lake-years with complete data for all proposed explanatory variables (Table 1). We log-transformed chl-a and TP concentrations due to the substantial positive skew of these data, and we Z-standardized all

explanatory variables. We fit linear mixed models for all possible combinations of explanatory variables and identified the best model using corrected Akaike Information Criterion (AICc). We report all selected models within two AICc units of the best model (Burnham & Anderson 2002). We assessed the multicollinearity of all models using the variance inflation factor, which we calculated using the *vif()* function from the package *car* in R (Fox et al. 2022).

We plotted the coefficient estimate for all fixed effects in the selected models to visually compare the magnitude of effect for each explanatory variable. For these visualizations, we calculated 95% confidence intervals of the fixed effects using the *confint.merMod()* function from *lme4* (Bates et al. 2023).

2.3.3 Operational definition of anoxia

We used an operational DO threshold to define hypolimnetic anoxia, following other studies on anoxia in lakes (e.g., Elshout et al. 2013; Nürnberg et al. 2019; LaBrie et al. 2023). To identify this threshold, we performed a breakpoint analysis and piecewise regression for hypolimnetic DO and TP using the package *segmented* in R (Muggeo, 2023; Appendix S6: Text S6.1). We then added slope-difference (U) and change-point (G0) parameters for the breakpoint relationship, and used the resulting breakpoint as a threshold value for our calculation of AF (Appendix S5).

Table 1: Explanatory variables used for mixed model regression. We tested several possible explanatory variables for each response variable using a mixed model approach. The time period over which mean values were calculated for each lake-year is provided for all water column variables. For information on lags used, see Appendix S7: Figures S1–S5. Epilimnion and hypolimnion are abbreviated as epi. and hypo. throughout.

Response variable	Proposed explanatory variables	Time period	Motivation for inclusion
Anoxic factor	Oxygen demand	Stratified	ABA feedback
	Spring average air temp.		Stratification onset
	Autumn average air temp.		Stratification end
	Winter average air temp.		Ice dynamics
	Hypo. temperature	Late-summer	Solubility, stratification end
Late-summer hypo. TP	Anoxic factor	Late-summer	ABA feedback
	Epi. TP	Stratified	Diffusion/sinking
	Maximum buoyancy frequency	Stratified	Diffusion
	Hypo. temp	Late-summer	Temperature dependence of sediment flux
	Spring precipitation	Late-summer	Catchment inputs/flushing
	Summer precipitation		Catchment inputs/flushing
	Winter precipitation		Catchment inputs/flushing
	Mean TP measurement date		Seasonal change
Stratified epi. TP	Hypo. TP	Late-summer	ABA feedback
	Hypo. TP (t-1)	Late-summer	Autumn mixing
	Epi. TP (t-1)	Late-summer	Legacy effect
	Spring precipitation		Catchment inputs/flushing
	Summer precipitation		Catchment inputs/flushing
	Winter precipitation		Catchment inputs/flushing
	Maximum buoyancy frequency	Stratified	Diffusion
	Mean TP measurement date	Stratified	Seasonal change
Stratified epi. chl-a	Epi. TP	Stratified	ABA feedback
	Epi. TN	Stratified	Potential limiting nutrient
	Spring average air temp.		Temperature-dependence of phytoplankton growth
	Summer average air temp.		
	Mean chl-a measurement date	Stratified	Seasonal change
Oxygen demand	Epi. chl-a	Stratified	ABA feedback
	Epi. chl-a (t-1)	Stratified	ABA feedback
	Hypolimnetic temp.	Stratified	Temperature-dependence of respiration
	Hypo. surface area to volume ratio	Stratified	Sediment oxygen demand
	Maximum buoyancy frequency	Stratified	Diffusion

2.3.4 Within-lake regressions

To assess whether the across-lake trends identified using mixed models were observable within individual lakes, we performed linear regressions separately at each lake. For each of our focal response variables (see Table 1), we used the same model formulations from the across-lakes analysis (i.e., the explanatory variables from Table 1 that were selected via AICc) to perform regressions within a lake. We saved the resulting coefficient estimates for each explanatory variable used to predict this focal response. We then plotted the distribution of coefficient estimates for all explanatory variables across all lakes, and we compared the median of these distributions to the mixed effect model coefficient estimates. For each response variable, we only included lakes that had at least 10 years of paired data for the response variable and all selected explanatory variables. We removed $n = 81$ lakes that never experienced anoxia (i.e., AF = 0 throughout the timeseries) from the within-lake analysis of the drivers of AF.

2.3.4.1 Driver analysis

The coefficient estimates for explanatory variables included in the ABA feedback (e.g., the coefficient of epilimnetic TP for predicting epilimnetic chl-a) indicates the magnitude of the response, while accounting for other drivers (Table 1). As an exploratory analysis to assess which lakes are most susceptible to the ABA feedback, we analyzed whether there were significant differences in these coefficients based on differences in lake characteristics. For this analysis, we developed linear models predicting the coefficient estimate for each focal variable in the ABA feedback (Table 1) based upon (individually) maximum depth, surface area, mean depth, residence time, dynamic ratio (square root of lake area divided by mean depth; Håkanson 1982), and mean concentrations of focal (ABA) variables (i.e., hypolimnetic DO, epilimnetic and

hypolimnetic TP, epilimnetic chl-a, and oxygen demand). We then used AICc to select the model(s) with the greatest explanatory power. We did not assess more complicated model structures (e.g., multiple drivers and interaction effects) due to the relatively small sample size for some of these analyses (e.g., $n = 35$ lakes for oxygen demand).

2.3.5 Climate effects

To summarize the effects of climatic variation on oxygen dynamics, we analyzed monthly and annual air temperature data. First, we calculated correlations between monthly air temperatures and, separately, hypolimnetic temperature, oxygen demand, AF, and late-summer DO concentrations (Appendix S8). Then, we summarized the effects of high and low annual air temperature anomalies on AF and late-summer oxygen concentrations (Appendix S8).

3. RESULTS

3.1 Operational definition of hypolimnetic anoxia

We identified a breakpoint relationship whereby hypolimnetic TP increased substantially after DO decreased below a threshold of 1.8 mg/L (56 $\mu\text{mol/L}$), averaged throughout the hypolimnion (Figure 3). Subsequently, we used 1.8 mg/L as our DO threshold for anoxia in all analyses. Of the 356 lakes with at least 10 years of hypolimnetic DO data, 146 lakes (34%) crossed the threshold of 1.8 mg/L during their time series (i.e., had at least one year with hypolimnion-averaged DO < 1.8 mg/L and at least one year with DO ≥ 1.8 mg/L). Lakes that crossed this threshold ($n = 146$) were more common than lakes that had consistently anoxic ($n = 120$) or consistently oxic ($n = 90$) hypolimnia. Furthermore, lakes that crossed the threshold of

1.8 mg/L had lower DO concentrations in the year following the first year of anoxia than in the year prior to the first year of anoxia (Appendix S9; Figure S9.1).

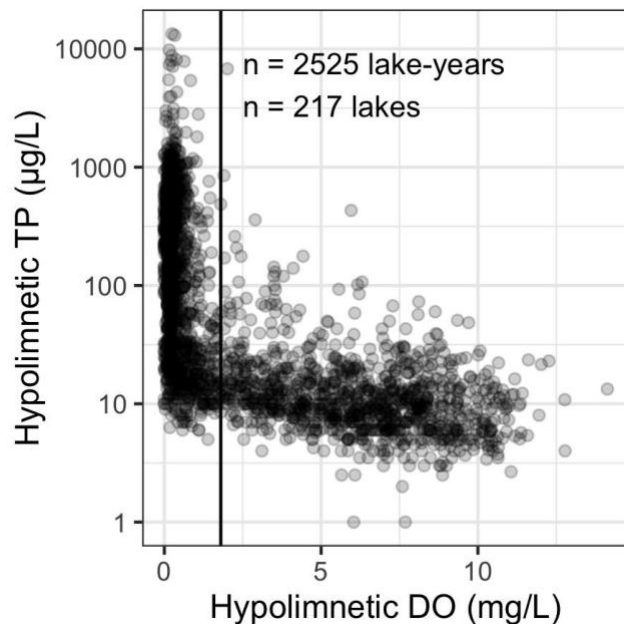


Figure 3: Piecewise mixed model regression identified a breakpoint in the relationship between hypolimnetic DO and TP at 1.8 mg/L DO. Here, points represent individual lake-years.

3.2 Regression analyses support expected relationships within and across lakes

Our analyses across 656 lakes provided support for the ABA feedback. Of the explanatory variables used in our model selection process (Table 1), all variables that were predicted to promote the ABA feedback were found to be statistically significant drivers of their predicted responses (Figure 4), with expected temporal lags as applicable (0–1 years; Appendix S7). High AF was associated with high hypolimnetic TP (Figure 4A), and high hypolimnetic TP was associated with high epilimnetic TP, both within and between years (i.e., both Hypo TP and Hypo TP_{t-1} had positive coefficients; Figure 4B). High epilimnetic TP was in turn associated with high chl-a within a year (Figure 4C), and high chl-a was associated with high oxygen

demand (both VHOD and $\text{VHOD}_{\text{std } 10^{\circ}\text{C}}$) the following year (Figure 4D; Appendix S10). Lastly, high oxygen demand was associated with greater AF in the lakes that experienced hypolimnetic anoxia (Figure 4E). For the lakes that did not exhibit anoxia during their time series, high oxygen demand was associated with low late-summer DO concentrations (Appendix S6).

All of the ABA relationships observed to be significant across hundreds of lakes ($n = 111\text{--}386$; Figure 4) were also supported by regression analyses conducted within individual lake time series (with $n = 35\text{--}157$ lakes for each analysis; Figure 5). The direction of each of the ABA relationships was identical within and across lakes (Figure 5). The magnitude of the median coefficient estimates for ABA explanatory variables within lakes (e.g., the coefficient for chl-a in the multiple linear regression with oxygen demand as a response variable) tended to be slightly smaller than the mixed model coefficient estimate (Figure 5) for each relationship, except for oxygen demand as a predictor of AF (Figure 5E).

While the hypothesized ABA feedback was supported by regression analyses, variability in the focal response variables (i.e., AF, TP, chl-a, and oxygen demand; Table 1) was also modulated by additional driving factors, as expected (Figure 1; Appendix S8). Specifically, climatic variables were selected as part of the optimal model for nearly all focal variables: spring air temperatures were important drivers of AF and chl-a, spring and summer precipitation were significant drivers of epilimnetic TP, and winter precipitation was a significant driver of hypolimnetic TP (Figure 4; Figure 5). Water temperature also played a role in explaining variation in several focal responses: hypolimnetic temperatures were a significant predictor of both AF and oxygen demand (Figure 4; Figure 5). For all responses, we found substantial variability in the random intercept of the mixed-model regressions among lakes (Table 2) and variability in within-lake regression coefficients (Figure 5), indicating external lake-specific

factors that influence the state of each response variable at a given lake. Random effects were largest for AF, and residual standard deviation from mixed-model analyses was highest for oxygen demand and epilimnetic chl-a (Table 2).

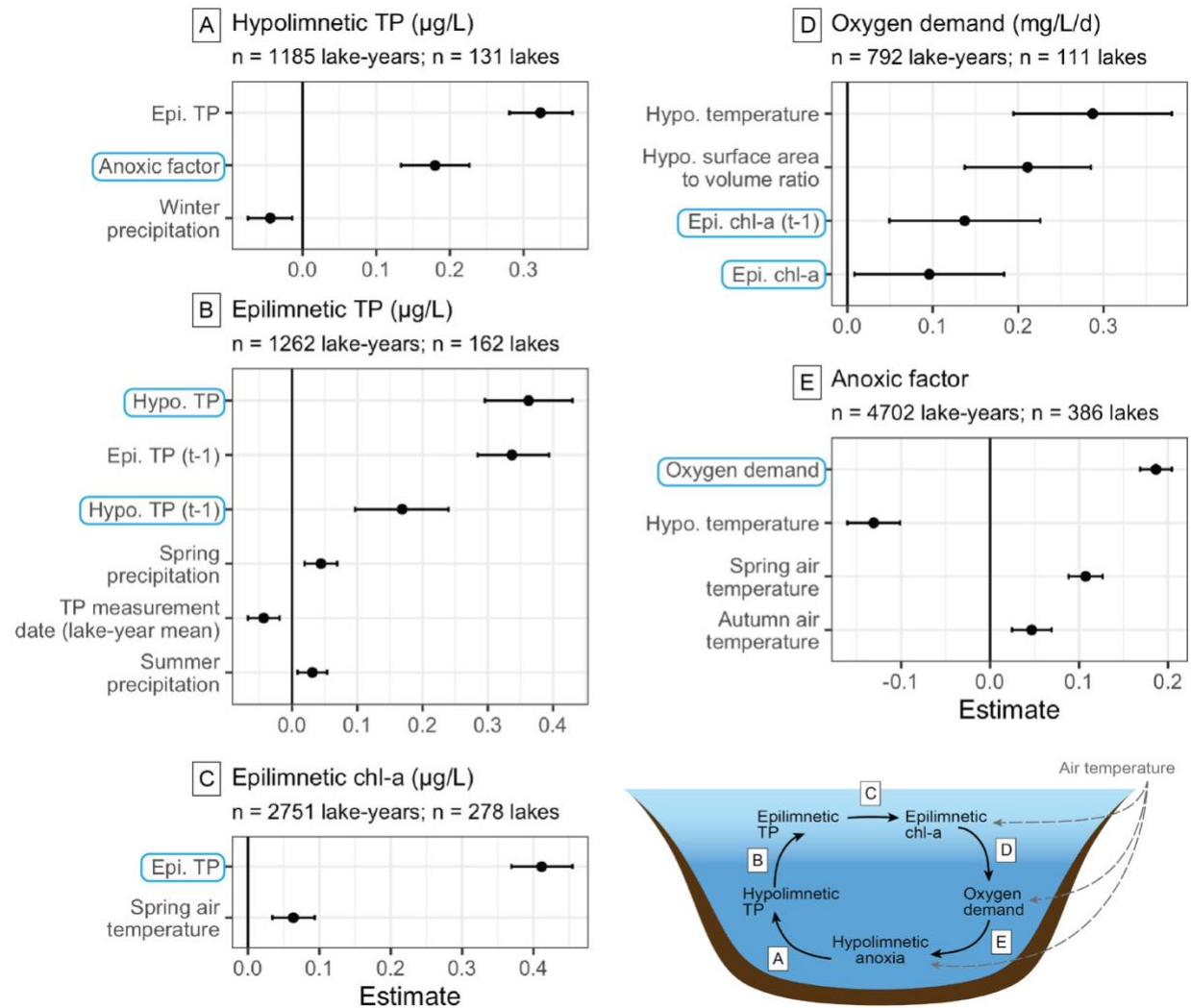


Figure 4: The proposed ABA feedback (bottom right) was supported by linear mixed model results across all variables (see Table 1). Here, panel titles indicate the response variable for each panel and y-axis labels indicate explanatory variables. X-axes indicate the magnitude and 95% confidence interval of the parameter estimate for each explanatory variable presented on the y-axis. The black vertical lines in panels A-E denote a parameter estimate of zero. Blue rectangles highlight drivers in the hypothesized ABA feedback (bottom right). Explanatory variables are ordered by the magnitude of the parameter estimate within each panel.

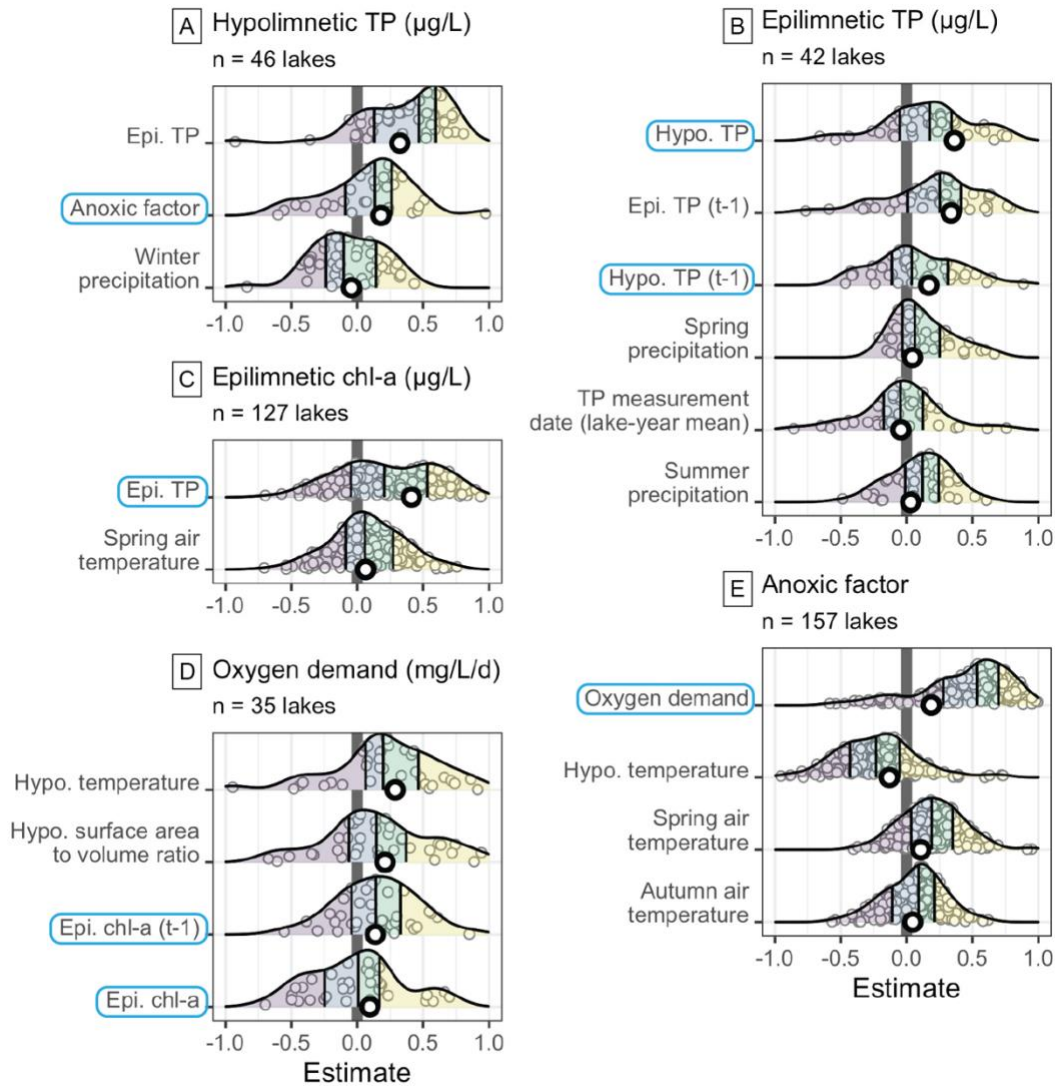


Figure 5: Linear regressions analyzing time series data within individual lakes provide further support for the ABA feedback. Here, panel titles indicate the response variable for each panel and y-axis labels indicate explanatory variables. Individual points represent regression coefficients from within one lake. Density distributions describe the distribution of parameter values across lakes, with colors delineating the quartiles of the distribution (purple: 0-25%, blue: 25-50%, green: 50-75%, and yellow: 75-100%). Black and white circles at the bottom of each distribution mark the parameter estimate from the mixed model analysis (Figure 4). The gray vertical lines in panels A-E denote a parameter estimate of zero. Blue rectangles highlight drivers in the hypothesized ABA feedback. Explanatory variables are ordered by the magnitude of the mixed-model parameter estimate for consistency with Figure 4. All x-axes range from -1 to 1 to enable comparison among panels.

Table 2: Random and residual variation from linear mixed models. Model structure and fixed effects are summarized in Figure 4.

Response variable	Random effect standard deviation (intercept)	Residual standard deviation
Anoxic factor (AF)	0.982	0.337
Hypolimnetic TP	0.665	0.286
Epilimnetic TP	0.248	0.340
Epilimnetic chl-a	0.635	0.415
Oxygen demand	0.630	0.597

Across lakes, our analyses indicate that the relative strength of ABA relationships varied with lake characteristics. Specifically, the coefficient for the effect of epilimnetic TP on chl-a was larger for lakes with high mean epilimnetic TP values; the coefficient for the effect of oxygen demand on AF was larger for lakes with deep mean depth; and the coefficient for the effect of chl-a on oxygen demand was larger for lakes with long residence time (Figure 6). The other ABA feedback relationships were not significantly mediated by any one of our candidate predictors (*Section 2.3.4.1*).

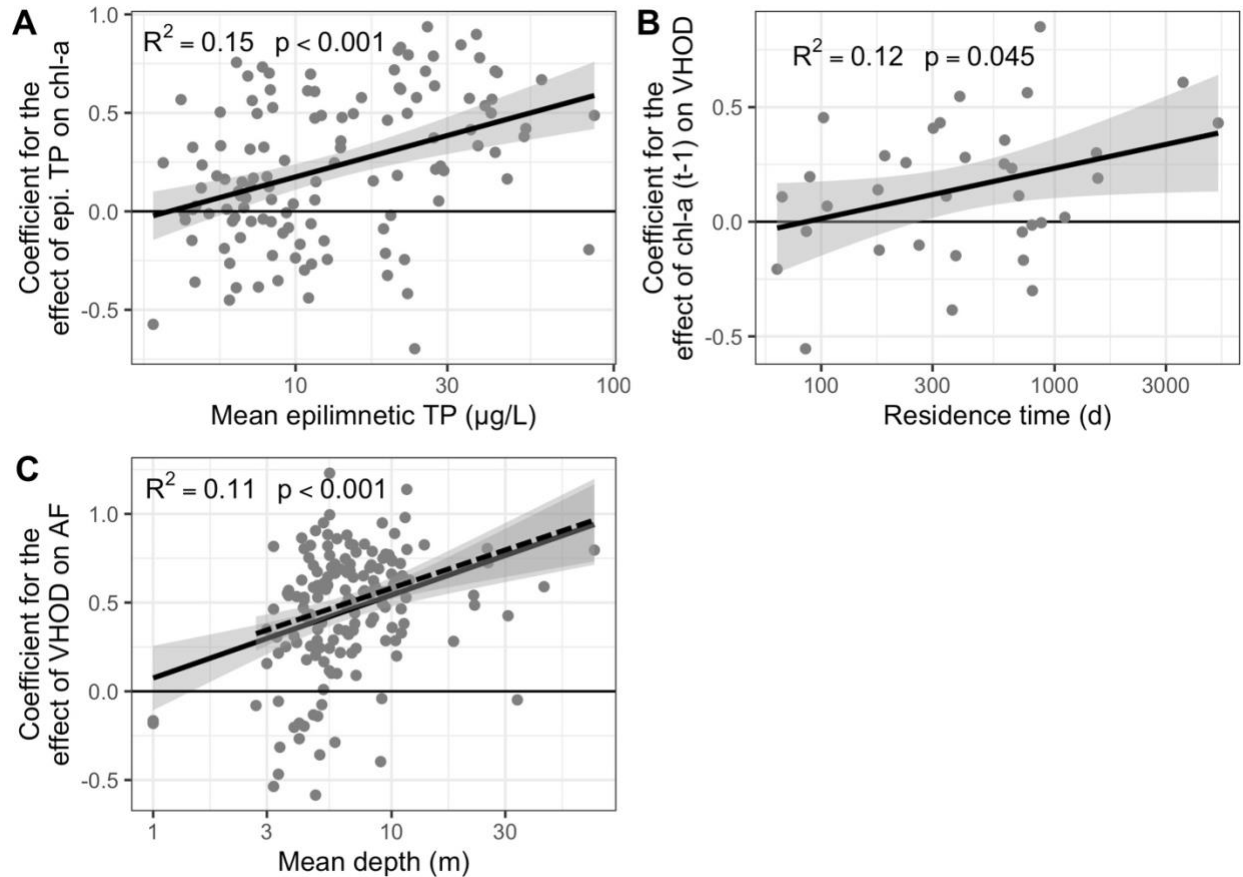


Figure 6: The strength of ABA feedback relationships may be modulated by lake characteristics. A: The coefficient for the effect of epilimnetic total phosphorus (epi. TP) on chlorophyll-*a* (chl-*a*) was most positive in lakes with high mean epilimnetic TP. B: The coefficient for the effect of the previous year's chlorophyll-*a* (chl-*a*) on volume-weighted hypolimnetic oxygen demand (VHOD) was most positive in lakes with long residence times. C: The coefficient for the effect of VHOD on anoxic factor (AF) was most positive in lakes with deep mean depths. This relationship was robust to including all data (solid regression line) and excluding disproportionately influential points (i.e., Cook's distance greater than $3 \times$ the mean, $n = 12$ lakes; shown as a dashed line). Linear regressions are presented as solid lines.

4. DISCUSSION

In analyzing ABA relationships both across and within 656 lakes, we found support for all linkages in the hypothesized ABA feedback (Figure 4; Figure 5). These results provide empirical support for the existence of a positive feedback mechanism that could intensify the development of anoxia in lakes around the world. Furthermore, our results indicate that the

strength of these relationships likely varies with lake characteristics, including mean depth, TP concentrations, and residence time. To our knowledge, our work is the first to quantitatively document all of the relationships that enable anoxia to beget increasingly frequent or more intense anoxia in future years across a large, multi-continental dataset of lakes.

4.1 Decades of research facilitate identification of ABA feedback

Individual relationships in the ABA feedback have been the subject of substantial research inquiry over the past century or longer (e.g., Sachs 1874; Thienemann 1928; Schindler 1974). While these previous studies primarily focused on examining biogeochemical dynamics within one lake, they provided support for the individual relationships in the ABA feedback (Figure 1). Modeling studies provided a means of simultaneously considering all ABA relationships, and have shown mechanistic support for the existence of an ABA feedback in seasonally-stratified lakes (Carpenter 2003; Carpenter and Lathrop 2008). However, model simulations have indicated that the susceptibility of individual lakes to a trophic regime shift, as a result of the ABA feedback, depends on multiple lake-specific parameters (i.e., macrophyte presence, temperature, mean depth; Genkai-Kato & Carpenter, 2005), highlighting the need for a multi-lake empirical approach.

By synthesizing data across many lakes, our mixed model approach allowed us to identify biogeochemical dynamics that likely would have been difficult to detect in individual lakes. The strength of this approach is reflected in the fact that coefficient estimates from our mixed model regressions, which integrate data from many lakes, were typically slightly larger in magnitude than the median coefficient estimates of regressions run within individual lakes (Figure 5), although both approaches showed support for the existence of the ABA feedback.

Across-lake regressions included a larger range of variation for predictor variables than is typically observed within individual lakes, which likely facilitated the detection of more substantial predictor-response effects. Through study of the hypothesized ABA feedback, we found support for several individual limnological relationships, some of which had not been previously analyzed on a widespread scale. Below we discuss our findings for each ABA relationship and their implications in the context of previous work (*Sections 4.1.1–4.1.5*).

4.1.1 Effect of anoxia on hypolimnetic TP (Figure 1A)

In this study, we observed a strong positive relationship between hypolimnetic anoxia and TP concentrations both within and across lakes. Across lakes, our breakpoint analysis detected a threshold relationship whereby hypolimnetic DO had a stronger effect on TP when DO concentrations decreased to levels approaching anoxia (<1.8 mg/L; Figure 3). Our results reinforce previous research affirming that AF (the duration and spatial extent of anoxia) may be strongly positively correlated with hypolimnetic TP concentrations (Figure 4; Figure 5; e.g., North et al. 2014; Nürnberg et al. 2019). A threshold relationship between DO and TP is well-supported by previous research across sediment core incubations, *in situ* sediment chamber measurements, and mass-balance whole ecosystem analyses (e.g., Einsele 1936; Mortimer 1942; Orihel et al. 2017; Anderson et al. 2021). Here, our threshold value of 1.8 mg/L DO, averaged throughout the entire hypolimnion, likely reflects DO conditions of ~0 mg/L near the sediment-water interface (which inherently is challenging to quantify empirically), resulting in enhanced TP loading (Nürnberg 2019). We note that our identified breakpoint of 1.8 mg/L is also remarkably similar to those identified in previous sediment incubation work (Matisoff et al. 2016; Doig et al. 2017; Orihel et al. 2017). Overall, this analysis indicates that the ABA

mechanism may require hypolimnetic DO concentrations to decrease to low levels (i.e., <1.8 mg/L) before a feedback effect will occur.

In our dataset, it was common for lakes to cross the threshold of 1.8 mg/L (34% of $n = 356$ lakes). Lakes where oxygen concentrations declined below 1.8 mg/L had lower DO concentrations in the year following the onset of anoxia than in the year prior to the onset of anoxia (Appendix S9; Figure S9.1). While our dataset was not a random or fully representative sample of global lakes, the large number of lakes which crossed the 1.8 mg/L threshold in this study suggests that the ABA feedback may be prevalent.

4.1.2 Effect of hypolimnetic TP on epilimnetic TP (Figure 1B)

We found moderately strong support for an effect of hypolimnetic TP on epilimnetic TP both within one year and between years (i.e., hypolimnetic TP influences epilimnetic TP the following year). While the directionality of this relationship can be difficult to identify in the absence of detailed nutrient input data (i.e., epilimnetic TP can affect hypolimnetic TP, vice versa, or a third driver may simultaneously influence both), existing research provides strong support for this effect. Elevated hypolimnetic TP concentrations can increase epilimnetic TP concentrations within a summer stratified period through organism-mediated transport, diffusion, and internal seiche dynamics (e.g., Carpenter et al. 1992; Soranno et al. 1997; Kamarainen et al. 2009; Nürnberg 2009; Haupt et al. 2010; Cottingham et al. 2015). At the onset of autumn mixing, the concentration of TP in the hypolimnion fundamentally determines the amount of potential TP input to the epilimnion, which can have legacy effects throughout the subsequent autumn, winter, and spring (e.g., Nürnberg and Peters 1984; Wang et al. 2019).

4.1.3 *Effect of epilimnetic nutrients on epilimnetic chl-a (Figure 1C)*

We found a strong positive association between surface water TP concentrations and surface water chl-a, both within and across lakes, likely reflecting the fact that interannual variability in phosphorus concentrations can play an important role in regulating phytoplankton growth in lakes (Figure 4; Figure 5). Our study follows many decades of data that illustrate the positive effect of TP on phytoplankton biomass (Schindler 1974; Smith 1982; MacKeigan et al. 2023). In this study, we were unable to identify an effect of epilimnetic TN concentrations on chl-a, suggesting that in these lakes, TP may play a more important role in regulating phytoplankton growth. However, we note that data availability was substantially greater for TP ($n = 387$ lakes) than for TN ($n = 86$ lakes), and complexities of nitrogen forms (not considered here) may hinder the detection of a nitrogen effect. Previous research has documented the importance of nitrogen for limiting or co-limiting phytoplankton growth in some lakes, over multiple timescales (Elser et al. 2007; Lewis Jr. and Wurtsbaugh 2008; Paerl et al. 2016; Scott et al. 2019; Lewis et al. 2020). Consequently, our study highlights the need for long-term, speciated nitrogen data to disentangle the role of nitrogen in the ABA feedback.

4.1.4 *Effect of epilimnetic chl-a on oxygen demand (Figure 1D)*

Support for the relationship between epilimnetic chl-a and oxygen demand was relatively weaker than for the other ABA relationships, although still consistent within and across lakes. We expected that this relationship would be more challenging to detect than the other ABA relationships due to high levels of spatio-temporal heterogeneity in chl-a and uncertainty associated with oxygen demand calculations (e.g., modeled bathymetry and the assumption of a closed system). Interestingly, the effect of chl-a appeared to occur at least as strongly between

years as within a year. Legacy effects of chl-a on oxygen demand are intuitive and expected, as decomposition of sediment organic matter (including settled phytoplankton biomass) may constitute the majority of the total hypolimnetic oxygen demand in many lakes (Steinsberger et al. 2020). Likewise, limited sampling of early-season bloom events could have partially obscured the role of within-year chl-a on oxygen demand. Regardless, our analyses provide support for both within-year and between-year effects of phytoplankton blooms in perpetuating anoxia.

4.1.5 Effect of oxygen demand on hypolimnetic anoxia (Figure 1E)

The positive relationship between oxygen demand and AF is well-supported by this study, and is also intuitive: as biological and chemical demand for oxygen increases, the onset of anoxia is likely to occur earlier in the stratified period, increasing the total duration of anoxia (Figure 4; Figure 5). Furthermore, in lakes that did not experience anoxia throughout the time series of data used in this study, oxygen demand was negatively associated with late-summer DO concentrations (Appendix S6: Text S6.2), supporting that oxygen demand and DO concentrations are closely coupled in both oxic and anoxic lakes. Across the dataset, the effect of oxygen demand on hypolimnetic oxygen conditions occurred simultaneously with an additional positive effect of spring air temperatures (Figure 4; Figure 5, Appendix S6: Text S6.2), and in anoxic lakes AF was further regulated by autumn air temperatures (Figure 4; Figure 5). Positive associations between anoxia and spring and autumn air temperatures may highlight the important role that stratification duration (i.e., both onset in spring and end in autumn) can play in driving the spatial and temporal extent of anoxia (e.g., Nürnberg, 1995; Jane et al. 2023). Previous work has identified that the duration of summer stratification is increasing across many lakes (Woolway et al. 2021), driving decreased late-summer oxygen concentrations (Jane et al. 2023).

However, the factors that control oxygen demand are changing less consistently: temporal trends in hypolimnetic temperature are highly variable across lakes (Pilla et al. 2020; Richardson et al. 2017), as are trends in chl-a from 1980–present (Kraemer et al. 2022). Consequently, it is not surprising that trends in oxygen demand appear to be inconsistent across lakes (Jane et al. 2023). In this study, our focus on annual and sub-annual timescales allowed us to more precisely investigate the mechanisms at play within and across 386 lakes (Figure 4E), identifying that variability in oxygen demand has the potential to drive a feedback effect in some lakes that experience hypolimnetic anoxia.

4.2 Lake characteristics can increase susceptibility to the ABA feedback

Through our cross-lake analyses, we identified that the ABA feedback may be stronger in some lakes than others. In particular, mean epilimnetic TP concentrations, mean depth, and residence time each modulated ABA feedback relationships (Figure 6).

First, the effect of TP on chl-a was strongest in lakes with high mean epilimnetic TP concentrations, especially for lakes with TP concentrations greater than $\sim 10 \mu\text{g/L}$ (Figure 6A). These mesotrophic to eutrophic/hypertrophic lakes also tended to experience substantial variability in epilimnetic TP concentrations, which likely made the effect of changing TP concentrations more detectable in our standardized linear regression analyses (Appendix S11: Figure S11.1). Ultimately, our finding that TP and chl-a are more closely correlated at high TP concentrations may provide some resistance to the initiation of the ABA feedback in oligotrophic lakes, while further accelerating the ABA feedback as eutrophication proceeds due to external or internal nutrient loading.

Second, the effect of the previous year's chl-a on oxygen demand was strongest in lakes with long residence times (Figure 6B). In these lakes, decomposing chl-a and autochthonous organic carbon may have more time to settle and accumulate on the hypolimnetic sediments, fueling oxygen demand the following year. Conversely, the effect of the previous year's chl-a on oxygen demand was negligible in lakes with residence time less than ~100 days (Figure 6B), as chl-a may be quickly flushed and exported downstream from these lakes. Consequently, lakes with longer residence time may be more susceptible to the ABA feedback.

Third, the magnitude of the effect of oxygen demand on AF generally increased with increasing mean depth of the lake (Figure 6C). Mechanistically, deeper lakes often have relatively lower oxygen demand due to low sediment area to hypolimnetic volume ratios (Livingstone and Imboden 1996; Müller et al. 2012; Steinsberger et al. 2020). Consequently, variation in oxygen demand can substantially affect the amount of time it takes to reach anoxia in these deep lakes. Conversely, in shallow lakes, hypolimnetic DO concentrations may be more strongly impacted by factors other than oxygen demand, including hypolimnetic primary production, stratification phenology, and mixing events (Wetzel 2001). Ultimately, deep lakes (i.e., mean depth > 5 m; Figure 6) appear to have a particularly strong coupling between oxygen demand and AF, strengthening the ABA feedback in these lakes.

Combined, these results suggest that deep mesotrophic or eutrophic lakes with long residence times are particularly likely to be susceptible to the ABA feedback, though more data are needed to test these hypotheses. Importantly, our identification of factors that may affect the strength of the ABA feedback across lakes would not have been possible without the use of a multi-lake dataset like the one analyzed in this study.

4.3 Climate change has the potential to trigger the ABA feedback

Our analysis of 656 widespread lakes suggests a strong relationship between climate variation and deoxygenation. Importantly, this climate variability may have the potential to push hypolimnetic DO below the ~1.8 mg/L threshold that is associated with increased hypolimnetic TP release from sediment, thereby initiating the ABA feedback.

4.2.1 High spring air temperatures are associated with anoxia

Our results suggest that increased spring air temperatures can contribute to DO declines not only by prolonging summer stratification, as demonstrated previously (Woolway et al. 2021; Jane et al. 2023), but also by increasing chl-a, hypolimnetic temperature, and oxygen demand (Figure 4C; Appendix S8). While we saw a clear effect of spring air temperatures on hypolimnetic DO dynamics, we did not observe a similar effect for summer temperatures (Appendix S8: Figure S8.1). Spring may be a particularly influential time period for the DO and temperature dynamics of warm monomictic and dimictic lakes, as this period sets the beginning of stratification and the initial heat and oxygen content of the hypolimnion (Shatwell et al. 2019; Woolway et al. 2021; Jane et al. 2023). While mean air temperatures are increasing around the world as a result of anthropogenic climate change, these impacts are not consistent across seasons or locations (Masson-Delmotte et al. 2021). Specifically, the time period during which temperatures fall in the historical range of spring temperatures is shortening across Northern Hemisphere mid-latitudes, which are representative of most of the lakes in this study (Wang et al. 2021). Conversely, the time period during which temperatures fall in the historical range of summer temperatures is lengthening (Wang et al. 2021; Woolway 2023). Our work highlights the importance of accounting for these differential changes in seasonal air temperatures, not just

annual means, when anticipating how changes in climate may affect hypolimnetic DO dynamics. Furthermore, as spring air temperatures continue to increase across many lakes, our work suggests that these climatic changes may play a role in causing hypolimnetic oxygen concentrations to decline, potentially initiating the ABA feedback.

4.4 Strengths and limitations of this analysis

Using regression models within and across lakes, we were able to simultaneously analyze the extent of support for each of the relationships in the hypothesized ABA feedback. Lakes analyzed in this study span five orders of magnitude in surface area and two orders of magnitude in maximum depth (Z_{\max} ; Lewis et al. 2023). Amidst these substantial differences, we found consistent support for the ABA feedback relationships within and across lakes.

While the dataset analyzed here is larger than those used in previous studies, data limitations continued to constrain our analysis. Specifically, we were unable to analyze the effects of external nutrient loads, or DOC concentrations on the ABA feedback due to lack of data, and we were unable to use causal inference methods to study ABA dynamics within individual lakes over time. Moreover, the majority (82%) of lakes analyzed here are temperate lakes located in the U.S.; consequently, results may not be fully generalizable to global lakes, and more research is needed to characterize DO dynamics in a broader, representative range of ecosystems, especially in tropical and southern hemisphere lakes. Our calculated AF values have substantial uncertainty, particularly with respect to stratification end dates, though we have done our best to minimize these uncertainties through detailed methodological testing (Appendix S5). To standardize across a wide range of lakes and sampling regimes, our analysis considered the entire hypolimnion as one homogenized layer, averaging over potentially meaningful variation in

DO dynamics across a depth gradient in the hypolimnion (e.g., LaBrie et al. 2023). Given the promising results we observed here, further exploration of depth-resolved DO declines across lakes likely has substantial potential to further our understanding of biogeochemical processing in lakes.

4.5 Conclusions and global change implications

We found widespread empirical support for the ABA feedback in analyzing time series data across 656 diverse lakes. Relationships were particularly strong between oxygen demand and AF; AF and hypolimnetic TP; and epilimnetic TP and chl-a. Conversely, the effect of epilimnetic chl-a on oxygen demand was comparatively less strong, though still detectable both within and across lakes. As oxygen concentrations are decreasing in many lakes around the world, accounting for the ABA feedback may help effectively prioritize restoration and conservation efforts. Notably, our work suggests that catchment-scale nutrient management may be particularly critical for preventing deterioration of water quality in lakes with late-summer hypolimnetic DO concentrations just above 1.8 mg/L that have not yet crossed this threshold. These lakes are less likely to currently experience feedback effects of anoxia, but may cross this threshold in the future, thereby initiating an ABA feedback that, once triggered, will make water quality management more challenging. As climate and land use continue to change on a global scale, understanding and accounting for the ABA feedback may enable more effective conservation of culturally, economically, and ecologically important lake ecosystems.

ACKNOWLEDGEMENTS

Many thanks to the Global Lake Ecological Observatory Network (GLEON) Metabolism Working Group for catalyzing this analysis. Specifically, Ted Harris, Paul Hanson, Jim Rusak, Oxana Erina, Jim Watkins, and April James contributed to the development of this manuscript. Thanks to Arpita Das for helping to match the lakes in this study with lake IDs from HydroLAKES and Filazzola et al. (2020), to Young Ho Yun for aiding in statistical analyses, and to the Virginia Tech Reservoir Group for feedback throughout the manuscript development process. We are grateful to Gertrud Nürnberg for providing constructive comments that substantially improved this manuscript.

This analysis would not have been possible without long-term data collection across many institutions. We thank the many researchers and community members who have collected, analyzed, and compiled the data used in this study. In particular, we would like to acknowledge Catherine Hein and Jacob Dickmann from the Wisconsin Department of Natural Resources who facilitated use of data from many Wisconsin lakes.

Data collection and manuscript development for this project have been supported by numerous grants. Abigail S. L. Lewis is supported by the U.S. National Science Foundation (NSF) graduate research fellowship program (DGE-1840995), NSF grant 1753639, the Institute for Critical Technology and Applied Science (ICTAS), and the College of Science Roundtable at Virginia Tech. Cayelan C. Carey receives support from NSF grants 1753639, 1933016, and 1737424. Stephen F. Jane is supported by the Cornell Atkinson Center for Sustainability. Rebecca L. North acknowledges support from the Missouri Department of Natural Resources, which funds the Missouri Statewide Lake Assessment Program (SLAP) coordinated by the University of Missouri (MU) Limnology Laboratory. Hans-Peter Grossart receives support from

the Leibniz Institute of Freshwater Biology and Inland Fisheries (IGB) and teams of scientists and technicians who run the Stechlin and Müggelsee long-term monitoring, as well as the German Research Foundation (DFG), which funds Project Pycnotrap (GR1540/37-1). Rachel M. Pilla notes that this research was supported by the U.S. Department of Energy (DOE), Office of Energy Efficiency and Renewable Energy, Water Power Technologies Office, and Environmental Sciences Division at Oak Ridge National Laboratory (ORNL). ORNL is managed by UT-Battelle, LLC, for the U.S. DOE under contract DE-AC05-00OR22725. Kevin C. Rose acknowledges support from NSF grants 1754265 and 2048031. Ruben Sommaruga acknowledges support from the LTSER platform Tyrolean Alps (LTER-Austria). Gesa A. Weyhenmeyer received financial support for this study from the Swedish Research Council (VR; Grant No. 2020-03222) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS; Grant No. 2020-01091). Piet Verburg acknowledges support from MBIE under grant number C01X2205. Jordi Delgado Martin acknowledges support from the EMALCSA Chair. Isabella Oleksy receives support from the NSF under grant EPS-2019528. Heidrun Feuchtmayr acknowledges support from the Natural Environmental Research Council award number NE/R016429/1 as part of the UK-SCaPE programme delivering National Capability. Many thanks to all of the funding sources that enabled this international lake analysis.

AUTHOR CONTRIBUTIONS

ASLL and MPL led the early conceptualization of this project, with significant contributions from SFJ, KCR, HPG, DWH, RS, and GAW. ASLL and MPL collated all data, which was contributed by ASLL, SFJ, KCR, YBS, SHB, FC, HF, HM, JDM, RLN, IAO, RMP, RS, PV,

774 DW, GAW, SES, APS, and CCC. Supplemental methods text was written and contributed by
775 ASLL, SFJ, YBS, SHB, FC, HF, HM, JDM, RLN, IAO, RMP, RS, PV, DW, GAW, SES, APS,
776 and CCC. ASLL led data analysis, developed figures, and wrote the manuscript with substantial
777 contributions from MPL and CCC. DWH and SHB reviewed the data publication and analysis
778 code. Additionally, SFJ, KCR, YBS, HF, HPG, DWH, HM, RLN, IAO, RMP, RS, DW, GAW,
779 and CCC made significant intellectual contributions to the development of methods and
780 interpretation of results in this analysis.

781

DATA AVAILABILITY

The in-lake data used in this study are published in the Environmental Data Initiative repository (EDI; Lewis et al. 2023), and include compiled data from multiple separately-published datasets (Maberly et al. 2017; Leach et al. 2018; Lentz et al. 2023; Winslow et al. 2018; Jones et al. 2020; Feuchtmayr et al. 2021; Stetler et al. 2021; Carey et al. 2022b, c, d, e; Williamson 2022; Solomon et al. 2022), in addition to other, previously-unpublished data. Additional data and metadata were drawn from openly accessible data sources, namely HydroLAKES (Messenger et al. 2016), Filazzola et al. (2020), and the ERA5 climate reanalysis (Hersbach and others 2019). Analysis code to reproduce the results in this manuscript is available in a Zenodo repository (Lewis & Lau, 2023).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Anderson, H. S., T. H. Johengen, R. Miller, and C. M. Godwin. 2021. Accelerated sediment phosphorus release in Lake Erie's central basin during seasonal anoxia. *Limnology and Oceanography* **66**: 3582–3595. doi:10.1002/lno.11900
- Bartosiewicz, M., A. Przytulska, J.-F. Lapierre, I. Laurion, M. F. Lehmann, and R. Maranger. 2019. Hot tops, cold bottoms: Synergistic climate warming and shielding effects increase carbon burial in lakes. *Limnology and Oceanography Letters* **4**: 132–144. doi:10.1002/lol2.10117

804 Bates, D., M. Maechler, B. Bolker, and others. 2023. lme4: Linear Mixed-Effects Models using
805 “Eigen” and S4.

806 Borchers, H. W. 2022. pracma: Practical Numerical Math Functions.

807 Breitburg, D., L. A. Levin, A. Oschlies, and others. 2018. Declining oxygen in the global ocean
808 and coastal waters. *Science* **359**: eaam7240. doi:10.1126/science.aam7240

809 Burns, N. M. (1995). Using hypolimnetic dissolved oxygen depletion rates for monitoring lakes.
810 *New Zealand Journal of Marine and Freshwater Research*, 29(1), 1–11.
811 doi:10.1080/00288330.1995.9516634

812 Carey, C. C., P. C. Hanson, R. Q. Thomas, and others. 2022. Anoxia decreases the magnitude of
813 the carbon, nitrogen, and phosphorus sink in freshwaters. *Global Change Biology* **28**:
814 4861–4881. doi:10.1111/gcb.16228

815 Carey, C. C., A. S. L. Lewis, D. W. Howard, W. M. Woelmer, P. A. Gantzer, K. A. Bierlein, J.
816 C. Little, and WVWA. 2022b. Bathymetry and watershed area for Falling Creek
817 Reservoir, Beaverdam Reservoir, and Carvins Cove Reservoir.
818 doi:10.6073/PASTA/352735344150F7E77D2BC18B69A22412

819 Carey, C. C., A. S. L. Lewis, R. P. McClure, A. B. Gerling, A. Breef-Pilz, and A. Das. 2022c.
820 Time series of high-frequency profiles of depth, temperature, dissolved oxygen,
821 conductivity, specific conductance, chlorophyll a, turbidity, pH, oxidation-reduction
822 potential, photosynthetic active radiation, and descent rate for Beaverdam Reservoir,
823 Carvins Cove Reservoir, Falling Creek Reservoir, Gatewood Reservoir, and Spring
824 Hollow Reservoir in Southwestern Virginia, USA 2013-2021.
825 doi:10.6073/PASTA/C4C45B5B10B4CB4CD4B5E613C3EFFBD0

826 Carey, C. C., H. L. Wander, D. W. Howard, B. R. Niederlehner, W. M. Woelmer, M. E. Lofton,
 827 A. B. Gerling, and A. Breef-Pilz. 2022d. Water chemistry time series for Beaverdam
 828 Reservoir, Carvins Cove Reservoir, Falling Creek Reservoir, Gatewood Reservoir, and
 829 Spring Hollow Reservoir in southwestern Virginia, USA 2013-2021.
 830 doi:10.6073/PASTA/7BD797155CDBB5F1ACDF0547C6BA9023

831 Carey, C. C., J. H. Wynne, M. E. Lofton, and others. 2022e. Filtered chlorophyll a time series for
 832 Beaverdam Reservoir, Carvins Cove Reservoir, Claytor Lake, Falling Creek Reservoir,
 833 Gatewood Reservoir, Smith Mountain Lake, Spring Hollow Reservoir in southwestern
 834 Virginia and Lake Sunapee in Sunapee, New Hampshire, USA during 2014-2021.
 835 doi:10.6073/PASTA/6BA5BEED2869A05C854C34251144A76E

836 Carpenter, S. R. 2003. Regime Shifts in Lake Ecosystems: Pattern and Variation: 15,
 837 International Ecology Institute.

838 Carpenter, S. R., K. L. Cottingham, and D. E. Schindler. 1992. Biotic feedbacks in Lake
 839 phosphorus cycles. *Trends in Ecology & Evolution* **7**: 332–336. doi:10.1016/0169-
 840 5347(92)90125-U

841 Carpenter, S. R., and R. C. Lathrop. 2008. Probabilistic Estimate of a Threshold for
 842 Eutrophication. *Ecosystems* **11**: 601–613.

843 Cottingham, K. L., H. A. Ewing, M. L. Greer, C. C. Carey, and K. C. Weathers. 2015.
 844 Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling. *Ecosphere*
 845 **6**: art1. doi:10.1890/ES14-00174.1

846 Doig, L. E., R. L. North, J. J. Hudson, C. Hewlett, K.-E. Lindenschmidt, and K. Liber. 2017.
 847 Phosphorus release from sediments in a river-valley reservoir in the northern Great Plains
 848 of North America. *Hydrobiologia* **787**: 323–339. doi:10.1007/s10750-016-2977-2

849 Downing, J. A., and E. McCauley. 1992. The nitrogen : phosphorus relationship in lakes.
850 Limnology and Oceanography **37**: 936–945. doi:10.4319/lo.1992.37.5.0936

851 Einsele, W. 1936. Über die Beziehungen des Eisenkreislaufs zum Phosphatkreislauf im
852 eutrophen See. Archiv für Hydrobiologie **29**: 664–686.

853 Elser, J. J., M. E. S. Bracken, E. E. Cleland, and others. 2007. Global analysis of nitrogen and
854 phosphorus limitation of primary producers in freshwater, marine and terrestrial
855 ecosystems. Ecology Letters **10**: 1135–1142. doi:10.1111/j.1461-0248.2007.01113.x

856 Elshout, P. M. F., Dionisio Pires, L. M., Leuven, R. S. E. W., Wendelaar Bonga, S. E., &
857 Hendriks, A. J. (2013). Low oxygen tolerance of different life stages of temperate
858 freshwater fish species. *Journal of Fish Biology*, 83(1), 190–206.
859 <https://doi.org/10.1111/jfb.12167>

860 Encinas Fernández, J., F. Peeters, and H. Hofmann. 2014. Importance of the Autumn Overturn
861 and Anoxic Conditions in the Hypolimnion for the Annual Methane Emissions from a
862 Temperate Lake. Environ. Sci. Technol. **48**: 7297–7304. doi:10.1021/es4056164

863 Feuchtmayr, H., M. A. Clarke, M. M. De Ville, B. A. Dodd, J. Fletcher, H. Guyatt, A. G. Hunt,
864 J. B. James, E. B. Mackay, G. Rhodes, S. J. Thackeray, S. C. Maberly. 2021. Surface
865 temperature, surface oxygen, water clarity, water chemistry and phytoplankton
866 chlorophyll a data from Blelham Tarn, 2014 to 2018. NERC Environmental Information
867 Data Centre. doi: 10.5285/ae8c850d-211e-4560-8b37-437b6e0e2a16

868 Filazzola, A., O. Mahdian, A. Shuvo, and others. 2020. A global database of chlorophyll and
869 water chemistry in freshwater lakes. doi:10.5063/F1JH3JKZ

870 Finlayson, C. M., R. S. de Groot, F. M. R. Hughes, and C. A. Sullivan. 2018. Freshwater
871 Ecosystem Services and Functions. *In* J. Hughes [ed.], *Freshwater Ecology and*
872 *Conservation: Approaches and Techniques*. Oxford University Press.

873 Foley, B., I. D. Jones, S. C. Maberly, and B. Rippey. 2012. Long-term changes in oxygen
874 depletion in a small temperate lake: effects of climate change and eutrophication.
875 *Freshwater Biology* **57**: 278–289. doi:10.1111/j.1365-2427.2011.02662.x

876 Forsythe, G. E., Malcolm, M. A., & Moler, C. B. (1977). *Computer Methods for Mathematical*
877 *Computations*. Prentice Hall Professional Technical Reference.

878 Fox, J., S. Weisberg, B. Price, and others. 2022. *car: Companion to Applied Regression*.

879 Håkanson, L. (2005). The Importance of Lake Morphometry for the Structure and Function of
880 Lakes. *International Review of Hydrobiology*, 90(4), 433–461.
881 <https://doi.org/10.1002/iroh.200410775>

882 Haupt, F., M. Stockenreiter, E. S. Reichwaldt, M. Baumgartner, W. Lampert, M. Boersma, and
883 H. Stibor. 2010. Upward phosphorus transport by *Daphnia* diel vertical migration.
884 *Limnology and Oceanography* **55**: 529–534. doi:10.4319/lo.2010.55.2.0529

885 Hersbach, H., B. Bell, P. Berrisford, and others. 2019. ERA5 monthly averaged data on single
886 levels from 1979 to present. doi:10.24381/CDS.F17050D7

887 Hounshell, A. G., R. P. McClure, M. E. Lofton, and C. C. Carey. 2021. Whole-ecosystem
888 oxygenation experiments reveal substantially greater hypolimnetic methane
889 concentrations in reservoirs during anoxia. *Limnology and Oceanography Letters* **6**: 33–
890 42.

891 Hupfer, M., and J. Lewandowski. 2008. Oxygen Controls the Phosphorus Release from Lake
 892 Sediments – a Long-Lasting Paradigm in Limnology. *International Review of*
 893 *Hydrobiology* **93**: 415–432. doi:10.1002/iroh.200711054
 894 Jagtman, E., D. T. Van der Molen, and S. Vermij. 1992. The influence of flushing on nutrient
 895 dynamics, composition and densities of algae and transparency in Veluwemeer, The
 896 Netherlands. *Hydrobiologia* **233**: 187–196. doi:10.1007/BF00016107
 897 Jane, S. F., G. Hansen, B. Kraemer, and others. 2021. Widespread deoxygenation of temperate
 898 lakes. *Nature* **594**. doi:10.1038/s41586-021-03550-y
 899 Jane, S. F., J. L. Mincer, M. P. Lau, A. S. L. Lewis, J. T. Stetler, and K. C. Rose. 2023. Longer
 900 duration of seasonal stratification contributes to widespread increases in lake hypoxia and
 901 anoxia. *Global Change Biology* **29**: 1009–1023. doi:10.1111/gcb.16525
 902 Jenny, J.-P., P. Francus, A. Normandeau, F. Lapointe, M.-E. Perga, A. Ojala, A. Schimmelmann,
 903 and B. Zolitschka. 2016a. Global spread of hypoxia in freshwater ecosystems during the
 904 last three centuries is caused by rising local human pressure. *Global Change Biology* **22**:
 905 1481–1489. doi:10.1111/gcb.13193
 906 Jenny, J.-P., A. Normandeau, P. Francus, and others. 2016b. Urban point sources of nutrients
 907 were the leading cause for the historical spread of hypoxia across European lakes.
 908 *Proceedings of the National Academy of Sciences* **113**: 12655–12660.
 909 doi:10.1073/pnas.1605480113
 910 Jones, J. R., A. Argerich, D. V. Obrecht, A. P. Thorpe, and R. L. North. 2020. Missouri Lakes
 911 and Reservoirs Long-term Limnological Dataset.
 912 doi:10.6073/PASTA/86D8D176E91410566B4DE51DF44C2624

913 Kamarainen, A. M., H. Yuan, C. H. Wu, and S. R. Carpenter. 2009. Estimates of phosphorus
 914 entrainment in Lake Mendota: a comparison of one-dimensional and three-dimensional
 915 approaches. *Limnology and Oceanography: Methods* **7**: 553–567.
 916 doi:10.4319/lom.2009.7.553

917 Kraemer, B. M., K. Kakouei, C. Munteanu, M. W. Thayne, and R. Adrian. 2022. Worldwide
 918 moderate-resolution mapping of lake surface chl-a reveals variable responses to global
 919 change (1997–2020). *PLOS Water* **1**: e0000051. doi:10.1371/journal.pwat.0000051

920 LaBrie, R., M. Hupfer, and M. P. Lau. 2023. Anaerobic duration predicts biogeochemical
 921 consequences of oxygen depletion in lakes. *Limnology and Oceanography Letters* **8**:
 922 666–674. doi:10.1002/lol2.10324

923 Ladwig, R., P. C. Hanson, H. A. Dugan, C. C. Carey, Y. Zhang, L. Shu, C. J. Duffy, and K. M.
 924 Cobourn. 2021. Lake thermal structure drives interannual variability in summer anoxia
 925 dynamics in a eutrophic lake over 37 years. *Hydrol. Earth Syst. Sci.* **25**: 1009–1032.
 926 doi:10.5194/hess-25-1009-2021

927 Leach, T. H., L. A. Winslow, F. W. Acker, and others. 2018. Long-term dataset on aquatic
 928 responses to concurrent climate change and recovery from acidification. *Sci Data* **5**:
 929 180059. doi:10.1038/sdata.2018.59

930 Lentz, M., S. Schmidt, J. Woodhouse, P. Kasprzak, S. Wollrab, S. A. Berger, U. Beyer, M.
 931 Bodenlos, M. Degebrodt, R. Degebrodt, T. Gonsiorczyk, E. Huth, M. Uta, M. Elke, J. C.
 932 Nejstgaard, M. Papke, S. Pinnow, R. Roßberg, M. Sachtleben, A. Scheffler, W. Scheffler,
 933 L. Krienitz, P. Casper, M. O Gessner, H-P. Grossart, R. Koschel. 2023. Lake Stechlin
 934 vertical profiles of multiparameter probe data 1970-2020. IGB Leibniz-Institute of
 935 Freshwater Ecology and Inland Fisheries. Dataset. doi:10.18728/igb-fred-823.1

936 Lewis, A. S. L. and M. P. Lau. 2023. abbylouis/Anoxia-Begets-Anoxia: Data analysis of
 937 biogeochemical dynamics in 656 lakes: v1.1.0. Zenodo. doi: 10.5281/zenodo.10064087.

938 Lewis, A. S. L., B. S. Kim, H. L. Edwards, and others. 2020. Prevalence of phytoplankton
 939 limitation by both nitrogen and phosphorus related to nutrient stoichiometry, land use,
 940 and primary producer biomass across the northeastern United States. *Inland Waters* 1–9.
 941 doi:10.1080/20442041.2019.1664233

942 Lewis, A. S. L., M. P. Lau, S. F. Jane, Y. Beeri-Shlevin, S. H. Burnet, F. Clayer, H. Feuchtmayr,
 943 H. Grossart, D. W. Howard, H. Mariash, J. Delgado-Martin, R. L. North, I. Oleksy, R. M.
 944 Pilla, K. C. Rose, A. P. Smagula, R. Sommaruga, S. E. Steiner, P. Verburg, D. Wain, G.
 945 A. Weyhenmeyer, and C. C. Carey. 2023. Dissolved oxygen, temperature, chlorophyll-a,
 946 total phosphorus, total nitrogen, and dissolved organic carbon at multiple depths in 822
 947 lakes from 1921-2022 ver 9. Environmental Data Initiative. [https://portal-](https://portal-s.edirepository.org/nis/mapbrowse?scope=edi&identifier=1029&revision=9)
 948 [s.edirepository.org/nis/mapbrowse?scope=edi&identifier=1029&revision=9](https://portal-s.edirepository.org/nis/mapbrowse?scope=edi&identifier=1029&revision=9)

949 Lewis Jr., W. M., and W. A. Wurtsbaugh. 2008. Control of Lacustrine Phytoplankton by
 950 Nutrients: Erosion of the Phosphorus Paradigm. *International Review of Hydrobiology*
 951 **93**: 446–465. doi:10.1002/iroh.200811065

952 Livingstone, D. M., & Imboden, D. M. 1996. The prediction of hypolimnetic oxygen profiles: A
 953 plea for a deductive approach. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:
 954 924–932. <https://doi.org/10.1139/f95-230>

955 Lynch, A. J., S. J. Cooke, A. H. Arthington, and others. 2023. People need freshwater
 956 biodiversity. *WIREs Water* **n/a**: e1633. doi:10.1002/wat2.1633

957 Maberly, S.C.; B. Brierley, H. T. Carter, M. A. Clarke, M. M. De Ville, J. M. Fletcher, J. B.
 958 James, P. Keenan, J. L. Kelly, E. B. Mackay, J. E. Parker, M. Patel, M. G. Pereira, G.

959 Rhodes, B. Tanna, S. J. Thackeray, C. Vincent, H. Feuchtmayr. 2017. Surface
 960 temperature, surface oxygen, water clarity, water chemistry and phytoplankton
 961 chlorophyll a data from Blelham Tarn, 1945 to 2013. NERC Environmental Information
 962 Data Centre. doi: 10.5285/393a5946-8a22-4350-80f3-a60d753beb00

963 MacKeigan, P. W., Z. E. Taranu, F. R. Pick, B. E. Beisner, and I. Gregory-Eaves. 2023. Both
 964 biotic and abiotic predictors explain significant variation in cyanobacteria biomass across
 965 lakes from temperate to subarctic zones. *Limnology and Oceanography* **68**: 1360–1375.
 966 doi:10.1002/lno.12352

967 Magnuson, J. J., D. M. Robertson, B. J. Benson, and others. 2000. Historical Trends in Lake and
 968 River Ice Cover in the Northern Hemisphere. *Science* **289**: 1743–1746.
 969 doi:10.1126/science.289.5485.1743

970 Matisoff, G., E. M. Kaltenberg, R. L. Steely, and others. 2016. Internal loading of phosphorus in
 971 western Lake Erie. *Journal of Great Lakes Research* **42**: 775–788.
 972 doi:10.1016/j.jglr.2016.04.004

973 Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen,
 974 Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R.,
 975 Maycock, T. K., Waterfield, T., Yelekçi, Ö., Yu, R., & Zhou, B. (Eds.). 2021. *Climate
 976 Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth
 977 Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge
 978 University Press. doi:10.1017/9781009157896

979 Messenger, M. L., B. Lehner, G. Grill, I. Nedeva, and O. Schmitt. 2016. Estimating the volume
 980 and age of water stored in global lakes using a geo-statistical approach. *Nat Commun* **7**:
 981 13603. doi:10.1038/ncomms13603

982 Middelburg, J. J., and L. A. Levin. 2009. Coastal hypoxia and sediment biogeochemistry.
 983 Biogeosciences **6**: 1273–1293. doi:10.5194/bg-6-1273-2009

984 Mortimer, C. H. 1941. The Exchange of Dissolved Substances Between Mud and Water in
 985 Lakes. Journal of Ecology **29**: 280–329. doi:10.2307/2256395

986 Mortimer, C. H. 1942. The Exchange of Dissolved Substances between Mud and Water in
 987 Lakes. Journal of Ecology **30**: 147–201. doi:10.2307/2256691

988 Moss, B. 2011. Allied attack: climate change and eutrophication. Inland Waters **1**: 101–105.
 989 doi:10.5268/IW-1.2.359

990 Muggeo, V. M. R. 2023. segmented: Regression Models with Break-Points / Change-Points
 991 (with Possibly Random Effects) Estimation (1.6-3). [https://CRAN.R-](https://CRAN.R-project.org/package=segmented)
 992 [project.org/package=segmented](https://CRAN.R-project.org/package=segmented)

993 Müller, B., Bryant, L. D., Matzinger, A., & Wüest, A. 2012. Hypolimnetic Oxygen Depletion in
 994 Eutrophic Lakes. Environmental Science & Technology, **46** 9964–9971.
 995 <https://doi.org/10.1021/es301422r>

996 Müller, B., T. Steinsberger, R. Schwefel, R. Gächter, M. Sturm, and A. Wüest. 2019. Oxygen
 997 consumption in seasonally stratified lakes decreases only below a marginal phosphorus
 998 threshold. Sci Rep **9**: 18054. doi:10.1038/s41598-019-54486-3

999 North, R. L., D. Barton, A. S. Crowe, and others. 2013. The state of Lake Simcoe (Ontario,
 1000 Canada): the effects of multiple stressors on phosphorus and oxygen dynamics. Inland
 1001 Waters **3**: 51–74. doi:10.5268/IW-3.1.529

1002 North, R. P., North, R. L., Livingstone, D. M., Köster, O., & Kipfer, R. 2014. Long-term changes
 1003 in hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake:

1004 Consequences of a climate regime shift. *Global Change Biology* **20**: 811–823.
 1005 <https://doi.org/10.1111/gcb.12371>
 1006 Nürnberg, G. K. 1984. The prediction of internal phosphorus load in lakes with anoxic
 1007 hypolimnia. *Limnology and Oceanography* **29**: 111–124. doi:10.4319/lo.1984.29.1.0111
 1008 Nürnberg, G., & Peters, R. H. 1984. The importance of internal phosphorus load to the
 1009 eutrophication of lakes with anoxic hypolimnia. *SIL Proceedings, 1922-2010* **22**: 190–
 1010 194. doi:10.1080/03680770.1983.11897287
 1011 Nürnberg, G. K. 1988. A simple model for predicting the date of fall turnover in thermally
 1012 stratified lakes. *Limnology and Oceanography* **33**: 1190–1195. doi:
 1013 10.4319/lo.1988.33.5.1190
 1014 Nürnberg, G. K. 1995. Quantifying anoxia in lakes. *Limnology and Oceanography* **40**: 1100–
 1015 1111. <https://doi.org/10.4319/lo.1995.40.6.1100>
 1016 Nürnberg, G. K. 2009. Assessing internal phosphorus load – Problems to be solved. *Lake and*
 1017 *Reservoir Management* **25**: 419–432. doi:10.1080/00357520903458848
 1018 Nürnberg, G. K. 2019. Quantification of Anoxia and Hypoxia in Water Bodies. In *Encyclopedia*
 1019 *of Water* (pp. 1–9). John Wiley & Sons, Ltd.
 1020 <https://doi.org/10.1002/9781119300762.wsts0081>
 1021 Nürnberg, G. K., Howell, T., & Palmer, M. 2019. Long-term impact of Central Basin hypoxia
 1022 and internal phosphorus loading on north shore water quality in Lake Erie. *Inland Waters*
 1023 **9**: 362–373. <https://doi.org/10.1080/20442041.2019.1568072>
 1024 Oleksy, I. A., and D. C. Richardson. 2021. Climate Change and Teleconnections Amplify Lake
 1025 Stratification With Differential Local Controls of Surface Water Warming and Deep

1026 Water Cooling. *Geophysical Research Letters* **48**: e2020GL090959.
 1027 doi:10.1029/2020GL090959
 1028 Orihel, D. M., H. M. Baulch, N. J. Casson, R. L. North, C. T. Parsons, D. C. M. Seckar, and J. J.
 1029 Venkiteswaran. 2017. Internal phosphorus loading in Canadian fresh waters: a critical
 1030 review and data analysis. *Can. J. Fish. Aquat. Sci.* **74**: 2005–2029. doi:10.1139/cjfas-
 1031 2016-0500
 1032 Pace, M. L., and Y. T. Prairie. 2005. Respiration in lakes, p. 103–121. *In* P. Del Giorgio and P.
 1033 Williams [eds.], *Respiration in Aquatic Ecosystems*. Oxford University Press.
 1034 Paerl, H. W., and J. Huisman. 2008. Blooms Like It Hot. *Science* **320**: 57–58.
 1035 doi:10.1126/science.1155398
 1036 Paerl, H. W., J. T. Scott, M. J. McCarthy, and others. 2016. It Takes Two to Tango: When and
 1037 Where Dual Nutrient (N & P) Reductions Are Needed to Protect Lakes and Downstream
 1038 Ecosystems. *Environ. Sci. Technol.* **50**: 10805–10813. doi:10.1021/acs.est.6b02575
 1039 Parmesan, C., M. D. Morecroft, Y. Trisurat, and others. 2022. Terrestrial and Freshwater
 1040 Ecosystems and Their Services H.O. Pörtner, D.C. Roberts, M. Tignor, et al. [eds.].
 1041 Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working
 1042 Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate
 1043 Change 197–378. doi:10.1017/9781009325844.004.198
 1044 Pilla, R. M., and C. E. Williamson. 2023. Multidecadal trends in ultraviolet radiation,
 1045 temperature, and dissolved oxygen have altered vertical habitat availability for *Daphnia*
 1046 in temperate Lake Giles, USA. *Freshwater Biology* **68**: 523–533. doi:10.1111/fwb.14044

1047 Pilla, R. M., C. E. Williamson, B. V. Adamovich, and others. 2020. Deeper waters are changing
 1048 less consistently than surface waters in a global analysis of 102 lakes. *Scientific Reports*
 1049 **10**: 20514. doi:10.1038/s41598-020-76873-x
 1050 Quinlan, R., Paterson, A. M., Smol, J. P., Douglas, M. S. V., & Clark, B. J. (2005). Comparing
 1051 different methods of calculating volume-weighted hypolimnetic oxygen (VWHO) in
 1052 lakes. *Aquatic Sciences*, 67(1), 97–103. <https://doi.org/10.1007/s00027-004-0717-6>
 1053 Reid, A. J., A. K. Carlson, I. F. Creed, and others. 2019. Emerging threats and persistent
 1054 conservation challenges for freshwater biodiversity. *Biological Reviews* **94**: 849–873.
 1055 doi:10.1111/brv.12480
 1056 Reinl, K. L., T. D. Harris, R. L. North, and others. 2023. Blooms also like it cold. *Limnology and*
 1057 *Oceanography Letters* **8**: 546–564. doi:10.1002/lol2.10316
 1058 Reynaud, A., and D. Lanza. 2017. A Global Meta-Analysis of the Value of Ecosystem
 1059 Services Provided by Lakes. *Ecological Economics* **137**: 184–194.
 1060 doi:10.1016/j.ecolecon.2017.03.001
 1061 Richardson, D. C., Melles, S. J., Pilla, R. M., Hetherington, A. L., Knoll, L. B., Williamson, C.
 1062 E., Kraemer, B. M., Jackson, J. R., Long, E. C., Moore, K., Rudstam, L. G., Rusak, J. A.,
 1063 Saros, J. E., Sharma, S., Strock, K. E., Weathers, K. C., & Wigdahl-Perry, C. R. 2017.
 1064 Transparency, Geomorphology and Mixing Regime Explain Variability in Trends in
 1065 Lake Temperature and Stratification across Northeastern North America (1975–2014).
 1066 *Water* **9**: 442. doi:10.3390/w9060442
 1067 Rosenberg, R., B. Hellman, and B. Johansson. 1991. Hypoxic tolerance of marine benthic fauna.
 1068 *Mar. Ecol. Prog. Ser.* **79**: 127–131. doi:10.3354/meps079127
 1069 Sachs, J. 1874. *Lehrbuch der botanik*, Engelmann.

1070 Schindler, D. E. 2017. Warmer climate squeezes aquatic predators out of their preferred habitat.
 1071 Proceedings of the National Academy of Sciences **114**: 9764–9765.
 1072 doi:10.1073/pnas.1712818114
 1073 Schindler, D. W. 1974. Eutrophication and Recovery in Experimental Lakes: Implications for
 1074 Lake Management. Science **184**: 897–899.
 1075 Schmidtko, S., L. Stramma, and M. Visbeck. 2017. Decline in global oceanic oxygen content
 1076 during the past five decades. Nature **542**: 335–339. doi:10.1038/nature21399
 1077 Scott, J. T., M. J. McCarthy, and H. W. Paerl. 2019. Nitrogen transformations differentially
 1078 affect nutrient-limited primary production in lakes of varying trophic state. Limnology
 1079 and Oceanography Letters **4**: 96–104. doi:10.1002/lol2.10109
 1080 Shatwell, T., W. Thiery, and G. Kirillin. 2019. Future projections of temperature and mixing
 1081 regime of European temperate lakes. Hydrology and Earth System Sciences **23**: 1533–
 1082 1551. doi:10.5194/hess-23-1533-2019
 1083 Smith, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An
 1084 empirical and theoretical analysis1. Limnology and Oceanography **27**: 1101–1111.
 1085 doi:10.4319/lo.1982.27.6.1101
 1086 Solomon, C., S. Jones, B. C. Weidel, and others. 2022. MFE database: Data from ecosystem
 1087 ecology research by Jones, Solomon, and collaborators on the ecology and
 1088 biogeochemistry of lakes and lake organisms in the Upper Midwest, USA.
 1089 doi:10.25390/caryinstitute.7438598.v6
 1090 Soranno, P. A., S. R. Carpenter, and R. C. Lathrop. 1997. Internal phosphorus loading in Lake
 1091 Mendota: response to external loads and weather. Can. J. Fish. Aquat. Sci. **54**: 1883–
 1092 1893. doi:10.1139/f97-095

1093 Steinsberger, T., R. Schwefel, A. Wüest, and B. Müller. 2020. Hypolimnetic oxygen depletion
 1094 rates in deep lakes: Effects of trophic state and organic matter accumulation. *Limnology*
 1095 and *Oceanography* **65**: 3128–3138. doi:10.1002/lno.11578

1096 Stetler, J. T., S. F. Jane, J. L. Mincer, M. N. Sanders, and K. C. Rose. 2021. Long-term lake
 1097 dissolved oxygen and temperature data, 1941-2018.
 1098 doi:10.6073/PASTA/C45EFE4826B5F615023B857DC59856F3

1099 Thienemann, A. 1928. Der Sauerstoff im eutrophen und obligotrophen See.

1100 Vachon, D., C. T. Solomon, and P. A. del Giorgio. 2017. Reconstructing the seasonal dynamics
 1101 and relative contribution of the major processes sustaining CO₂ emissions in northern
 1102 lakes. *Limnol. Oceanogr.* **62**: 706–722. doi:10.1002/lno.10454

1103 Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity.
 1104 PNAS **105**: 15452–15457. doi:10.1073/pnas.0803833105

1105 Wang, J., Y. Guan, L. Wu, X. Guan, W. Cai, J. Huang, W. Dong, and B. Zhang. 2021. Changing
 1106 Lengths of the Four Seasons by Global Warming. *Geophysical Research Letters* **48**:
 1107 e2020GL091753. doi:10.1029/2020GL091753

1108 Wang, M., X. Xu, Z. Wu, and others. 2019. Seasonal Pattern of Nutrient Limitation in a
 1109 Eutrophic Lake and Quantitative Analysis of the Impacts from Internal Nutrient Cycling.
 1110 *Environ. Sci. Technol.* **53**: 13675–13686. doi:10.1021/acs.est.9b04266

1111 Wetzel, R. G. 2001. 13 - THE PHOSPHORUS CYCLE, p. 239–288. *In* R.G. Wetzel [ed.],
 1112 *Limnology* (Third Edition). Academic Press.

1113 Wetzel, R. G., and G. E. Likens. 2000. Estimates of Whole Lake Metabolism: Hypolimnetic
 1114 Oxygen Deficits and Carbon Dioxide Accumulation, p. 373–382. *In* R.G. Wetzel and
 1115 G.E. Likens [eds.], *Limnological Analyses*. Springer.

1116 Williamson, C. E., E. P. Overholt, R. M. Pilla, T. H. Leach, J. A. Brentrup, L. B. Knoll, E. M.
 1117 Mette, and R. E. Moeller. 2015. Ecological consequences of long-term browning in lakes.
 1118 Sci Rep **5**: 1–10. doi:10.1038/srep18666
 1119 Williamson, C. E. 2022. Three decades of limnological data from lakes in the Pocono Mountains
 1120 region, Pennsylvania USA, 1988-2021.
 1121 doi:10.6073/PASTA/0D764453DD98D7FA978D517E6787538F
 1122 Wilson, H. L., Ayala, A. I., Jones, I. D., Rolston, A., Pierson, D., de Eyto, E., Grossart, H.-P.,
 1123 Perga, M.-E., Woolway, R. I., & Jennings, E. (2020). Variability in epilimnion depth
 1124 estimations in lakes. Hydrology and Earth System Sciences **24**: 5559–5577.
 1125 Doi:10.5194/hess-24-5559-2020
 1126 Winslow, L., T. Leach, and T. Hahn. 2018. adklakedata: Adirondack Long-Term Lake Data.
 1127 Winslow, L., J. Read, R. Woolway, J. Brentrup, T. Leach, J. Zwart, S. Albers, and D. Collinge.
 1128 2019. rLakeAnalyzer: Lake Physics Tools.
 1129 Woolway, R. I. 2023. The pace of shifting seasons in lakes. Nat Commun **14**: 2101.
 1130 doi:10.1038/s41467-023-37810-4
 1131 Woolway, R. I., S. Sharma, G. A. Weyhenmeyer, and others. 2021. Phenological shifts in lake
 1132 stratification under climate change. Nat Commun **12**: 2318. doi:10.1038/s41467-021-
 1133 22657-4
 1134 Zhao, L., R. Zhu, Q. Zhou, E. Jeppesen, and K. Yang. 2023. Trophic status and lake depth play
 1135 important roles in determining the nutrient-chlorophyll a relationship: Evidence from
 1136 thousands of lakes globally. Water Research 120182. doi:10.1016/j.watres.2023.120182
 1137 Zhi, W., Klingler, C., Liu, J., & Li, L. (2023). Widespread deoxygenation in warming rivers.
 1138 Nature Climate Change, 13(10). doi: 10.1038/s41558-023-01793-3