

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

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40

41 ABSTRACT

42 Declining oxygen concentrations in the deep waters of lakes worldwide pose a pressing
43 environmental and societal challenge. Existing theory suggests that low deep-water dissolved
44 oxygen (DO) concentrations could trigger a positive feedback through which anoxia (i.e., very
45 low DO) during a given summer begets increasingly severe occurrences of anoxia in following
46 summers. Specifically, anoxic conditions can promote nutrient release from sediments, thereby
47 stimulating phytoplankton growth, and subsequent phytoplankton decomposition can fuel
48 heterotrophic respiration, resulting in increased spatial extent and duration of anoxia. However,
49 while the individual relationships in this feedback are well established, to our knowledge there
50 has not been a systematic analysis within or across lakes that simultaneously demonstrates all of
51 the mechanisms necessary to produce a positive feedback that reinforces anoxia. Here, we
52 compiled data from 656 widespread temperate lakes and reservoirs to analyze the proposed
53 Anoxia Begets Anoxia (ABA) feedback. Lakes in the dataset span a broad range of surface area
54 (1–126,909 ha), maximum depth (6–370 m), and morphometry, with a median time series
55 duration of 30 years at each lake. Using linear mixed models, we found support for each of the
56 positive feedback relationships between anoxia, phosphorus concentrations, chlorophyll-*a*
57 concentrations, and oxygen demand across the 656-lake dataset. Likewise, we found further
58 support for these relationships by analyzing time series data from individual lakes. Our results
59 indicate that the strength of these feedback relationships may vary with lake-specific
60 characteristics: for example, we found that surface phosphorus concentrations were more
61 positively associated with chlorophyll-*a* in high-phosphorus lakes, and oxygen demand had a
62 stronger influence on the extent of anoxia in deep lakes. Taken together, these results support the

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

65

66 **KEYWORDS:**

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

69

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77

78 1. INTRODUCTION

79 Dissolved oxygen (DO) concentrations are declining in the bottom-waters of many
80 aquatic ecosystems around the world (Jenny et al. 2016a; Schmidtko et al. 2017; Breitburg et al.
81 2018; Jane et al. 2021; Zhi et al. 2023). These declines pose a significant threat to both marine
82 and freshwater ecosystems, as low DO conditions can decrease habitat suitability for numerous
83 aquatic organisms (e.g., Rosenberg et al. 1991; Vaquer-Sunyer and Duarte 2008; Schindler 2017;
84 Pilla and Williamson 2023), and decrease redox potential, promoting methane production (e.g.,
85 Encinas Fernández et al. 2014; Vachon et al. 2017; Hounshell et al. 2021), and altering aquatic
86 nutrient cycling (e.g., Hupfer and Lewandowski 2008; Middelburg and Levin 2009; Carey et al.
87 2022a). In freshwater lakes, the trend of decreasing DO concentrations may be particularly
88 severe, with rates of decline up to 10 times higher than those observed in marine ecosystems
89 (Jane et al. 2021). As freshwaters are critical ecosystems for drinking water, recreation,
90 irrigation, and biodiversity (Reynaud and Lanzasova 2017; Finlayson et al. 2018; Reid et al.
91 2019; Lynch et al. 2023), understanding and addressing changes in freshwater DO is essential to
92 ensuring water security and ecosystem functioning in the face of global change.

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

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

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

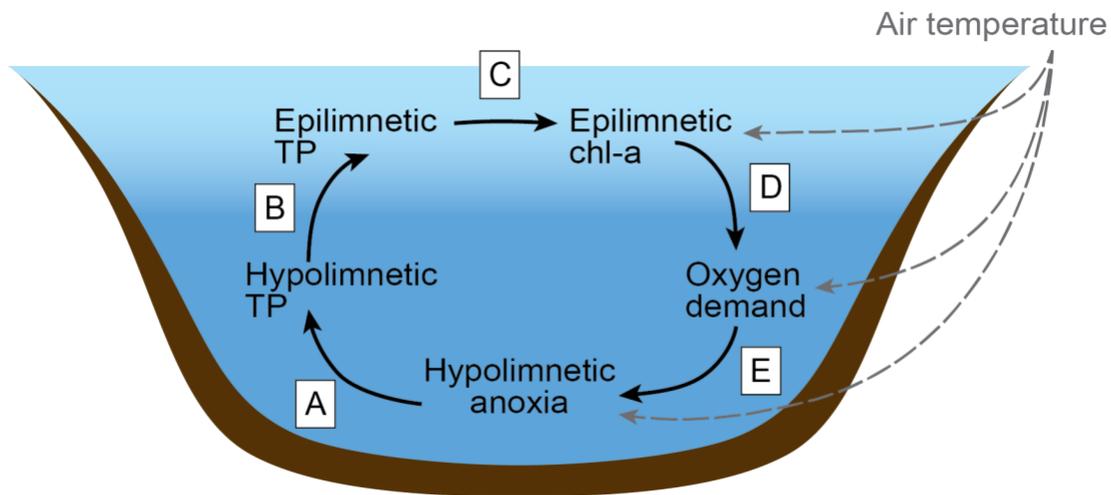
118 While the individual relationships in the ABA feedback cycle (Figure 1) are well-
119 established, these relationships occur over multiple timescales and amidst numerous other
120 interacting factors (e.g., climate variation) that could prevent the detection of the overall
121 feedback. Hypolimnetic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

124 characteristics, microbial processing, and catchment inputs may also play important roles in
125 phosphorus dynamics (e.g., Hupfer and Lewandowski 2008; Orihel et al. 2017). Increases in
126 hypolimnetic phosphorus are expected to increase surface water (epilimnetic) phosphorus
127 concentrations within a summer stratified period through both biological and physical processes
128 (e.g., organism-mediated transport, diffusion, and internal seiche dynamics; Carpenter et al.
129 1992; Kamarainen et al. 2009; Haupt et al. 2010; Cottingham et al. 2015) or during autumn mixis
130 when epilimnetic and hypolimnetic waters homogenize (e.g., Nürnberg and Peters 1984, Wetzel
131 2001; Figure 1B). Higher epilimnetic phosphorus concentrations in turn can stimulate
132 phytoplankton growth in many lakes, thereby increasing chlorophyll-*a* (chl-*a*, Figure 1C;
133 Schindler 1974), though many other important factors, including nitrogen concentrations,
134 climate, and light availability, also contribute to phytoplankton growth (e.g., Paerl and Huisman
135 2008; Reinl et al. 2023). Increased phytoplankton biomass and subsequent decomposition may
136 fuel increased biological oxygen demand (Figure 1D; Pace and Prairie 2005; Müller et al. 2019;
137 Ladwig et al. 2021) and result in earlier onset of anoxia (Figure 1E), although climate can also
138 play an important role in driving DO dynamics in many lakes, as discussed above. Given the
139 substantial complexity to each of these relationships, all operating on different time scales, it
140 remains unclear the extent to which the full positive feedback plays a role in controlling DO
141 dynamics within lakes around the world.

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

147 well as the influence of hypolimnetic DO on hypolimnetic TP (e.g., Jagtman et al. 1992).
148 Likewise, lake size may control the importance of mixing dynamics between the epilimnion and
149 hypolimnion, and residence time may affect the extent to which chl-a and hypolimnetic TP
150 influence biogeochemical dynamics the following year (Wetzel 2001). While many of these
151 expected relationships have not been assessed across lakes, an empirical analysis of data from
152 2849 lakes suggests that the impact of phosphorus concentrations on chlorophyll-a may be
153 stronger in shallow lakes relative to deep lakes, potentially due to differences in light availability
154 and macrophyte cover (Zhao et al. 2023). Characterizing the effect of lake characteristics on the
155 ABA feedback relationships is needed to identify which lakes are most susceptible to the
156 feedback, enabling managers to prioritize conservation efforts across lakes.

157



158

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

165

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

179

180 2. METHODS

181 2.1 Overview of data compilation and analysis

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

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

192

193 **2.2 Dataset compilation**

194 *2.2.1 In-lake data*

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

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

212 In sum, the complete dataset consisted of 108,736 distinct water temperature and DO
213 profiles across 656 lakes during 1938-2022 (Appendix S2: Figure S2.1). The median data
214 duration was 30 years at each lake (range: 3–81 years). Lakes in the dataset had a median depth
215 of 14 m (Z_{\max} ; range: 6–370 m), median surface area of 100 ha (range: 1–126,909 ha), and
216 median elevation of 264 m (range: -215–2804 m). The lakes were located in 18 countries across
217 5 continents, with latitudes ranging from -42.6 to 68.3 (Lewis et al. 2023).

218

219 *2.2.1.1 HydroLAKES*

220 We collated additional metadata for each lake using HydroLAKES, a global database of
221 1.4 million lakes (with surface area ≥ 10 ha; Messenger et al. 2016). For lakes with missing mean
222 or maximum depth (i.e., the depths were not reported with the data; $n = 43$), we used
223 HydroLAKES data to fill in these values (Lewis et al. 2023). We also compiled residence time
224 estimates from HydroLAKES to assess whether the strength of ABA feedback relationships may
225 vary with differences in residence time across lakes.

226

227 *2.2.2 Epilimnetic and hypolimnetic concentrations*

228 *2.2.2.1 Profile interpolation*

229 We interpolated all temperature and DO profiles to a 1-m resolution following Jane et al.
230 (2021). Briefly, we selected all profiles with at least three depths, then used the *pchip()* function
231 of the *pracma* R package (Borchers 2022) to interpolate measurements from the surface to the
232 deepest sampled depth.

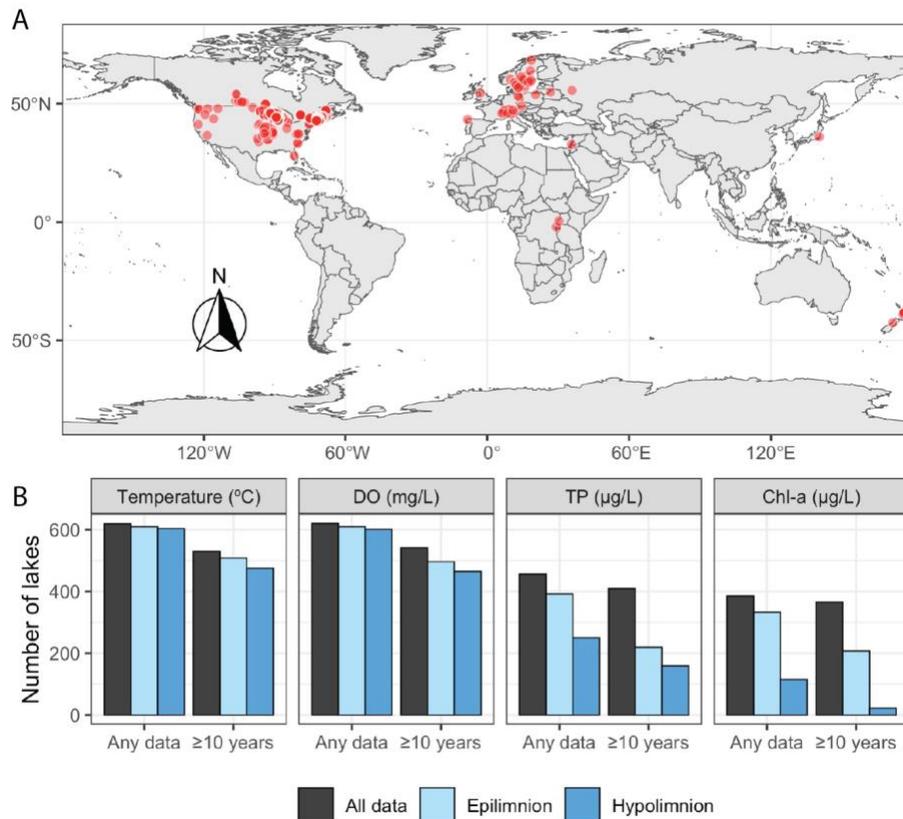
233 To account for variation and error in sampling procedures, we implemented a
234 standardized screening protocol to remove temperature and DO profiles that were substantially
235 shallower or deeper than the reported maximum depth of the lake (Appendix S3).

236

237 2.2.2.2 Mean concentrations

238 We averaged data for all focal variables to an annual timestep using data from the entire
239 stratified period and, separately, the late-summer period at each lake (Appendix S1: Text S1.2).
240 The late summer (i.e., mid-July through August in the northern hemisphere, following Jane et al.
241 2021) is when DO concentrations are likely to approach their lowest value (Wetzel 2001), and
242 may consequently be a critical time period for some processes in the ABA feedback. Conversely,
243 other processes occurring throughout the entire summer stratified period (e.g., oxygen demand,
244 hypolimnetic temperature) can also be critical to the ABA feedback, motivating the study of both
245 periods within a year.

246 For each profile during either the entire summer stratified period or the late-summer
247 period, we calculated the depths of the top and bottom of the metalimnion (the middle thermal
248 layer of the lake) using the *rLakeAnalyzer* R package (Winslow et al. 2019). We used mean
249 metalimnion depths to estimate the bottom of the epilimnion and top of the hypolimnion for each
250 lake-year. We then averaged all hypolimnetic and epilimnetic water quality measurements
251 throughout the time-period of analysis, using interpolated profiles for temperature and DO and
252 all measurements for TP, chl-a, TN, and DOC. To estimate the strength of stratification at the
253 thermocline, we calculated maximum buoyancy frequency using *rLakeAnalyzer* (Read et al.,
254 2011; Winslow et al. 2019) for each temperature profile. Maximum buoyancy frequency was
255 averaged throughout the stratified period for each lake-year (Table 1).



256

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

263

264 2.2.3 Volume-weighted hypolimnetic oxygen demand

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

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

273

274 *2.2.4 Anoxic Factor*

275 Anoxic factor (AF) describes the spatial and temporal extent of anoxia within a lake, and
276 is therefore a useful metric of deoxygenation in lakes that experience hypolimnetic anoxia
277 (Nürnberg 1995; Nürnberg 2019). AF is expected to increase with increased oxygen demand,
278 and can predict internal TP loading in lakes that experience hypolimnetic anoxia (Nürnberg
279 1995; Nürnberg 2019; Figure 1). Here, we calculated AF within each lake-year following
280 Nürnberg (1988) and Nürnberg (2019), modified to address limited data availability across and
281 within lakes (Appendix S5). Briefly, we estimated the duration of anoxia using oxygen profiles,
282 oxygen demand, and modeled turnover dates, and we used modeled or measured bathymetry to
283 quantify the spatial extent of anoxia within each lake-year. The DO threshold for anoxia was
284 defined operationally, as described below (*2.3.3 Operational definition of anoxia*), with detailed
285 methods provided in Appendix S5.

286

287 *2.2.5 Climate data*

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

291 Centre for Medium-Range Weather Forecasts (ECMWF), and provides meteorological data from
292 1959–2022 on a 0.25-degree global grid (Hersbach et al. 2019). For our analysis, we used the
293 monthly 2-m air temperature and total precipitation ERA5 data products, and found the closest
294 gridded values for every lake in our dataset. We summarized “seasonal” air temperature and
295 precipitation values by averaging across multiple months for each lake-year, with southern
296 hemisphere data offset by six months. Spring values were calculated as the average of March and
297 April air temperature or precipitation (following, e.g., Williamson et al. 2015). While
298 stratification onset varies across latitudes and lakes, these spring months are the most likely to
299 correspond to ice melt and spring mixing across the temperate lakes in this study (Woolway et al.
300 2021; Appendix S1: Figure S1.2). Summer values were calculated as the average of July and
301 August air temperature or precipitation, as these summer months most closely correspond with
302 our late-summer in-lake data and were the warmest two months on average across the dataset
303 (Appendix S2: Figure S2.4). Winter temperature and precipitation were calculated as the average
304 of January and February air temperature and precipitation. These winter months were, on
305 average, the coldest months in our dataset (Appendix S2: Figure S2.4), and likely constituted a
306 significant portion of the ice-covered period in lakes that experience seasonal ice cover
307 (Magnuson et al. 2000).

308

309 **2.3 Data analysis**

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

314

315 2.3.1 Lag analysis

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

323

324 2.3.2 Mixed effects modeling

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

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

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

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

346

347 2.3.3 Operational definition of anoxia

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

355

356 Table 1: Explanatory variables used for mixed model regression. We tested several possible
 357 explanatory variables for each response variable using a mixed model approach. The time period
 358 over which mean values were calculated for each lake-year is provided for all water column
 359 variables. For information on lags used, see Appendix S7: Figures S1–S5. Epilimnion and
 360 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 | Stratified | Catchment inputs/flushing |
| | Summer precipitation | | Catchment inputs/flushing |
| | Winter precipitation | | Catchment inputs/flushing |
| | Maximum buoyancy frequency | | 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. | Stratified | Temperature-dependence of phytoplankton growth |
| | Summer average air temp. | | Seasonal change |
| | 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 |

361

362 *2.3.4 Within-lake regressions*

363 To assess whether the across-lake trends identified using mixed models were observable
364 within individual lakes, we performed linear regressions separately at each lake. For each of our
365 focal response variables (see Table 1), we used the same model formulations from the across-
366 lakes analysis (i.e., the explanatory variables from Table 1 that were selected via AICc) to
367 perform regressions within a lake. We saved the resulting coefficient estimates for each
368 explanatory variable used to predict this focal response. We then plotted the distribution of
369 coefficient estimates for all explanatory variables across all lakes, and we compared the median
370 of these distributions to the mixed effect model coefficient estimates. For each response variable,
371 we only included lakes that had at least 10 years of paired data for the response variable and all
372 selected explanatory variables. We removed $n = 81$ lakes that never experienced anoxia (i.e., AF
373 = 0 throughout the timeseries) from the within-lake analysis of the drivers of AF.

374

375 *2.3.4.1 Driver analysis*

376 The coefficient estimates for explanatory variables included in the ABA feedback (e.g.,
377 the coefficient of epilimnetic TP for predicting epilimnetic chl-a) indicates the magnitude of the
378 response, while accounting for other drivers (Table 1). As an exploratory analysis to assess
379 which lakes are most susceptible to the ABA feedback, we analyzed whether there were
380 significant differences in these coefficients based on differences in lake characteristics. For this
381 analysis, we developed linear models predicting the coefficient estimate for each focal variable
382 in the ABA feedback (Table 1) based upon (individually) maximum depth, surface area, mean
383 depth, residence time, dynamic ratio (square root of lake area divided by mean depth; Håkanson
384 1982), and mean concentrations of focal (ABA) variables (i.e., hypolimnetic DO, epilimnetic and

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

389

390 *2.3.5 Climate effects*

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

396

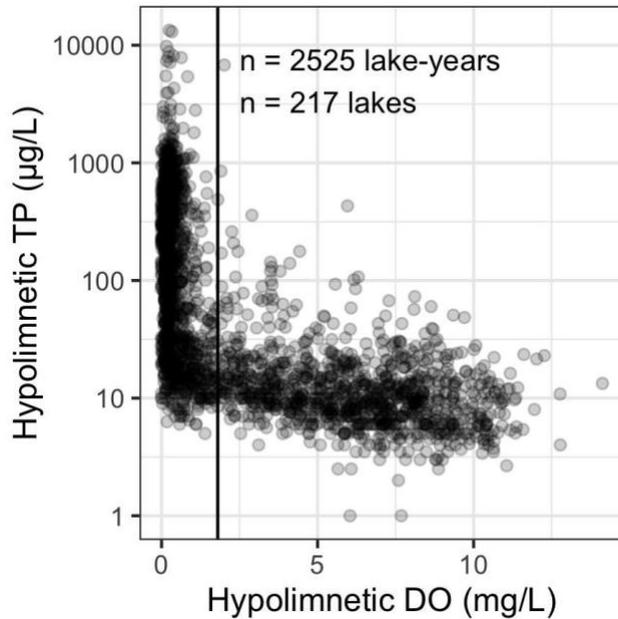
397 3. RESULTS

398 **3.1 Operational definition of hypolimnetic anoxia**

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

407 1.8 mg/L had lower DO concentrations in the year following the first year of anoxia than in the
408 year prior to the first year of anoxia (Appendix S9; Figure S9.1).

409



410

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

413

414

415 3.2 Regression analyses support expected relationships within and across lakes

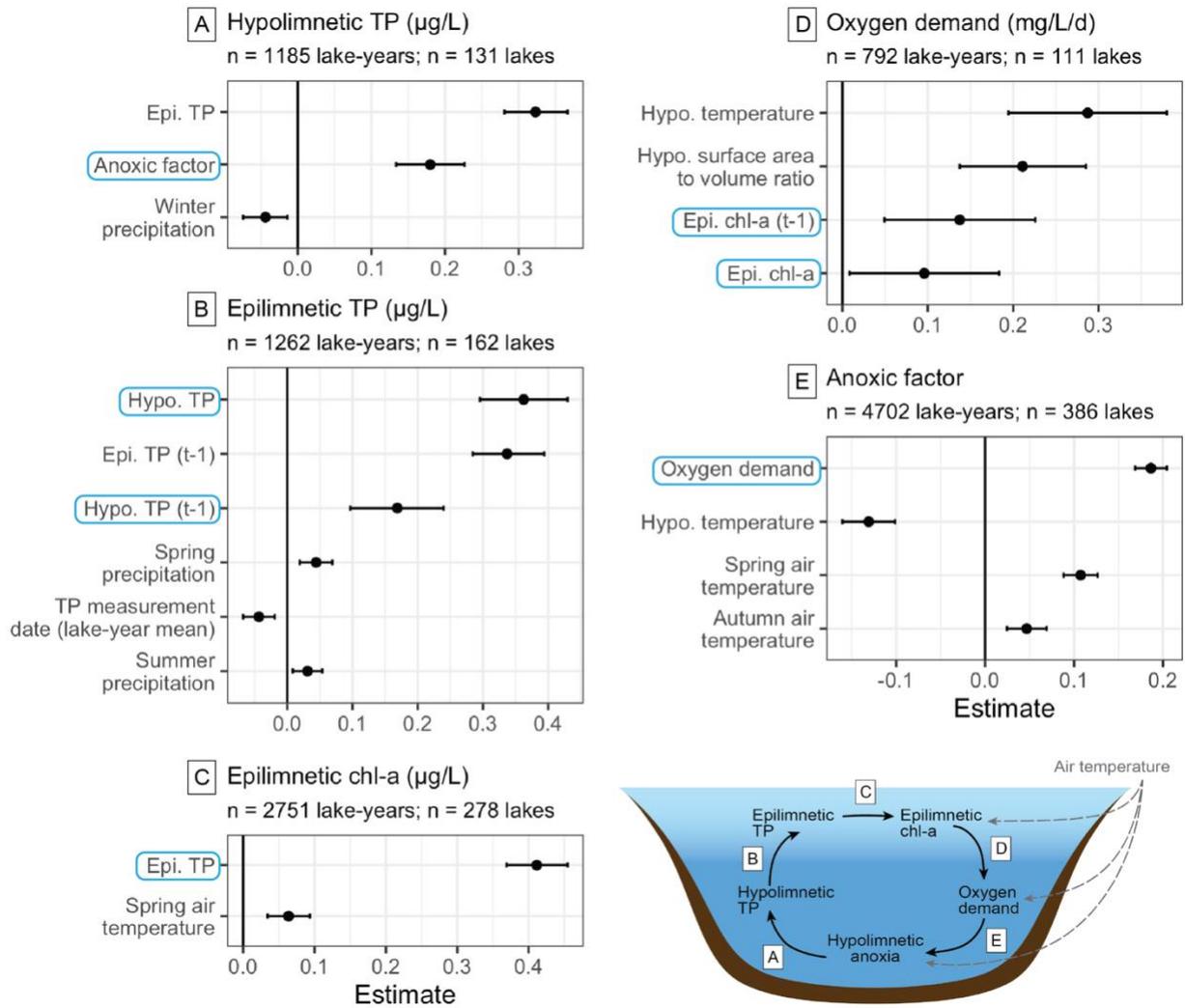
416 Our analyses across 656 lakes provided support for the ABA feedback. Of the
417 explanatory variables used in our model selection process (Table 1), all variables that were
418 predicted to promote the ABA feedback were found to be statistically significant drivers of their
419 predicted responses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

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

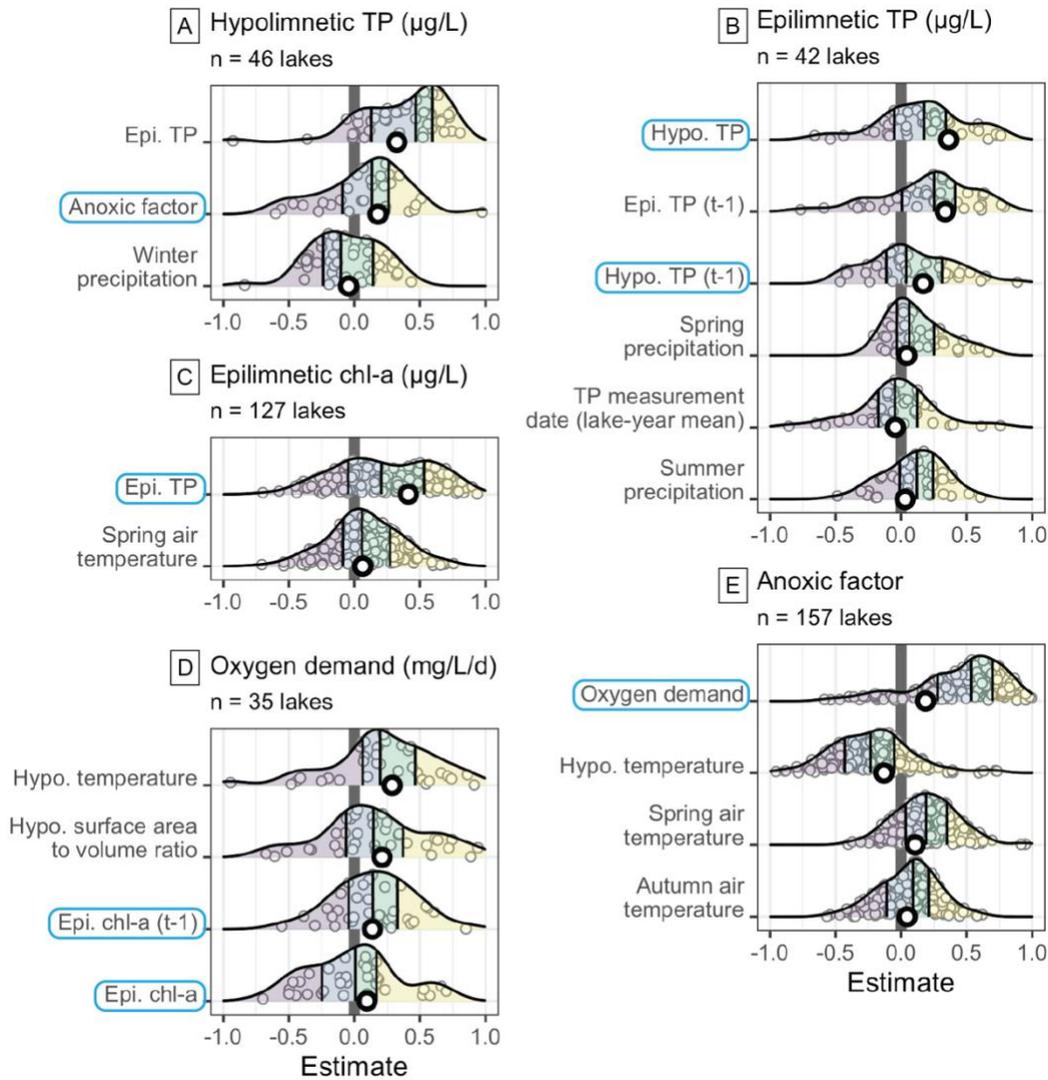
428 All of the ABA relationships observed to be significant across hundreds of lakes ($n =$
429 111–386; Figure 4) were also supported by regression analyses conducted within individual lake
430 time series (with $n = 35–157$ lakes for each analysis; Figure 5). The direction of each of the ABA
431 relationships was identical within and across lakes (Figure 5). The magnitude of the median
432 coefficient estimates for ABA explanatory variables within lakes (e.g., the coefficient for chl-a in
433 the multiple linear regression with oxygen demand as a response variable) tended to be slightly
434 smaller than the mixed model coefficient estimate (Figure 5) for each relationship, except for
435 oxygen demand as a predictor of AF (Figure 5E).

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

447 factors that influence the state of each response variable at a given lake. Random effects were
 448 largest for AF, and residual standard deviation from mixed-model analyses was highest for
 449 oxygen demand and epilimnetic chl-a (Table 2).
 450



451
 452 Figure 4: The proposed ABA feedback (bottom right) was supported by linear mixed model
 453 results across all variables (see Table 1). Here, panel titles indicate the response variable for each
 454 panel and y-axis labels indicate explanatory variables. X-axes indicate the magnitude and 95%
 455 confidence interval of the parameter estimate for each explanatory variable presented on the y-
 456 axis. The black vertical lines in panels A-E denote a parameter estimate of zero. Blue rectangles
 457 highlight drivers in the hypothesized ABA feedback (bottom right). Explanatory variables are
 458 ordered by the magnitude of the parameter estimate within each panel.
 459



460

461 Figure 5: Linear regressions analyzing time series data within individual lakes provide further
 462 support for the ABA feedback. Here, panel titles indicate the response variable for each panel
 463 and y-axis labels indicate explanatory variables. Individual points represent regression
 464 coefficients from within one lake. Density distributions describe the distribution of parameter
 465 values across lakes, with colors delineating the quartiles of the distribution (purple: 0-25%, blue:
 466 25-50%, green: 50-75%, and yellow: 75-100%). Black and white circles at the bottom of each
 467 distribution mark the parameter estimate from the mixed model analysis (Figure 4). The gray
 468 vertical lines in panels A-E denote a parameter estimate of zero. Blue rectangles highlight drivers
 469 in the hypothesized ABA feedback. Explanatory variables are ordered by the magnitude of the
 470 mixed-model parameter estimate for consistency with Figure 4. All x-axes range from -1 to 1 to
 471 enable comparison among panels.
 472

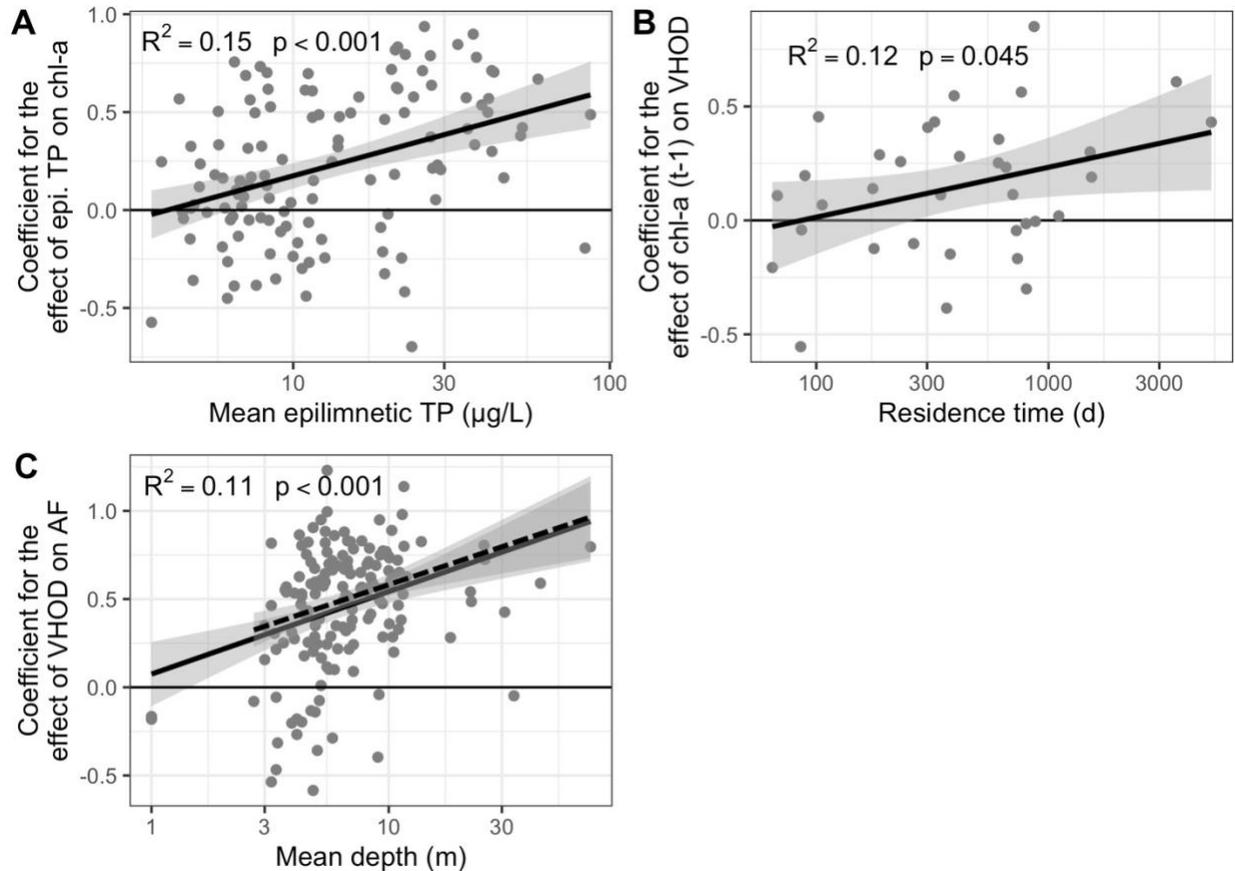
473 Table 2: Random and residual variation from linear mixed models. Model structure and fixed
474 effects are summarized in Figure 4.

| 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 |

475

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

483



484

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

494

495

496 4. DISCUSSION

497

498

499

500

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

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

505

506 **4.1 Decades of research facilitate identification of ABA feedback**

507 Individual relationships in the ABA feedback have been the subject of substantial
508 research inquiry over the past century or longer (e.g., Sachs 1874; Thienemann 1928; Schindler
509 1974). While these previous studies primarily focused on examining biogeochemical dynamics
510 within one lake, they provided support for the individual relationships in the ABA feedback
511 (Figure 1). Modeling studies provided a means of simultaneously considering all ABA
512 relationships, and have shown mechanistic support for the existence of an ABA feedback in
513 seasonally-stratified lakes (Carpenter 2003; Carpenter and Lathrop 2008). However, model
514 simulations have indicated that the susceptibility of individual lakes to a trophic regime shift, as
515 a result of the ABA feedback, depends on multiple lake-specific parameters (i.e., macrophyte
516 presence, temperature, mean depth; Genkai-Kato & Carpenter, 2005), highlighting the need for a
517 multi-lake empirical approach.

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

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

530

531 *4.1.1 Effect of anoxia on hypolimnetic TP (Figure 1A)*

532 In this study, we observed a strong positive relationship between hypolimnetic anoxia
533 and TP concentrations both within and across lakes. Across lakes, our breakpoint analysis
534 detected a threshold relationship whereby hypolimnetic DO had a stronger effect on TP when
535 DO concentrations decreased to levels approaching anoxia (<1.8 mg/L; Figure 3). Our results
536 reinforce previous research affirming that AF (the duration and spatial extent of anoxia) may be
537 strongly positively correlated with hypolimnetic TP concentrations (Figure 4; Figure 5; e.g.,
538 North et al. 2014; Nürnberg et al. 2019). A threshold relationship between DO and TP is well-
539 supported by previous research across sediment core incubations, *in situ* sediment chamber
540 measurements, and mass-balance whole ecosystem analyses (e.g., Einsele 1936; Mortimer 1942;
541 Orihel et al. 2017; Anderson et al. 2021). Here, our threshold value of 1.8 mg/L DO, averaged
542 throughout the entire hypolimnion, likely reflects DO conditions of ~0 mg/L near the sediment-
543 water interface (which inherently is challenging to quantify empirically), resulting in enhanced
544 TP loading (Nürnberg 2019). We note that our identified breakpoint of 1.8 mg/L is also
545 remarkably similar to those identified in previous sediment incubation work (Matisoff et al.
546 2016; Doig et al. 2017; Orihel et al. 2017). Overall, this analysis indicates that the ABA

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

549 In our dataset, it was common for lakes to cross the threshold of 1.8 mg/L (34% of $n =$
550 356 lakes). Lakes where oxygen concentrations declined below 1.8 mg/L had lower DO
551 concentrations in the year following the onset of anoxia than in the year prior to the onset of
552 anoxia (Appendix S9; Figure S9.1). While our dataset was not a random or fully representative
553 sample of global lakes, the large number of lakes which crossed the 1.8 mg/L threshold in this
554 study suggests that the ABA feedback may be prevalent.

555

556 *4.1.2 Effect of hypolimnetic TP on epilimnetic TP (Figure 1B)*

557 We found moderately strong support for an effect of hypolimnetic TP on epilimnetic TP
558 both within one year and between years (i.e., hypolimnetic TP influences epilimnetic TP the
559 following year). While the directionality of this relationship can be difficult to identify in the
560 absence of detailed nutrient input data (i.e., epilimnetic TP can affect hypolimnetic TP, vice
561 versa, or a third driver may simultaneously influence both), existing research provides strong
562 support for this effect. Elevated hypolimnetic TP concentrations can increase epilimnetic TP
563 concentrations within a summer stratified period through organism-mediated transport, diffusion,
564 and internal seiche dynamics (e.g., Carpenter et al. 1992; Soranno et al. 1997; Kamarainen et al.
565 2009; Nürnberg 2009; Haupt et al. 2010; Cottingham et al. 2015). At the onset of autumn
566 mixing, the concentration of TP in the hypolimnion fundamentally determines the amount of
567 potential TP input to the epilimnion, which can have legacy effects throughout the subsequent
568 autumn, winter, and spring (e.g., Nürnberg and Peters 1984; Wang et al. 2019).

569

570 *4.1.3 Effect of epilimnetic nutrients on epilimnetic chl-a (Figure 1C)*

571 We found a strong positive association between surface water TP concentrations and
572 surface water chl-a, both within and across lakes, likely reflecting the fact that interannual
573 variability in phosphorus concentrations can play an important role in regulating phytoplankton
574 growth in lakes (Figure 4; Figure 5). Our study follows many decades of data that illustrate the
575 positive effect of TP on phytoplankton biomass (Schindler 1974; Smith 1982; MacKeigan et al.
576 2023). In this study, we were unable to identify an effect of epilimnetic TN concentrations on
577 chl-a, suggesting that in these lakes, TP may play a more important role in regulating
578 phytoplankton growth. However, we note that data availability was substantially greater for TP
579 ($n = 387$ lakes) than for TN ($n = 86$ lakes), and complexities of nitrogen forms (not considered
580 here) may hinder the detection of a nitrogen effect. Previous research has documented the
581 importance of nitrogen for limiting or co-limiting phytoplankton growth in some lakes, over
582 multiple timescales (Elser et al. 2007; Lewis Jr. and Wurtsbaugh 2008; Paerl et al. 2016; Scott et
583 al. 2019; Lewis et al. 2020). Consequently, our study highlights the need for long-term, speciated
584 nitrogen data to disentangle the role of nitrogen in the ABA feedback.

585

586 *4.1.4 Effect of epilimnetic chl-a on oxygen demand (Figure 1D)*

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

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

599

600 *4.1.5 Effect of oxygen demand on hypolimnetic anoxia (Figure 1E)*

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

616 However, the factors that control oxygen demand are changing less consistently: temporal trends
617 in hypolimnetic temperature are highly variable across lakes (Pilla et al. 2020; Richardson et al.
618 2017), as are trends in chl-a from 1980–present (Kraemer et al. 2022). Consequently, it is not
619 surprising that trends in oxygen demand appear to be inconsistent across lakes (Jane et al. 2023).
620 In this study, our focus on annual and sub-annual timescales allowed us to more precisely
621 investigate the mechanisms at play within and across 386 lakes (Figure 4E), identifying that
622 variability in oxygen demand has the potential to drive a feedback effect in some lakes that
623 experience hypolimnetic anoxia.

624

625 **4.2 Lake characteristics can increase susceptibility to the ABA feedback**

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

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

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

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

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

660

661 **4.3 Climate change has the potential to trigger the ABA feedback**

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

666

667 *4.2.1 High spring air temperatures are associated with anoxia*

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

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

688

689 **4.4 Strengths and limitations of this analysis**

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

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

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

711

712 **4.5 Conclusions and global change implications**

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

727

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770 AUTHOR CONTRIBUTIONS

771 ASLL and MPL led the early conceptualization of this project, with significant contributions
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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
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781

782 DATA AVAILABILITY

783 The in-lake data used in this study are published in the Environmental Data Initiative
784 repository (EDI; Lewis et al. 2023), and include compiled data from multiple separately-
785 published datasets (Maberly et al. 2017; Leach et al. 2018; Lentz et al. 2023; Winslow et al.
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790 (Hersbach and others 2019). Analysis code to reproduce the results in this manuscript is
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792

793 CONFLICT OF INTEREST

794 The authors declare no conflict of interest.

795

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