

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

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5 AUTHORS:

6 Abigail S. L. Lewis<sup>1\*</sup>, Maximilian P. Lau<sup>2</sup>, Stephen F. Jane<sup>3</sup>, Kevin C. Rose<sup>4</sup>, Yaron Be’eri-  
7 Shlevin<sup>5</sup>, Sarah H. Burnet<sup>6</sup>, François Clayer<sup>7</sup>, Heidrun Feuchtmayr<sup>8</sup>, Hans-Peter Grossart<sup>9, 10</sup>,  
8 Dexter W. Howard<sup>1</sup>, Heather Mariash<sup>11</sup>, Jordi Delgado Martin<sup>12</sup>, Rebecca L. North<sup>13</sup>, Isabella  
9 Oleksy<sup>14</sup>, Rachel M. Pilla<sup>15</sup>, Amy P. Smagula<sup>16</sup>, Ruben Sommaruga<sup>17</sup>, Sara E. Steiner<sup>16</sup>, Piet  
10 Verburg<sup>18</sup>, Danielle Wain<sup>19</sup>, Gesa A. Weyhenmeyer<sup>20</sup>, and Cayelan C. Carey<sup>1</sup>

11  
12 AFFILIATIONS:

13 <sup>1</sup> Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA

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

16 <sup>3</sup> Department of Natural Resources and the Environment, Cornell University, Ithaca, NY 14853,  
17 USA

18 <sup>4</sup> Department of Biological Sciences, Rensselaer Polytechnic Institute, Troy, NY 12180 USA

19 <sup>5</sup> The Kinneret Limnological Laboratory, Israel Oceanographic and Limnological Research,  
20 Migdal 14950, Israel

21 <sup>6</sup> Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA

22 <sup>7</sup> Norwegian Institute of Water Research, Oslo, Norway

23 <sup>8</sup> Lake Ecosystems Group, UK Centre for Ecology & Hydrology, Lancaster, UK

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

26 <sup>10</sup> Department of Biochemistry and Biology, Potsdam University, 14469 Potsdam, Germany

27 <sup>11</sup> Prince Albert National Park, Parks Canada, SK, Canada

28 <sup>12</sup> Department of Civil Engineering, Universidade da Coruña, A Coruña, Spain

29 <sup>13</sup> School of Natural Resources, University of Missouri-Columbia, Columbia, Missouri, USA

30 <sup>14</sup> Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA

31 <sup>15</sup> Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

32 <sup>16</sup> New Hampshire Department of Environmental Services, Concord, NH, USA

33 <sup>17</sup> Department of Ecology, Universität Innsbruck, Technikerstr. 25. 6020 Innsbruck, Austria

34 <sup>18</sup> National Institute of Water and Atmospheric Research, Wellington, New Zealand.

35 <sup>19</sup> 7 Lakes Alliance, Belgrade Lakes, Maine, USA

36 <sup>20</sup> 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.  
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## 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 ( $<1$  mg/L DO) during a given summer begets increasingly frequent and severe occurrences of anoxia in following summers. Specifically, anoxic conditions can promote nutrient release from sediments, thereby stimulating phytoplankton growth and subsequent decomposition, which in turn fuels heterotrophic respiration and accelerates deep-water DO declines. 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 necessary mechanisms 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 length of 30 years at each lake. Using linear mixed models, we found support for each of the feedback relationships between lower DO concentrations, higher phosphorus concentrations, higher chlorophyll-*a* concentrations, and greater volume-weighted deep-water oxygen demand. Likewise, we found further support for these relationships within time series data at 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 late-summer DO concentrations in large (high-surface-area) 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, oxygen demand, phosphorus, residence time, surface area

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## 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). 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 Lanzaova 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. 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 across 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 ( $<1$  mg/L DO) 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. Declines in DO concentrations have been shown to enhance internal loading of phosphorus from sediments, particularly when hypolimnetic DO concentrations decrease to anoxic levels (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 fall mixis when epilimnetic and hypolimnetic waters homogenize (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 lower end of summer DO concentrations (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, depth, 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 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.

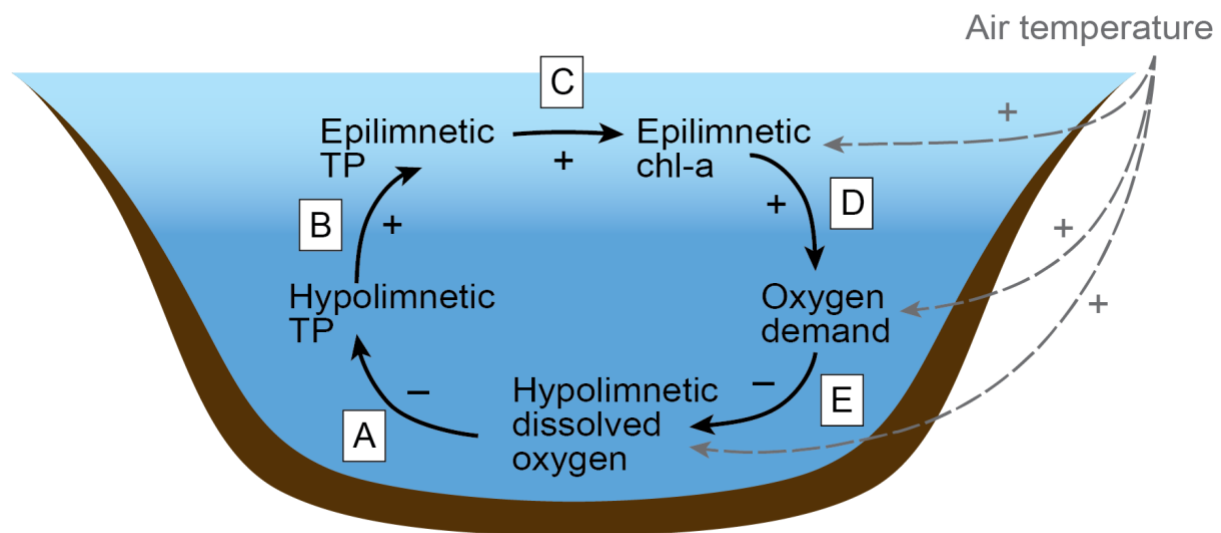


Figure 1: The proposed positive feedback through which “anoxia begets anoxia” (ABA). Declines in hypolimnetic dissolved oxygen result in internal hypolimnetic phosphorus (TP) loading (A), which in turn increases epilimnetic TP (B) and stimulates phytoplankton growth, resulting in increased chlorophyll-a (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. Symbols next to each arrow (+/-) indicate the directionality of the relationship (i.e., a positive or negative effect).

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 DO concentrations, hypolimnetic phosphorus concentrations, epilimnetic phosphorus concentrations, epilimnetic chl-a, and oxygen demand within and across widespread 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 size 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). 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 solicited from 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 that did not previously have contributed 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 when available, but were more limited in availability ( $n = 111$  lakes for DOC and  $n = 119$  lakes for TN), motivating us to primarily focus on TP 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 111,903 distinct water temperature and DO profiles across 656 lakes during 1938-2022 (Appendix S2: Figure S1). 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  $\geq 10$  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 lake.

#### 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 S2). 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 2000), and may consequently be a particularly 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 package (Winslow et al. 2019). We used mean metalimnion depths for each lake-year to estimate the bottom of the epilimnion and top of the hypolimnion. 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.

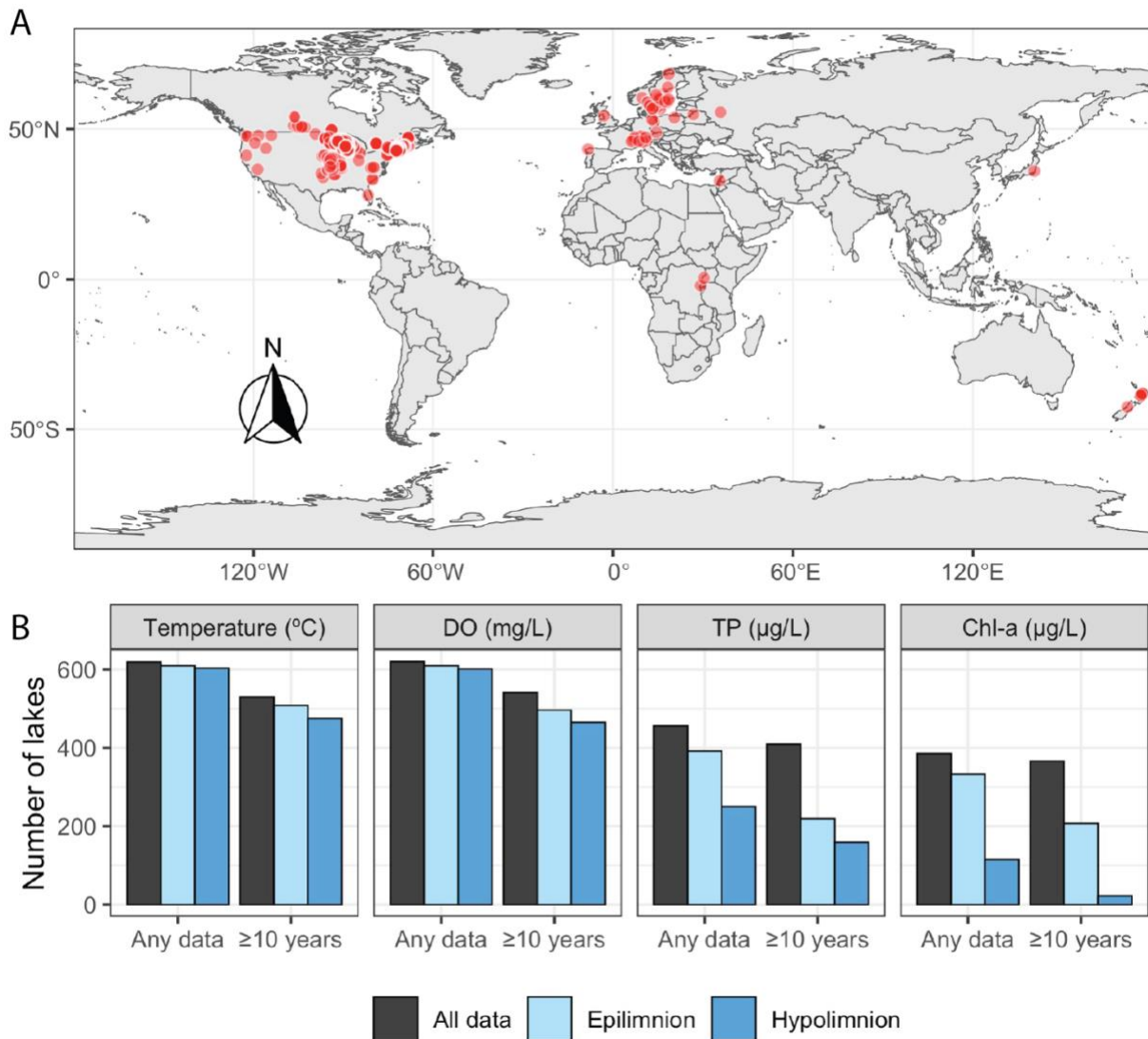


Figure 2: Data were compiled from a total of 656 widespread temperate lakes, with data availability differing across sites. A: map of all sites included in this dataset. Note that due to overlapping data points, many sites are not visible. More detailed maps of the United States and Europe are provided 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. For a description of how late-summer epilimnetic and hypolimnetic data were calculated, see Appendix S1: Text S2.

### 2.2.3 Volume-weighted hypolimnetic oxygen demand

We calculated volume-weighted hypolimnetic oxygen demand (VHOD) 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 entire summer stratified period. We calculated a VHOD rate based on the raw data as well as a temperature-corrected VHOD (following Pace & Prairie 2005). Detailed methods for both calculations are provided in Appendix S4.

#### 2.2.4 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 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 S2). 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 S4).

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 S4), 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 VHOD and chl-a) 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 DO declines could create a positive feedback that promotes anoxia (Figure 1), we used linear mixed models to estimate the

magnitude and direction of effect for drivers of VHOD, DO, epilimnetic and hypolimnetic TP, and epilimnetic chl-a among lake-years. Lake ID was included as a random effect on the intercept in all models. Mixed effect models were run using 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 Z-standardized explanatory variables, then 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 the *lme4* package in R (Bates et al. 2023).

While conducting regressions, we accounted for the expected non-linearity of investigated relationships. First, we log-transformed chl-a and TP concentrations due to the substantial positive skew of these data. Because we expected a non-linear relationship between hypolimnetic DO and TP (i.e., TP increases most under anoxic conditions), we performed a breakpoint analysis and piecewise regression for DO and TP (Appendix S5). Similarly, we expected that increased VHOD would result in decreased late-summer DO concentrations only until DO was functionally zero, beyond which DO cannot decrease further within a summer. We used a piecewise regression to confirm this nonlinear effect (described in Appendix S5), then

338 removed  $n = 160$  consistently anoxic lakes (lakes with maximum late-summer hypolimnetic DO  
 339 values  $< 1$  mg/L) from the hypolimnetic DO driver analysis.

340 Table 1: Explanatory variables used for mixed model regression. We tested several possible  
 341 explanatory variables for each response variable using a mixed model approach. The time period  
 342 over which mean values were calculated for each lake-year is provided for all water column  
 343 variables. For information on lags used, see Appendix S6: Figures S1–S6. Epilimnion and  
 344 hypolimnion are abbreviated as epi. and hypo. throughout.

Response variable	Proposed explanatory variables	Time period	Motivation for inclusion
Late-summer hypo. DO	VHOD	Stratified	ABA feedback
	Spring average air temp.		Stratification onset
	Summer average air temp.		Saturation
	Winter average air temp.		Ice dynamics
	Hypo. temperature	Late-summer	Saturation
	Mean DO measurement date	Late-summer	Modeling control
Late-summer hypo. TP	Hypo. DO	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		Catchment inputs/flushing
	Summer precipitation		Catchment inputs/flushing
	Winter precipitation		Catchment inputs/flushing
	Mean TP measurement date	Late-summer	Modeling control
Stratified epi. TP	Hypo. TP	Late-summer	ABA feedback
	Hypo. TP (t-1)	Late-summer	Fall mixing
	Epi. TP (t-1)	Late-summer	Persistence
	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	Modeling control
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.		Temperature-dependence of phytoplankton growth
	Mean chl-a measurement date	Stratified	Modeling control
Volume-weighted hypolimnetic	Epi. chl-a	Stratified	ABA feedback
	Epi. chl-a (t-1)	Stratified	ABA feedback



oxygen demand (VHOD)	Hypolimnetic temp.	Stratified	Temperature-dependence of respiration
	Hypo. surface area to volume ratio	Stratified	Sediment oxygen demand
	Maximum buoyancy frequency	Stratified	Diffusion

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### 2.3.3 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.

#### 2.3.3.1 Driver analysis

The coefficient estimates for explanatory variables included in the ABA feedback (e.g., the coefficient of VHOD for predicting lake-summer DO) 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, and mean concentrations of focal (ABA) variables (i.e., hypolimnetic DO, epilimnetic and hypolimnetic TP, epilimnetic chl-a, and VHOD). 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 VHOD).

#### 2.3.4 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, and late-summer oxygen concentrations (Appendix S7). Then, we summarized the effects of high and low annual air temperature anomalies on late-summer oxygen concentrations (Appendix S7).

### 3. RESULTS

#### 3.1 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 3), with expected temporal lags as applicable (0–1 years; Appendix S6). Low DO concentrations were associated with high hypolimnetic TP (Figure 3A), particularly when hypolimnetic DO concentrations were below a threshold of 1.7 mg/L (Figure 4), and high hypolimnetic TP was associated with high epilimnetic TP, both within and between years (i.e., both Hypo TP and Hypo TP<sub>t-1</sub> had positive coefficients; Figure 3B). High epilimnetic

TP was in turn associated with high chl-a within a year (Figure 3C), and high chl-a was associated with high VHOD and  $\text{VHOD}_{\text{std } 10^{\circ}\text{C}}$  the following year (Figure 3D; Appendix S8). Lastly, high VHOD was associated with low late-summer DO concentrations (Figure 3E).

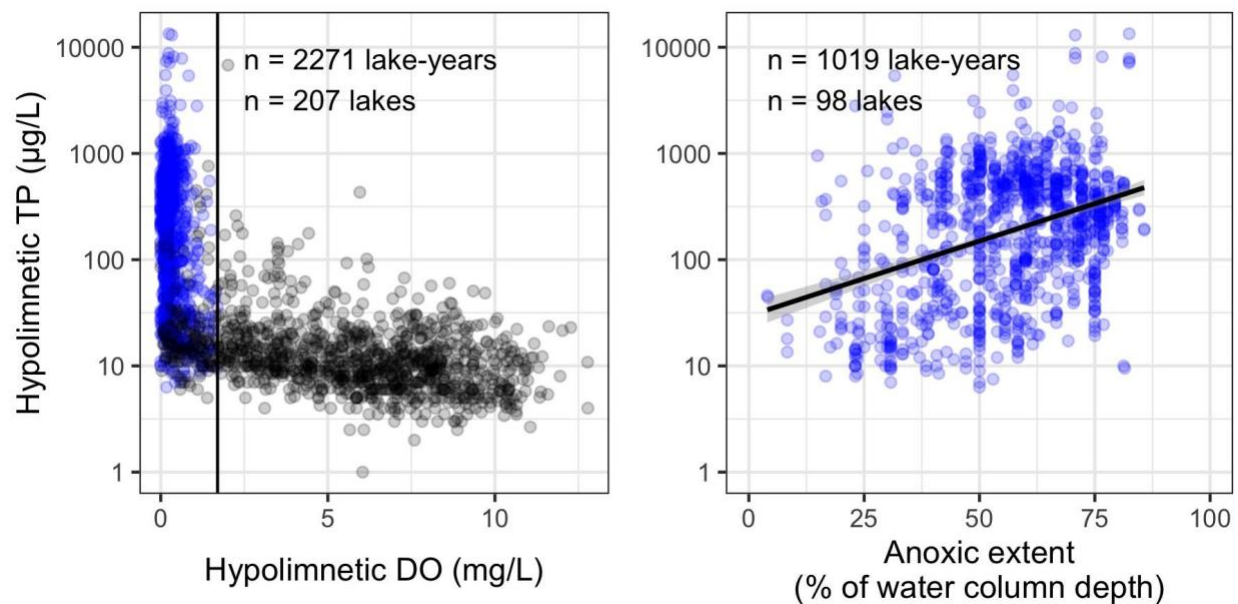
Of the 379 lakes with at least 10 years of hypolimnetic DO data, 176 lakes crossed the threshold of 1.7 mg/L during the time series (i.e., had at least one year with  $\text{DO} < 1.7$  mg/L and at least one year with  $\text{DO} > 1.7$  mg/L). This was more common than lakes that had consistently anoxic ( $n = 100$ ) or consistently oxic ( $n = 102$ ) hypolimnia. Lakes that crossed the threshold of 1.7 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 S1).

All of the ABA relationships observed to be significant across hundreds of lakes were also supported by regression analyses conducted within individual lake time series (with  $n = 48$ –158 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 (e.g., the coefficient for chl-a in the multiple linear regression with VHOD as a response variable) tended to be slightly smaller than the mixed model coefficient estimate (Figure 5) for each relationship, except for VHOD as a predictor of DO (Figure 5E).

While the hypothesized ABA feedback was supported by regression analyses, variability in the focal response variables (i.e., VHOD, DO, TP, chl-a; Table 1) was also modulated by additional driving factors, as expected (Figure 1; Appendix S7). Specifically, climatic variables were selected as part of the optimal model for nearly all focal variables: spring air temperatures were important drivers of hypolimnetic DO and chl-a, winter precipitation was a significant driver of hypolimnetic TP, and winter and spring precipitation were significant drivers of

epilimnetic TP (Figure 3, Figure 5). Water temperature and stratification also played a role in explaining variation in several focal responses: hypolimnetic temperatures were a significant predictor of both hypolimnetic DO and VHOD, and buoyancy frequency at the thermocline was a significant predictor of epilimnetic TP (Figure 3, Figure 5). For all responses, we found substantial variability in the random intercept of the mixed-model regressions among lakes (Table 2) and significant variation in within-lake regression coefficients (Figure 5), indicating external lake-specific factors that influence the state of each response at a given lake. Random effects were largest for VHOD and late-summer DO concentrations, and residual standard deviation from mixed-model analyses was highest for VHOD and the two epilimnetic response variables (chl-a and TP; Table 2).





432

433 Figure 4: Hypolimnetic TP varied as a function of hypolimnetic DO across lakes. Left:  
 434 Breakpoint relationship between late-summer hypolimnetic dissolved oxygen (DO) and total  
 435 phosphorus (TP). Vertical line indicates the breakpoint of 1.7 mg/L, as identified by piecewise  
 436 mixed model regression analyses. Right: Relationship between the vertical extent of anoxia and  
 437 hypolimnetic TP concentrations, for lakes with mean hypolimnetic DO < 1.7 mg/L ( $R^2 = 0.14$ ;  $p$   
 438 < 0.001). Points represent individual lake-years, and points that appear in both panels are plotted  
 439 in blue.

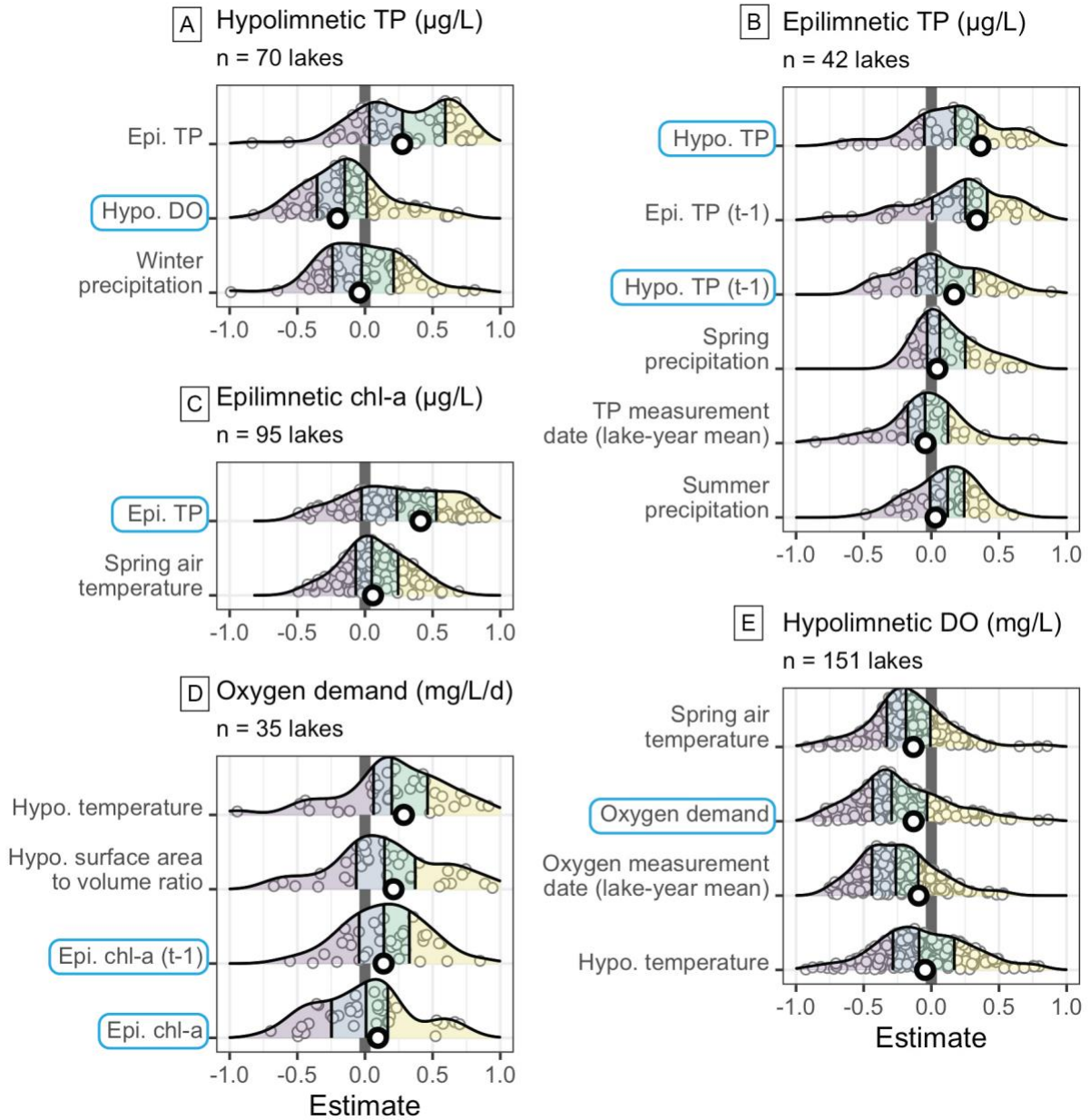


Figure 5: Linear regressions analyzing time series data within individual lakes provide further support for the ABA feedback. Here, panel titles indicate the response variable for each panel and y-axis labels indicate explanatory variables. Individual points represent regression coefficients from within 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 3). 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 3.

Table 2: Random and residual variation from linear mixed models. Model structure and fixed effects are summarized in Figure 3.

Response variable	Random effect standard deviation	Residual standard deviation
Hypolimnetic DO	0.806	0.338
Hypolimnetic TP	0.683	0.267
Epilimnetic TP	0.243	0.396
Epilimnetic chl-a	0.545	0.420
Oxygen demand	0.941	0.412

Across lakes, our analyses indicate that the relative strength of ABA relationships varied with lake characteristics. The coefficient for the effect of epilimnetic TP on chl-a was larger (more positive) for lakes with high mean epilimnetic TP values; the coefficient for the effect of VHOD on DO was larger (more negative) for lakes with large surface area; and the coefficient for the effect of chl-a on VHOD was larger (more positive) for lakes with long residence time (Figure 6). Other ABA feedback relationships were not significantly mediated by any one of our candidate predictors (maximum depth, surface area, mean depth, residence time, and mean concentrations of focal variables).



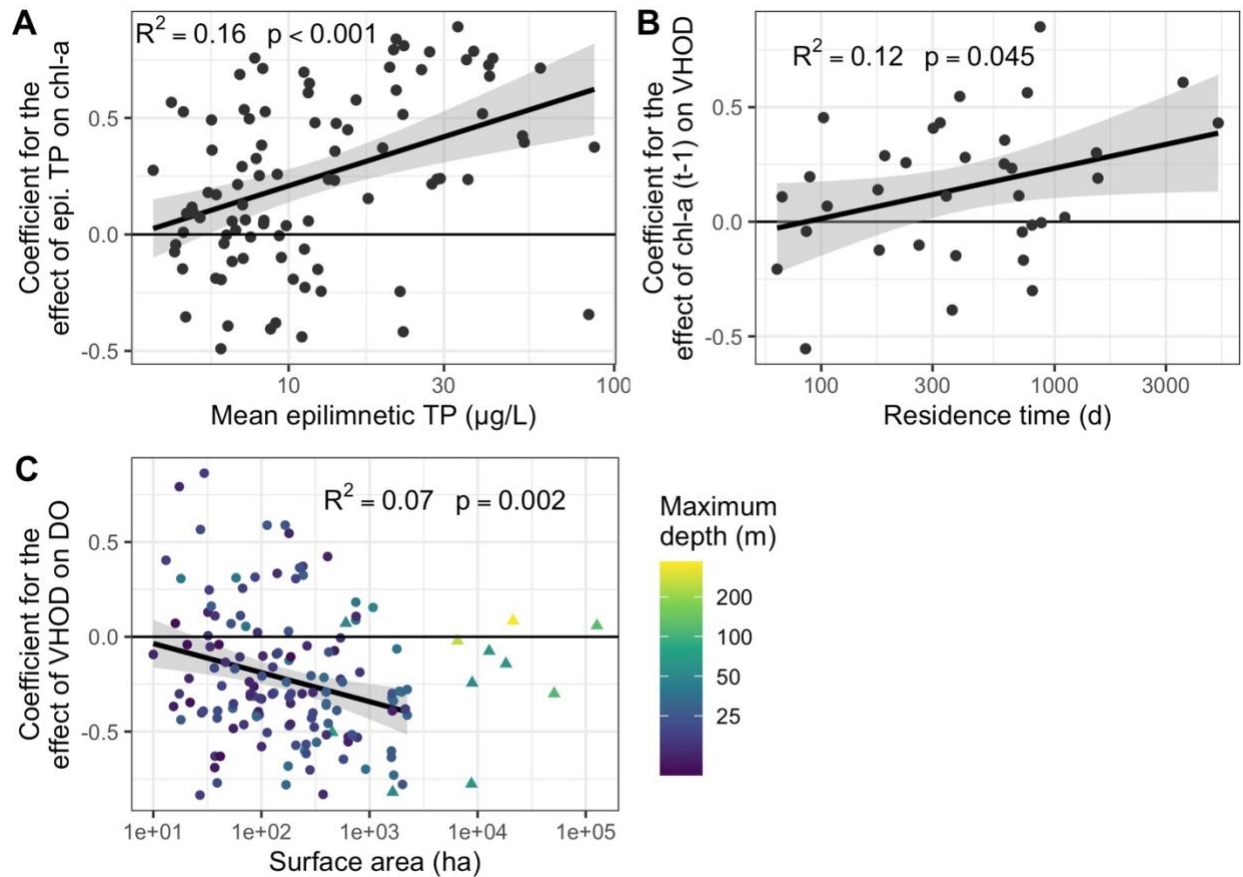


Figure 6: The strength of ABA feedback relationships may be modulated by lake characteristics. A: the coefficient for the effect of epilimnetic total phosphorus (epi. TP) on chlorophyll-*a* (chl-*a*) was most positive in lakes with high mean epilimnetic TP. B: the coefficient for the effect of the previous 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 volume-weighted hypolimnetic oxygen demand (VHOD) on dissolved oxygen (DO) was most negative in lakes with large surface areas. Linear regressions are presented as solid lines. In panel C, lakes with maximum depth > 50 m are omitted from the regression.

#### 4. DISCUSSION

In analyzing ABA relationships both across and within 656 lakes, we found support for all linkages in the hypothesized ABA feedback (Figure 3; 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 (surface area, TP

concentrations, 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 approach. These previous single-lake and modeling studies provided the mechanistic framework for analysis, although they had not been tested empirically across multiple lakes prior to this work.

By synthesizing data across many lakes, our mixed model approach allowed us to better 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 DO on hypolimnetic TP (Figure 1A)*

In this study, we observed a strong negative relationship between hypolimnetic DO 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 (here, <1.7 mg/L; Figure 4). 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). Notably, our identified breakpoint of 1.7 mg/L is remarkably similar to those identified in previous sediment incubation work (Matisoff et al. 2016; Doig et al. 2017; Orihel et al. 2017). Furthermore, our study identified that increasing spatial extent of anoxia within the hypolimnion may increase P flux after the onset of anoxia (Figure 4). Overall, this analysis indicates that the ABA mechanism may require hypolimnetic DO concentrations to decrease to low levels (< 1.7 mg/L) before a feedback effect will occur.

In our dataset, it was common for lakes to cross the threshold of 1.7 mg/L. Of the 379 lakes for which we had at least 10 years of hypolimnetic DO data, 46% of lakes crossed this threshold at some point during the time series (i.e., had at least one year with DO < 1.7 mg/L and at least one year with DO > 1.7 mg/L). Lakes where oxygen concentrations declined below 1.7 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 S1). While our dataset was not a random or fully representative sample of global lakes, the large number of lakes which crossed the 1.7 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 is 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 an effect of hypolimnetic TP concentrations on epilimnetic TP concentrations within a summer stratified period (Carpenter et al. 1992; Soranno et al. 1997; Kamarainen et al. 2009; Haupt et al. 2010; Cottingham et al. 2015), and it is intuitive that hypolimnetic TP may have a continuing legacy effect on full water column TP concentrations during mixing throughout the fall, winter, and spring (e.g., Wang et al. 2019).

#### 4.1.3 Effect of epilimnetic TP 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 (Figures 3, 5). Our study follows many decades of data that illustrate the positive effect of phosphorus on phytoplankton biomass (Schindler 1974; Smith 1982; MacKeigan et al. 2023). We note that while we were unable to identify an effect of nitrogen on the ABA feedback (likely due to lack of data and complexities of nitrogen forms), previous research has documented the importance of nitrogen for limiting or co-limiting phytoplankton growth in some lakes (Elser et al. 2007; Lewis Jr. and Wurtsbaugh 2008; Paerl et al. 2016; Scott et al. 2019; Lewis et al. 2020), so it is likely that nitrogen does play an important role in promoting lake anoxia by increasing phytoplankton growth and decomposition. Our study highlights the need for long-term nitrogen data time series 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 VHOD 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 VHOD 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 VHOD 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 VHOD. Regardless, our analyses provide support for both with-year and between-year effects of phytoplankton blooms in perpetuating low-DO conditions.

#### *4.1.5 Effect of VHOD on hypo DO (Figure 1E)*

The negative relationship between VHOD and late-summer DO concentrations is well-supported by this study, and is also intuitive: as biological and chemical demand for oxygen increases, hypolimnetic DO concentrations decrease (Figure 3, Figure 5). This association occurred simultaneously with an additional and comparably strong effect of spring air temperatures on late-summer DO concentrations. Previous work has identified that the duration of summer stratification is increasing across many lakes (Jane et al. 2023), driving decreased late-summer oxygen concentrations. 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), 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 hundreds of lakes, 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, lake surface area, 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 high-TP 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 S10: Figure S1). Our results suggest that the ABA feedback may be particularly influential in lakes with substantial external nutrient loading and may continue to intensify with greater eutrophication.

Second, the effect of the previous year's chl-a on VHOD 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  $\sim 100$  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 VHOD on hypolimnetic DO generally increased with increasing lake surface area (Figure 6C). Controlling for maximum depth, lakes with large surface area are likely to have high sediment area to volume ratios, leading to a greater influence of sediment oxygen demand on hypolimnetic oxygen concentrations (Wetzel 2001). Conversely, in lakes with small surface areas, hypolimnetic oxygen concentrations may be more strongly

controlled by other factors, including stratification phenology and mixing events. Notably, a few very large lakes (lakes with maximum depth > 50 m) did not follow the same pattern seen in shallower lakes (Figure 6C), as expected due to the buffering effect of greater hypolimnetic volume in these lakes.

Combined, these results suggest that large 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 this hypothesis. Importantly, this analysis of which factors explain the strength of the ABA feedback across lakes would not have been possible without the type of multi-lake dataset analyzed in this study.

#### **4.3 Climate change has the potential to trigger the ABA feedback**

Our analysis of hundreds of 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 ~1.7 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 VHOD (Figure 3C; Appendix S7). 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 S7: Figure S1). 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 regression modeling approach**

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. Because of limited sampling in fall, winter, and spring months, we did not consider the influence that the duration of summer anoxia or presence of winter anoxia could play in driving biogeochemical cycling. Furthermore, 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 higher temporally- and 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 VHOD and hypolimnetic DO; hypolimnetic DO and TP; and epilimnetic TP and chl-a. Conversely, the effect of epilimnetic chl-a on VHOD 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 1.7 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.

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

## 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; 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.

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