

Widespread deoxygenation of temperate lakes

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2 Widespread deoxygenation of temperate lakes

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83 **Summary paragraph:**

84 The concentration of dissolved oxygen in aquatic systems helps regulate biodiversity^{1, 2}, nutrient
85 biogeochemistry³, greenhouse gas emissions⁴, and drinking water quality⁵. The long-term
86 declines in dissolved oxygen concentrations in coastal and ocean waters have been linked to
87 climate warming and human activity^{6, 7}, but little is known about changes in dissolved oxygen
88 concentrations in lakes. While dissolved oxygen solubility decreases with increasing water
89 temperatures, long-term lake trajectories are not necessarily predictable. Oxygen losses in
90 warming lakes may be amplified by enhanced decomposition and stronger thermal stratification⁸,
91 ⁹ or they may increase as a result of enhanced primary production¹⁰. Here we analyse 45,148
92 dissolved oxygen and temperature profiles from 393 temperate lakes spanning 1941-2017. We
93 find that a decline in dissolved oxygen is widespread in surface and deep-water habitats. The
94 decline in surface waters is primarily associated with reduced solubility under warmer water
95 temperatures, although surface dissolved oxygen increased in a subset of highly-productive
96 warming lakes, likely due to increasing phytoplankton production. In contrast, the decline in
97 deep waters is associated with stronger thermal stratification and water clarity losses, but not
98 with changes in gas solubility. Our results suggest that climate change and declining water
99 clarity have altered the physical and chemical environment of lakes. Freshwater dissolved
100 oxygen losses are 2.5-10 times greater than observed in the world's oceans^{6, 7} and could threaten
101 essential lake ecosystem services^{2, 3, 5, 11}.

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105 **Main text:**

106 The concentration of dissolved oxygen (DO) in aquatic systems influences biodiversity¹,
107 ², nutrient biogeochemistry³, greenhouse gas emissions⁴, drinking water quality⁵, and, ultimately,
108 human health¹². Many aquatic species require well-oxygenated habitat^{11, 13} and cool water to
109 survive warm summers^{2, 11}. Loss of deep-water DO degrades water quality by promoting the
110 release of accumulated nutrients from sediments into water^{1, 3}, which can increase phytoplankton
111 biomass. This process can also facilitate harmful algal blooms⁵, which can compromise water
112 supplies and harm human health¹². Despite clear evidence of large-scale deoxygenation in ocean
113 waters^{6, 7}, there are no systematic large-scale studies of this phenomenon in lakes³.

114 DO concentrations should decline with increasing water temperature due to reduced gas
115 solubility. However, other mechanisms can alter DO, potentially amplifying or counteracting
116 losses predicted from solubility changes alone. For example, rates of heterotrophic respiration
117 increase with temperature faster than primary production⁹, and surface-temperature warming can
118 increase the strength and duration of thermal stratification, reducing water circulation, and
119 preventing deep-water DO replenishment^{8, 14, 15}. Studies of individual lakes demonstrate deep-
120 water DO concentrations can decrease with lake warming^{3, 8, 15, 16}, reducing access to cold-water
121 habitat essential to many organisms¹¹. However, given the many feedbacks and processes
122 regulating DO, overall trajectories currently defy *a priori* prediction.

123 We addressed this critical issue by compiling and analyzing an extensive database of lake
124 temperature and DO profiles to characterize widespread and long-term changes in DO
125 concentration and its causes. We used data from 393 temperate lake and reservoir basins, each
126 with a minimum of 15 years of observation (median: 24 years), and report population medians
127 from long-term surface- (epilimnion) and deep-water (hypolimnion) trends in temperature, DO

128 concentration, and DO saturation during the late summer period when seasonal DO depletion is
129 expected to be pronounced¹⁷. Our analyses revealed that lake DO concentrations have declined in
130 both surface and deep waters from 1980 to 2017 by 0.45 and 0.42 mg L⁻¹, respectively (Fig. 1).
131 These rates represent losses of 5.1 and 20.2% for surface and deep waters, respectively, and were
132 substantially greater than those observed for the oceans, where total water-column DO has
133 declined about 2% since 1960⁶.

134 While deep-water temperatures have been virtually stable since observations began (Fig.
135 1a; $-0.01^{\circ}\text{C decade}^{-1}$), both deep-water DO concentration and percent saturation declined
136 through time ($-0.12 \text{ mg L}^{-1} \text{ decade}^{-1}$ and $-1.2\% \text{ decade}^{-1}$; respectively, Fig. 1b, c). Declines were
137 unrelated to solubility as predicted changes based on solubility (slight increase of 0.01 mg L^{-1})
138 were negligible compared with observed losses (median -0.23 mg L^{-1} based on last five years
139 relative to first five years of each time series, Fig. 2b) Declining DO, despite essentially
140 unchanging solubility, implies deep-water habitats have become increasingly inhospitable for
141 organisms with aerobic metabolism, including fishes. We quantified potential impacts of such
142 declines on habitat availability by calculating trends in $T_{\text{DO}3}$, the minimum water column
143 temperature where DO was at least 3 mg L^{-1} . This metric was developed to quantify oxy-thermal
144 habitats for cold-water fisheries¹¹. In lakes where DO was below 3 mg L^{-1} anywhere in the water
145 column at least once in the time series ($n = 369$), $T_{\text{DO}3}$ increased by $0.17^{\circ}\text{C decade}^{-1}$, with 68.0%
146 of lakes having positive trends and declining habitat for many cold-water species.

147 In contrast to trends observed for deep waters, variation in surface-water DO
148 concentrations was well explained by changes in gas solubility. Consistent with other global-
149 scale lake studies¹⁸, median air temperatures warmed at $0.30^{\circ}\text{C decade}^{-1}$ and median lake surface
150 waters warmed at $0.39^{\circ}\text{C decade}^{-1}$. Additionally, median wind speed and precipitation declined

151 (trends of $-0.04 \text{ m s}^{-1} \text{ decade}^{-1}$ and $-4.23 \text{ mm decade}^{-1}$, respectively), while shortwave radiation
152 increased ($1.88 \text{ W m}^2 \text{ decade}^{-1}$; Table S1). Surface-water temperature increases were best
153 explained by spring and summer air temperature increases and by summer wind speed declines
154 (Table S2). Surface-water DO concentrations declined at $-0.11 \text{ mg L}^{-1} \text{ decade}^{-1}$ (Fig. 1b).
155 Comparing the last five years relative to first five years of each time series revealed that the
156 median change predicted due to solubility loss was $\sim 63\%$ of the median observed decline in DO
157 concentration, with solubility-predicted loss of 0.12 versus observed losses of 0.19 mg L^{-1} (Fig.
158 2a).

159 Despite a strong influence of water temperature on DO concentration in surface-waters,
160 there was substantial variability among lakes (Fig. 2a), and a large subset of lakes exhibited
161 increases in both water temperature and DO concentration ($n=87$; Fig. 3d). Analysis of the
162 interaction between DO concentration, surface temperature, and water clarity (measured as
163 Secchi depth, a proxy for trophic status¹⁹) showed that DO concentration generally decreased
164 with increasing temperature. However, in lakes with low water clarity ($< 2 \text{ m}$), DO concentration
165 increased when average mean summer surface-water temperatures exceeded $\sim 24^\circ\text{C}$ (Fig. 3c).
166 Similarly, in a subset of lakes with chlorophyll data (a proxy for phytoplankton biomass; $n =$
167 162), positive DO trends were observed when chlorophyll was high and surface temperatures
168 exceeded $\sim 25^\circ\text{C}$, (Fig. 3b; $P < 0.001$). Thus, we suggest that eutrophication and warming interact
169 to increase surface-water DO concentration despite reduced gas solubility.

170 Lakes with increasing DO concentration in warming surface waters had significantly
171 higher surface-water temperatures (Fig. 3a; $P = 0.016$) and their watersheds contained a
172 significantly higher proportion of agriculture ($P = 0.046$) and developed land cover ($P < 0.001$)
173 compared with other lakes. When developed land exceeded $\sim 50\%$ of a watershed and surface

174 water temperature exceeded $\sim 25^{\circ}\text{C}$, the probability of a warming lake having an increasing DO
175 trend was $>50\%$. Combined, these analyses highlight a potential threshold above which water
176 temperatures and lake productivity interact to elevate DO concentration in surface waters despite
177 declining gas solubility. While we lack data on phytoplankton taxonomic composition, evidence
178 indicates that phytoplankton blooms are increasing globally²⁰, in particular due to
179 cyanobacteria²¹. High temperatures and elevated nutrient loading can promote surface
180 cyanobacteria blooms whose photosynthesis leads to DO supersaturation, particularly in
181 eutrophic lakes as temperatures exceed $\sim 23\text{-}25^{\circ}\text{C}$ ^{10, 21}. Consistent with this inferred mechanism,
182 we note these same lakes exhibited consistently low deep-water DO concentration (median: 0.64
183 mg L^{-1}) relative to other lakes (median: 3.42 mg L^{-1}), as is expected when a large phytoplankton
184 biomass sinks and is decomposed in deep-water habitats²². Deep water DO changes are described
185 in more detail below.

186 Decadal-scale trends in DO were associated with non-linear changes in surface-water
187 temperature (Fig. 2c-f; Fig. S1). For example, although surface-water temperatures generally
188 increased from 1980 onwards, there was a period of accelerated increase during 1990-2000, with
189 slower warming thereafter (Fig. 2c), consistent with the “warming hiatus” observed during 1998-
190 2012²³. This trend occurs across the population of all lakes, as well as the subset of lakes
191 sampled continuously throughout this period. Similarly, surface-water DO exhibited periodic
192 deviations from an overarching trend of declining DO concentration (Fig. 2d), mainly due to the
193 productive lakes exhibiting increasing DO levels in surface waters (Fig. 2d, blue line). Excluding
194 these lakes, analysis of the remaining sites showed a consistent long-term decline in surface-
195 water DO (Fig. 2d, red line). Deep-water temperatures exhibited a pronounced multi-decadal

196 oscillation since 1980 (Fig. 2e) as has been observed in some lakes previously²⁴, whereas deep-
197 water DO concentration declined consistently through time (Fig. 2f).

198 While surface-water DO concentration changes were generally well predicted by
199 solubility changes, deep-water DO changes were more strongly associated with changes in water
200 clarity and water-column density differences (Figs. 4 and S2). For example, water clarity losses
201 exceeding 1 m were associated with substantial reductions in deep-water DO saturation (Fig.
202 S2). Mechanistically, increases in phytoplankton biomass or dissolved organic matter (DOM)
203 reduce water clarity while increasing oxygen-consuming respiration^{19, 22, 25}. Increases in
204 phytoplankton biomass and DOM are often caused by land use change and recovery from acid
205 deposition, respectively²⁶. However, there was no overarching decline in water clarity across
206 study lakes. Indeed, 51% of lakes had clarity increases and 49% had decreases, and only 39% of
207 lakes exhibited both water clarity loss and DO saturation loss (Fig. 4a).

208 Deep-water DO decreased substantially in lakes where the water column density
209 difference between surface and deep waters increased by more than $\sim 0.5 \text{ kg m}^{-3}$ (Fig 4b; Fig.
210 S2b). Strong increases in the density difference indicate intensified stratification that reduces
211 vertical mixing and replenishment of deep-water DO from the atmosphere, and may reduce
212 nutrient upwelling to surface waters^{3, 15}. Water column density differences increase due to water
213 clarity losses as well as other factors that increase heat gain in near-surface waters, including
214 climate warming²⁶ and atmospheric stilling²⁷. Increased water column density differences may
215 also be associated with earlier onset of seasonal stratification and thus more time for oxygen
216 consumption before the summer sampling period²². We found that changes in water-column
217 density differences were best explained by changes in deep water temperature and climate
218 characteristics (Fig. S3). Despite no overarching among-lake trend in water clarity or deep-water

219 temperature, stratification strength increased in 84% of lakes that stratified, with 61% of basins
220 exhibiting both increased density difference and DO saturation loss (Fig 4b). Warming surface-
221 water temperatures combined with unchanging deep-water temperatures (Fig. 1a) increases the
222 density difference in lake water columns (median rate: $0.10 \text{ kg m}^{-3} \text{ decade}^{-1}$). We observed
223 unchanging deep-water DO in lakes where both clarity and stratification were unchanged (Fig.
224 4c, d). Therefore, we anticipate further DO losses in deep waters of lakes where water clarity
225 continues to decline or thermal stratification intensifies, whether due to atmospheric warming,
226 stilling, or both^{26, 27}.

227 Despite a wide range of lake and catchment characteristics, the overall trend of temperate
228 lake deoxygenation is clear, with climate changes and water clarity losses contributing to
229 declines in lake DO concentration at rates ~ 2.5 -10 times greater than those observed in the global
230 oceans^{6, 7}. We find deep-water lake habitats are especially threatened, and deep-water DO trends
231 may portend future losses of cold-water and oxygen-sensitive species², increased internal
232 nutrient loading which exacerbates eutrophication³ and the formation of harmful algal blooms⁵,
233 and potentially increased outgassing of stored methane⁴. While already rapid, future losses in
234 lake DO may accelerate due to continued anthropogenic modifications of the environment,
235 including eutrophication²², salinization²⁸, and hydrological management²⁸. While many lakes
236 have undergone active management to reduce nutrient loads, in part to mitigate phytoplankton
237 growth and deep-water oxygen loss²⁸, our findings suggest such actions will likely require more
238 rigorous efforts in the future to counter the effects of climate and land use change.

239

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365

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367 analyses, and drafted the manuscript. GJAH, BMK, PRL, JLM, RLN, RMP, JTS, CEW and RIW
368 helped design the study and conduct analyses, contributed data, and edited the manuscript. All
369 other authors contributed data, edited the manuscript, or both.

370

371 **Author information:** Derived statistics used in our analyses are publicly available via the
372 Environmental Data Initiative (EDI) repository at:

373 <https://doi.org/10.6073/pasta/ac8b05bb0da19032b3df3efc21f83874>.

374 Reprints and permissions information is available at www.nature.com/reprints. The authors
375 declare no competing interests.

376 Correspondence and requests for materials should be addressed to KCR (rosek4@rpi.edu).

377

378 **Figures and Figure Captions:**

379 **Fig. 1 | Trends in dissolved oxygen and temperature. a-c,** Density plots of trend magnitudes
380 for **a** temperature ($^{\circ}\text{C decade}^{-1}$), **b** DO concentration ($\text{mg L}^{-1} \text{ decade}^{-1}$) and **c** DO percent
381 saturation ($\% \text{ decade}^{-1}$). Red distribution indicates surface water trends and blue indicates deep-
382 water trends. The x-axis range for each plot covers two standard deviations from the median, or
383 approximately 95% of data. Vertical dashed lines indicate median trends, and the zero trend is
384 highlighted with a black vertical line.

385

386 **Fig. 2 | Solubility effects and changes in temperature and DO concentration through time.**
387 **a, b,** Observed vs. predicted change in DO concentration (mg L^{-1}) due to solubility for surface
388 **(a)** and deep **(b)** waters. Solid black line is the 1:1 line and the blue line is loess smoothed, while
389 the gray regions are 95% confidence intervals. **c-f,** Smoothed curves of GAMM models, showing
390 deviation from the mean model predictions for selected response variables with year as the
391 predictor variable. Gray regions represent one standard error from the predicted line for **c,**
392 temperature ($^{\circ}\text{C}$) and **d,** DO (mg L^{-1}) through time for surface waters. The red line represents
393 lakes where both surface temperature and DO were increasing ($n = 87$) and the blue line is all
394 other lakes ($n = 332$). **e,** Temperature and **f,** DO for deep waters.

395

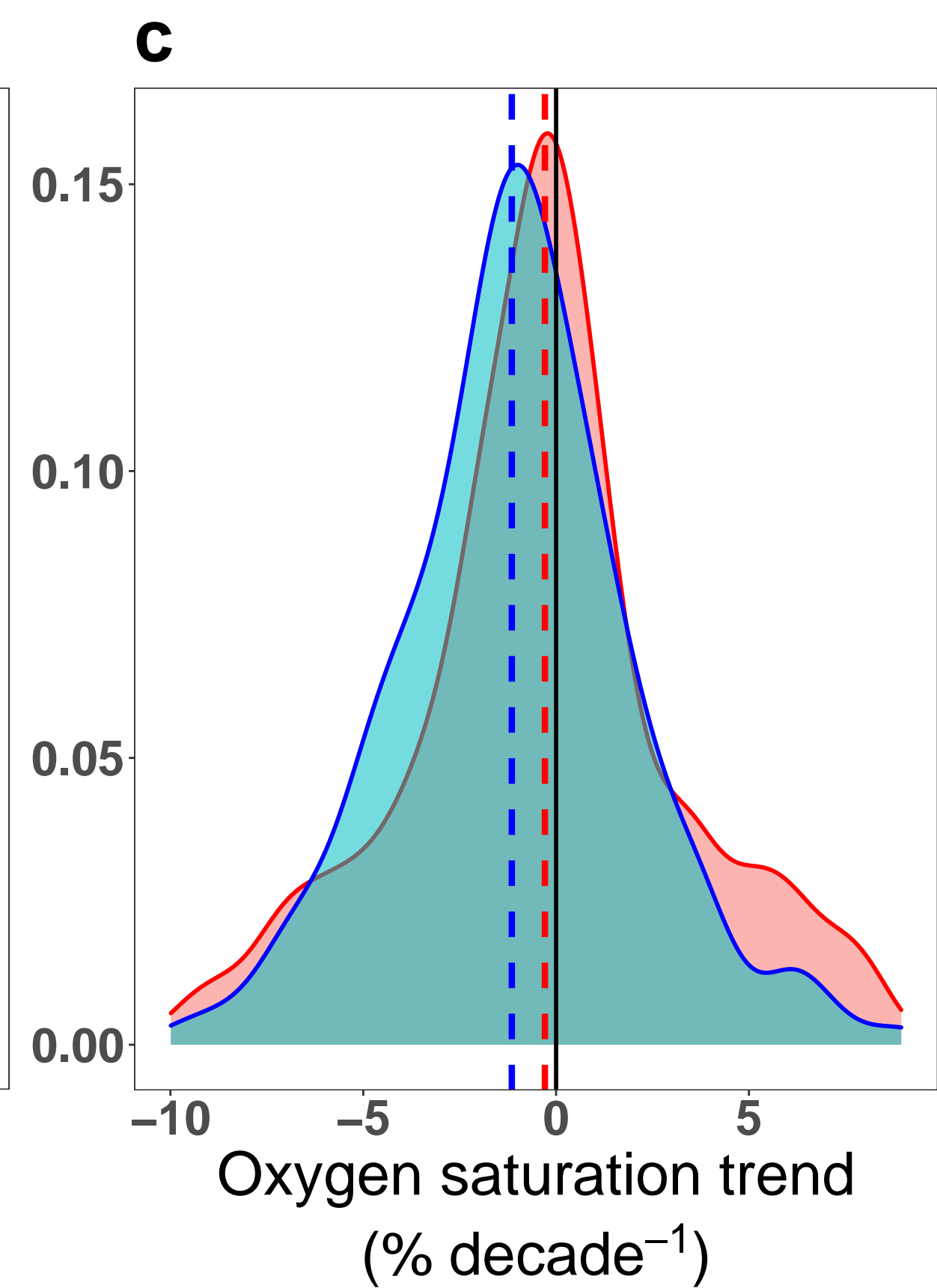
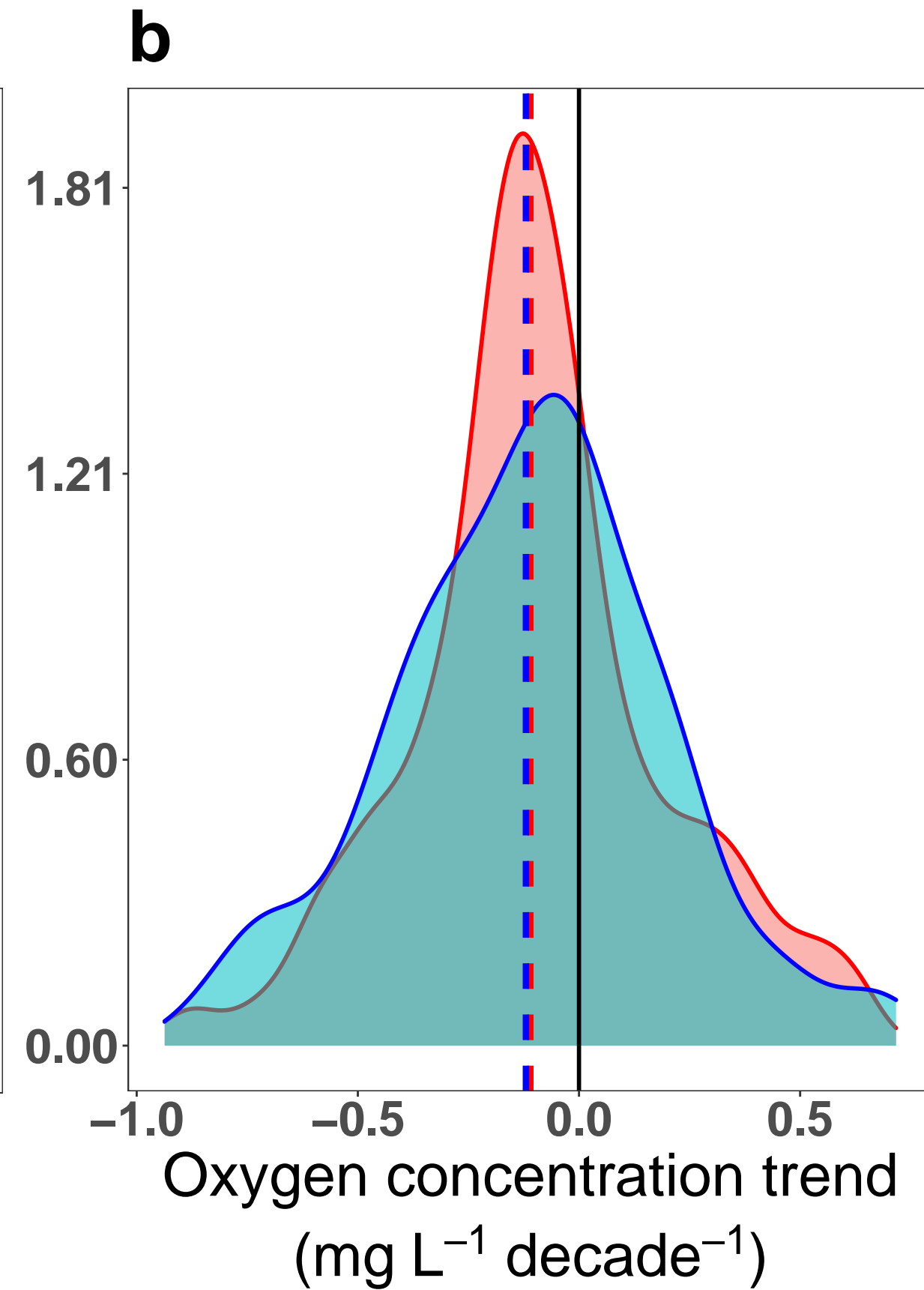
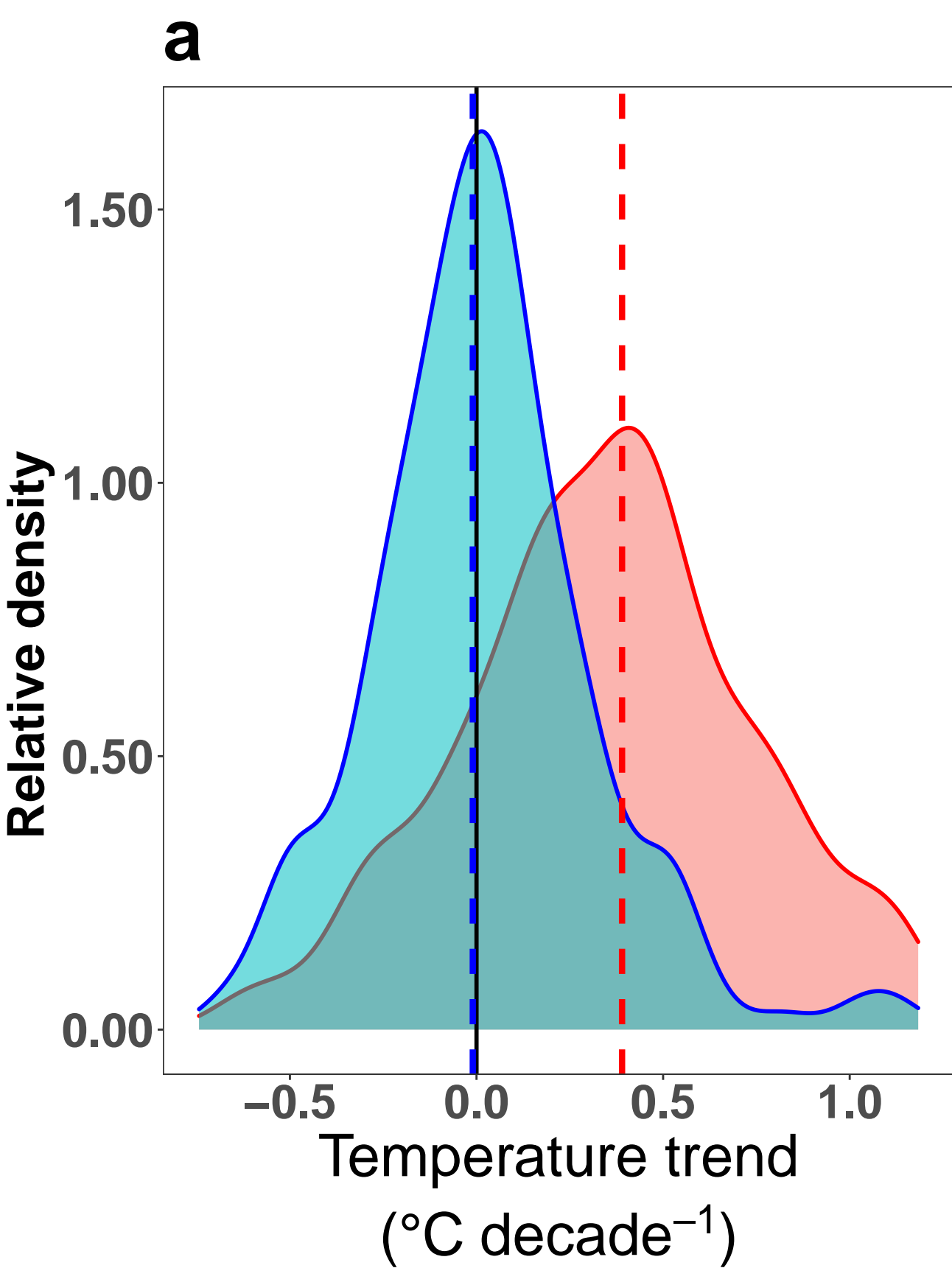
396 **Fig. 3 | Interaction of productivity and temperature in surface waters. a,** Predicted
397 probability of a lake having both increasing surface temperature and DO concentration from a
398 fitted logistic regression model at three different mean surface water temperatures: 21°C (blue),
399 25°C (black), 28°C (red) **b,** Predictions of DO trends from a fitted multiple regression model for

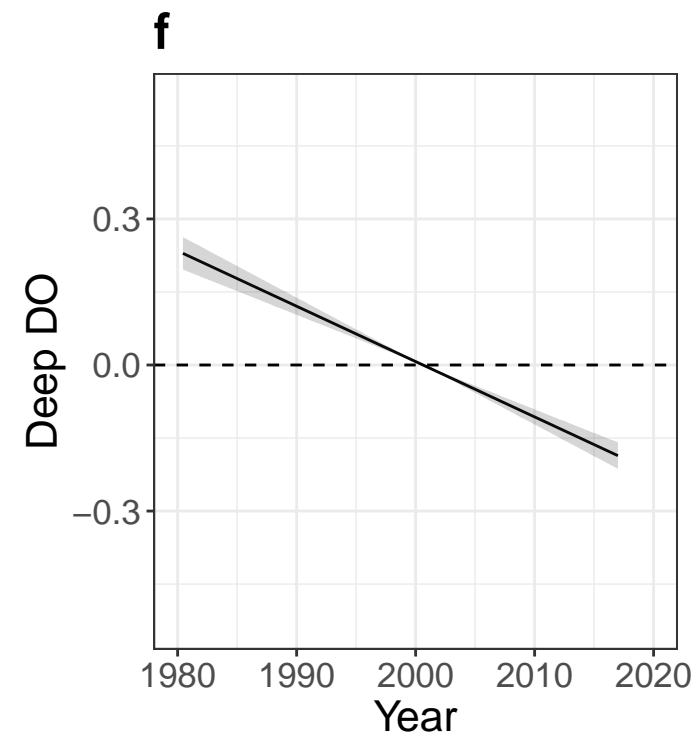
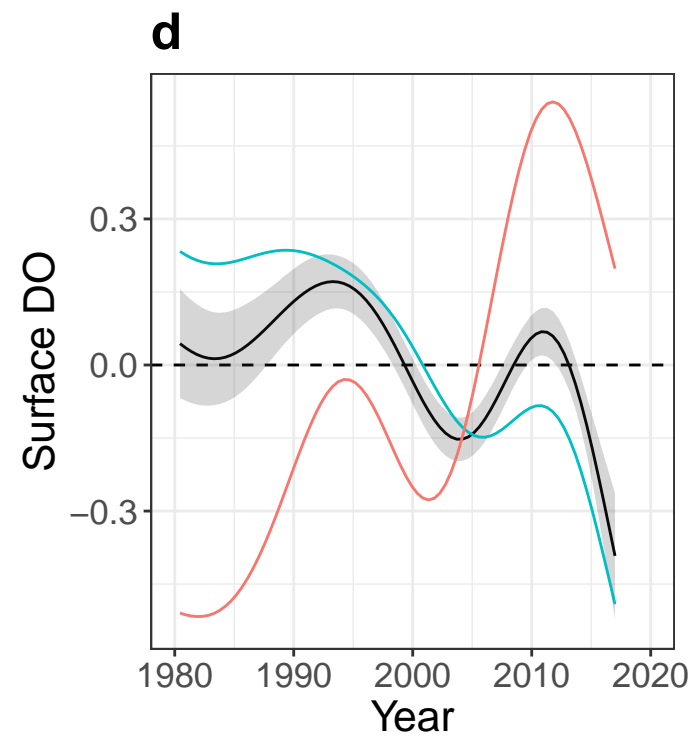
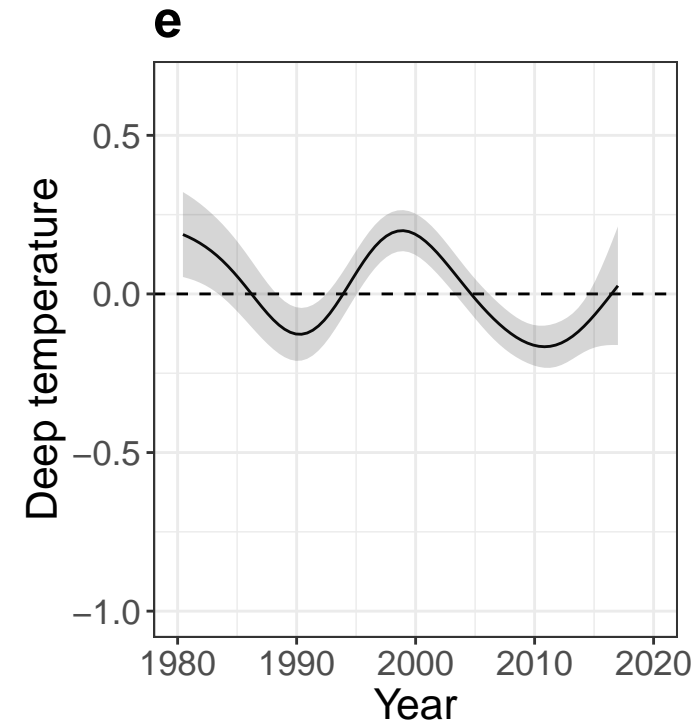
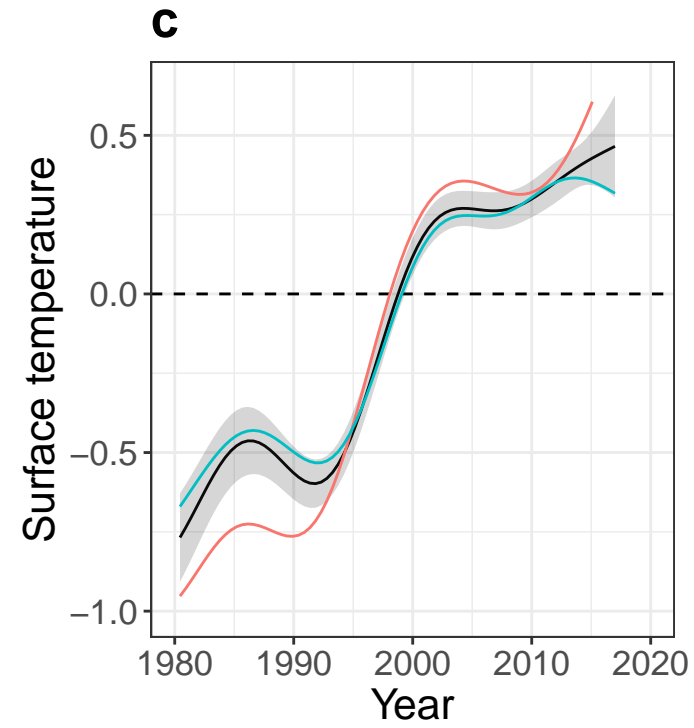
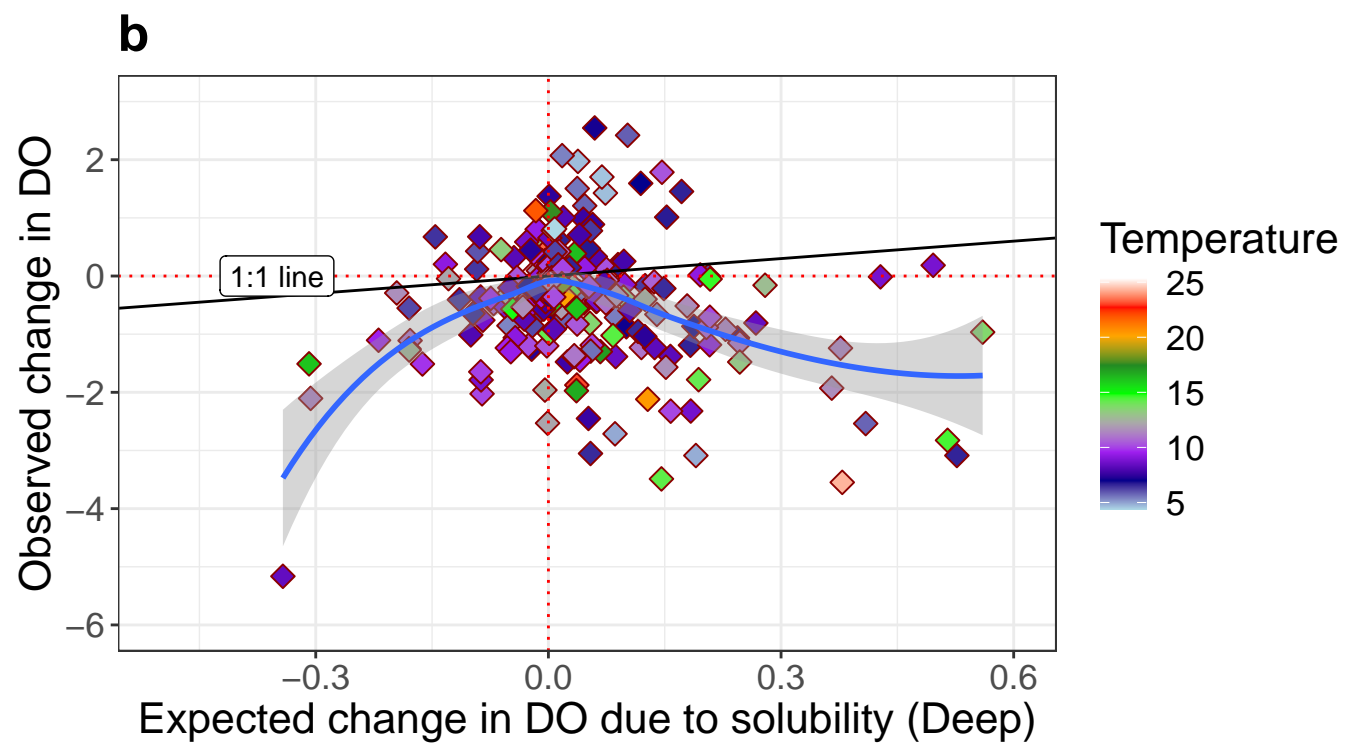
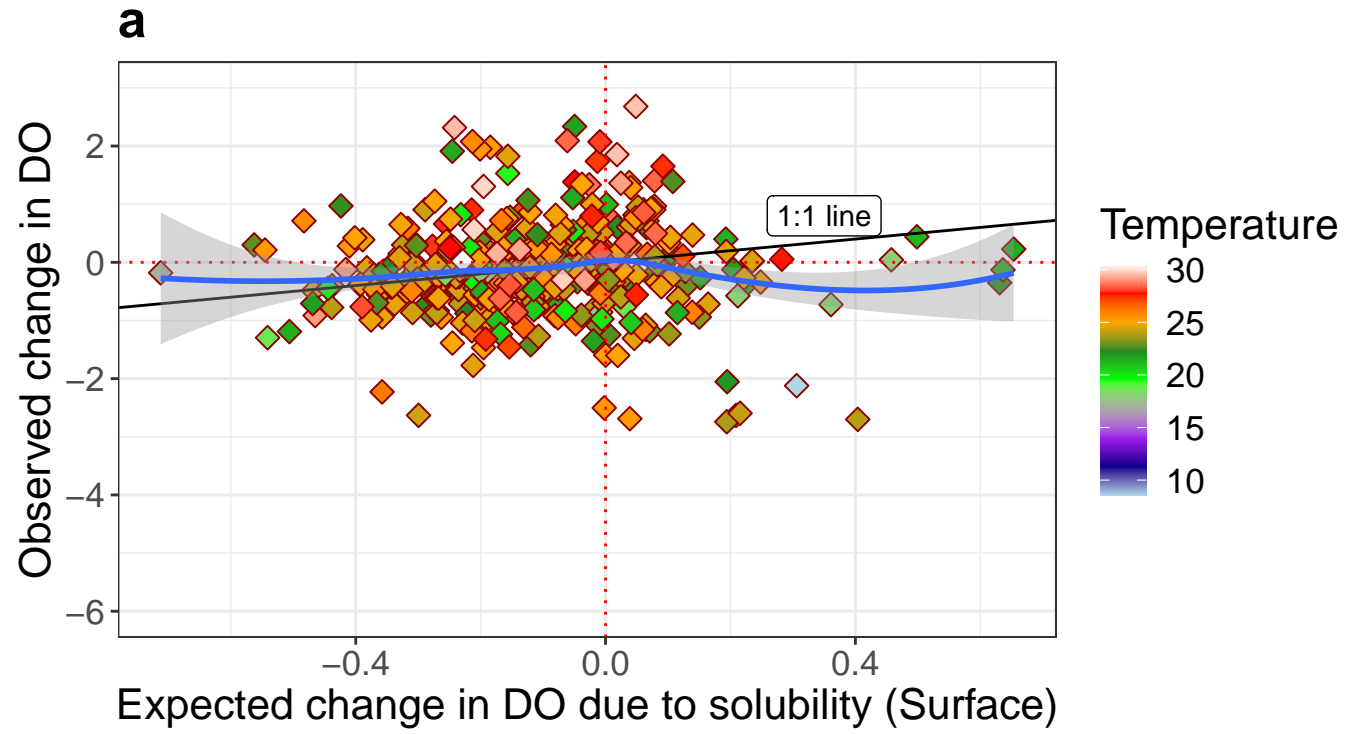
400 chlorophyll (used as a surrogate for primary productivity) at these same temperatures (legend
401 same as **a**) **c**, The interaction of water clarity (measured as Secchi depth in m) and surface-water
402 temperature ($^{\circ}\text{C}$) and their effects on surface DO (mg L^{-1}) from fitted generalized additive mixed
403 models (GAMM) **d**, Most lakes exhibited increasing surface temperatures and decreasing DO
404 concentration consistent with solubility effects, but a subset of lakes ($n = 87$) have both
405 increasing surface temperature and DO concentration.

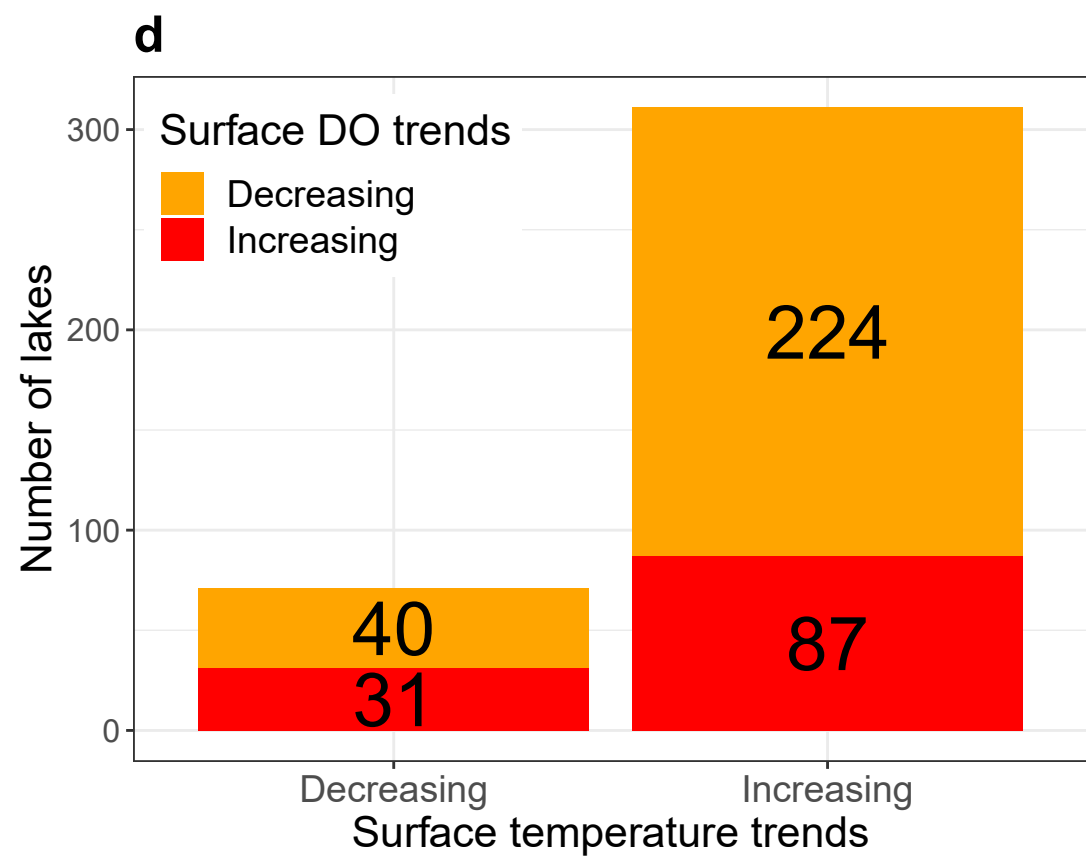
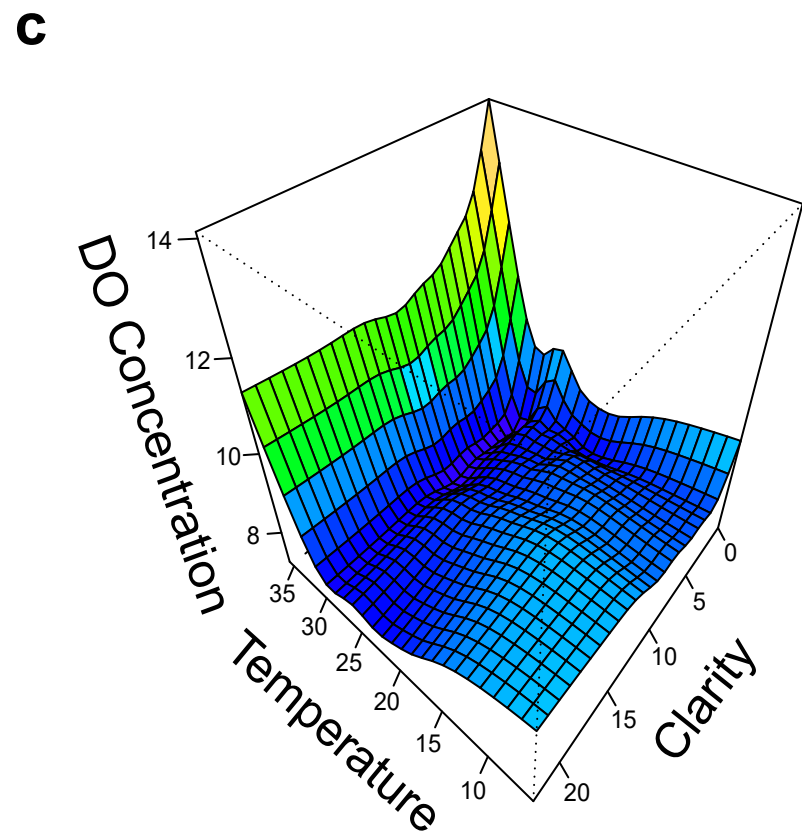
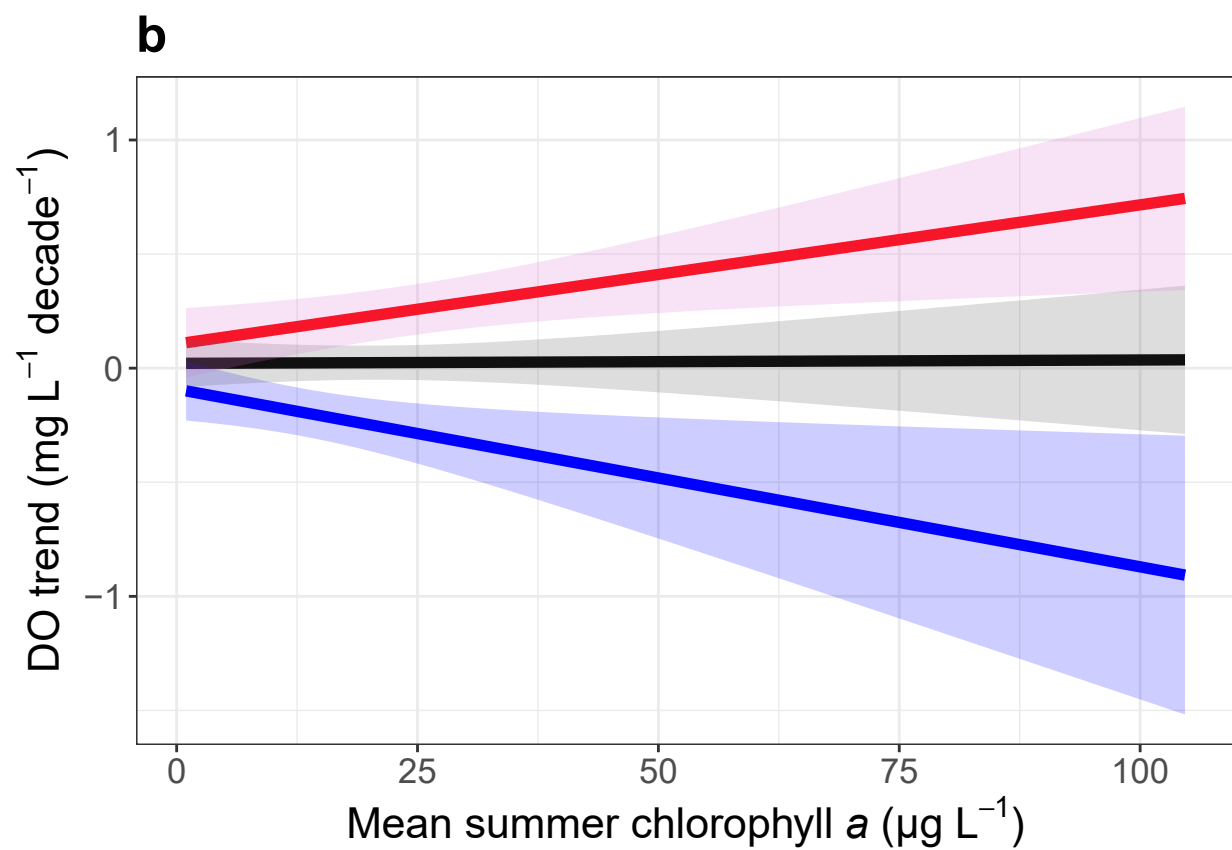
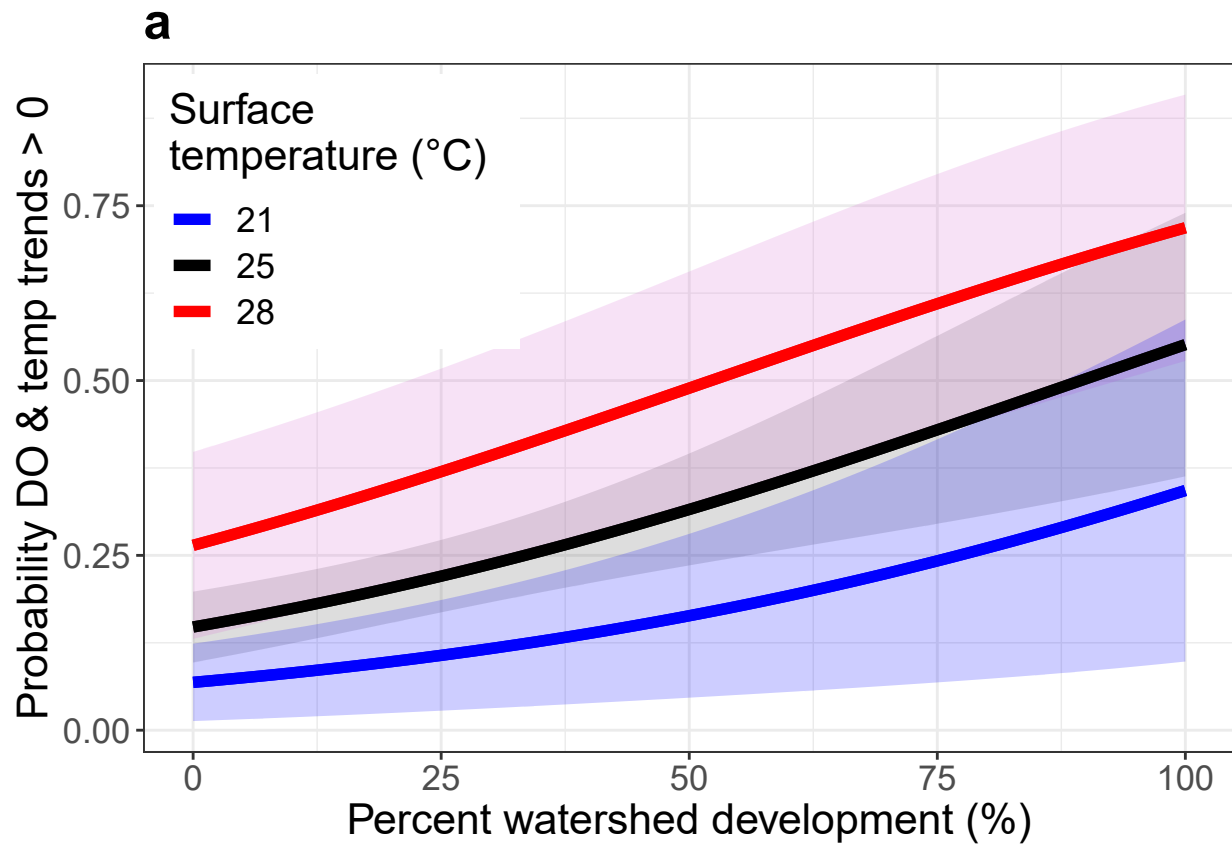
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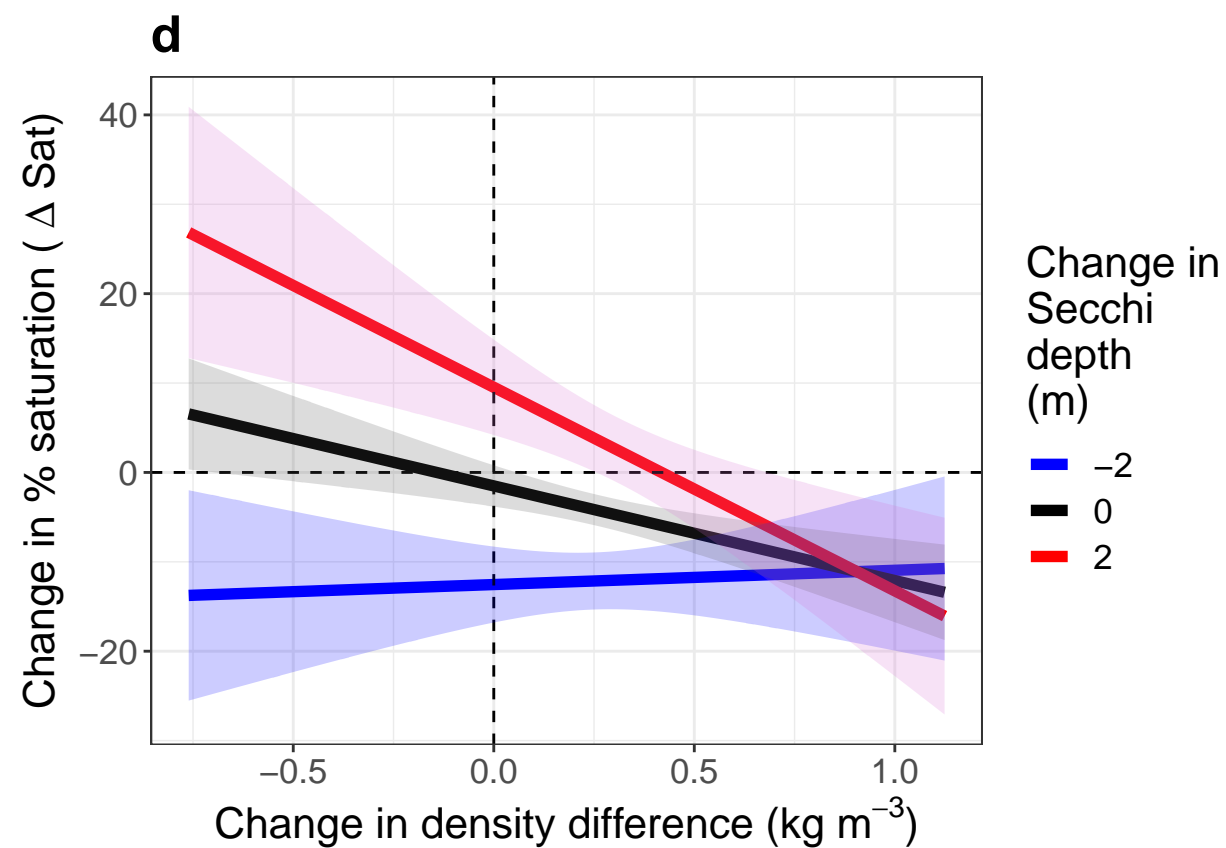
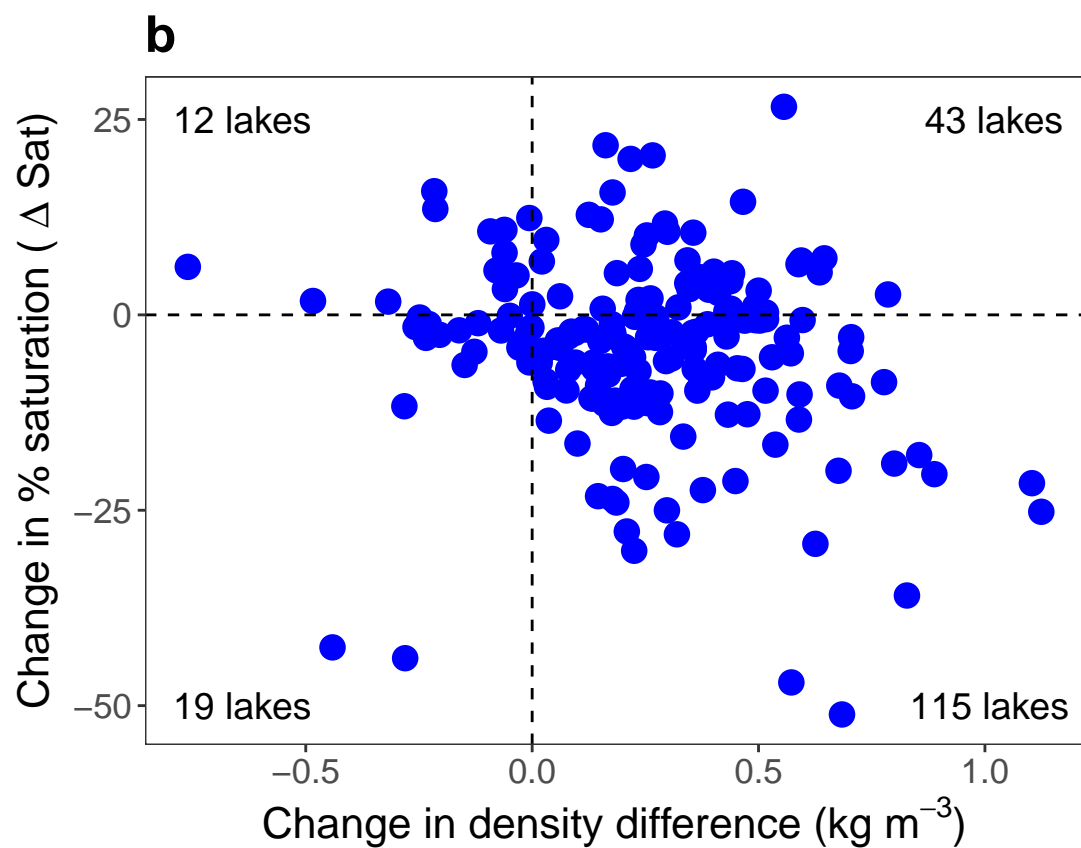
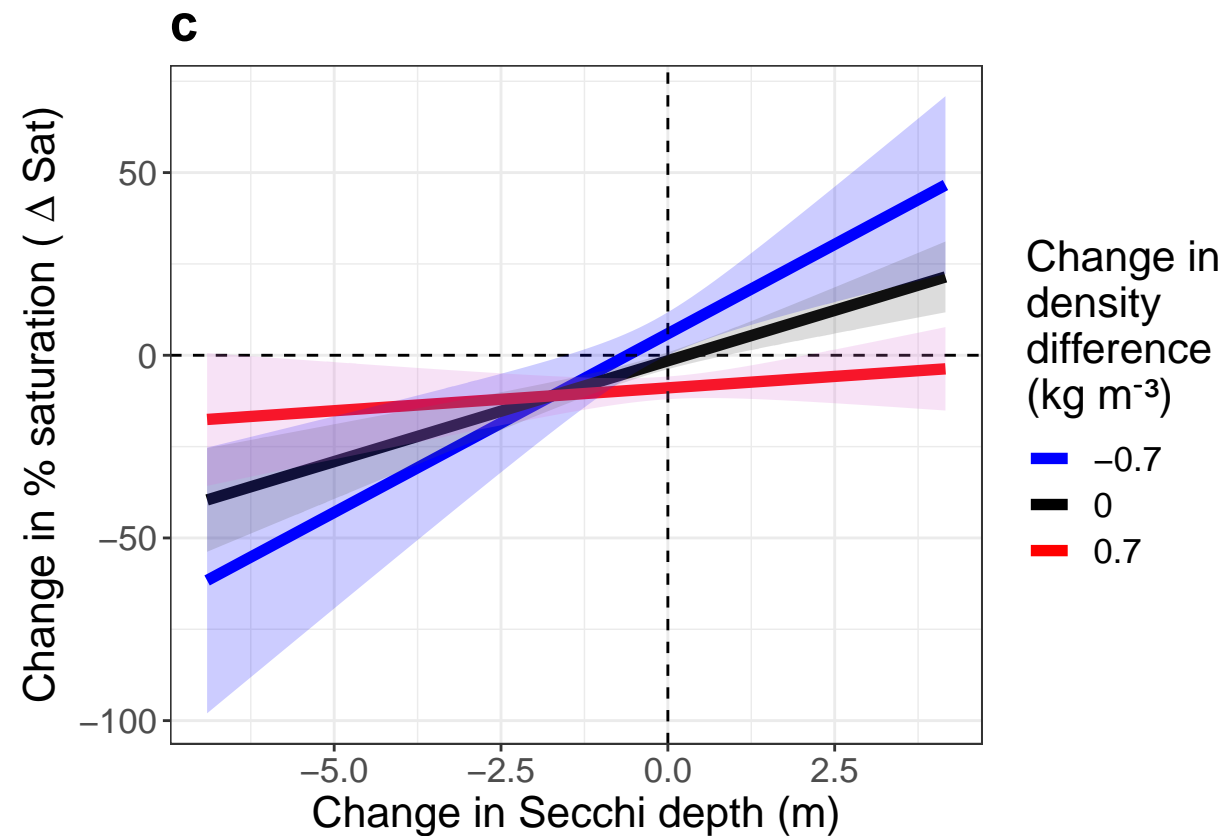
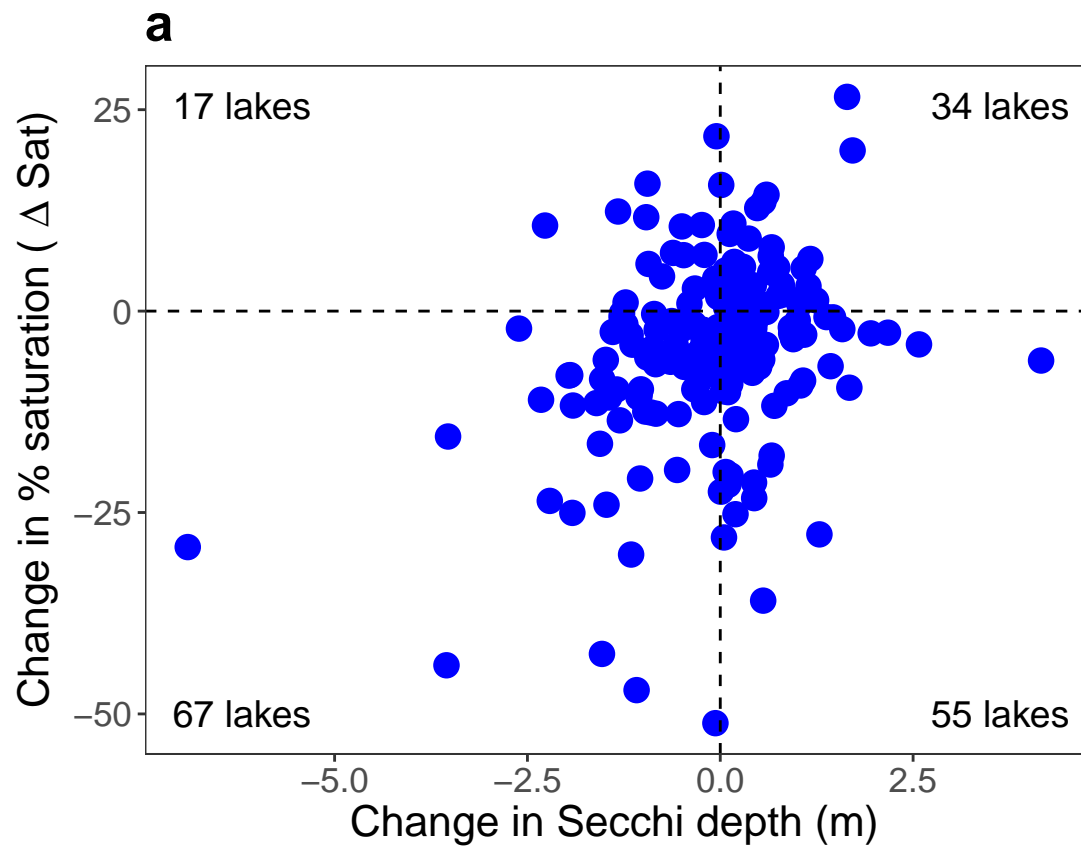
407 **Fig. 4 | Effect of changes in water clarity and density difference on deep-water DO**
408 **saturation change. a**, Change in % saturation versus change in water clarity (Secchi depth). **b**,
409 Change in % saturation versus change in water column density difference between surface and
410 deep waters. The number of lakes in each quadrant in **a** and **b** are indicated by text. **c**, Predictions
411 of change in % saturation from a fitted multiple regression model for change in water clarity at
412 three density changes. **d**, Predictions of change in % saturation from a fitted multiple regression
413 model for change in density difference at three clarity changes. Note that for both **c** and **d** the
414 origin sits at no change in either predictor.

415









416 **Supplemental information**

417 There are seven supplemental information tables and four supplemental information
418 figures. Tables S1 and S2 are referenced in text. Table S3 describes data contributors for this
419 project and Table S4 provides location and trend information for each lake. Trend data were not
420 reported for a) two lakes where providers did not provide permission to publish data but that
421 were included in trend analyses (Annecy and Geneva; ‘NP’ in table S4), b) lakes had less than 15
422 years of data at a given depth (not shown in table), or c) deep-water trends in lakes that did not
423 thermally stratify (‘NA’ in table S4). In one lake (T Bird), epilimnetic water was artificially
424 aerated and this depth layer was excluded from analysis. Table S5 presents statistics associated
425 with spatial autocorrelation analyses. Table S6 describes trends over the entire population of
426 lakes versus a sub-sample of lakes after accounting for the large numbers of samples obtained in
427 lake-rich regions. Table S7 describes trends and uncertainty in trends over two time periods for
428 subsets of lakes having data for at least 80% of years: 1980-2017 and 1990-2017. Fig. S1
429 presents the results of GAMM analysis of trends zoomed out to visualize distribution of residuals
430 for surface and deep-water temperature and dissolved oxygen trends. Fig. S2 presents the partial
431 dependency plots for the top predictors of changes in deep-water DO percent saturation as
432 determined by a random forest analysis. Fig. S3 presents partial dependency plots for the top
433 predictors of changes in water column density difference between surface and deep waters as
434 determined by a random forest analysis. Fig. S4 presents the locations of lakes used in this study
435 (n=393).

436

437 **Figure S1** | Results of GAMM analysis of trends zoomed out to visualize distribution of
438 residuals. **a**, Surface-water temperature (°C) **b**, Deep-water temperature (°C) **c**, Surface-water
439 DO (mg L⁻¹) and **d**, Deep-water DO concentration (mg L⁻¹).

440

441 **Figure S2** | **a-f**, Partial dependency plots from a random forest algorithm of deep-water change
442 in % dissolved oxygen saturation (Δ Sat) in the last five years of record relative to the first five
443 years of record for each lake. Plots are ordered by predictor variable importance, decreasing in
444 importance from the upper left to lower right (a to f). Vertical red lines indicate zero change in
445 predictor variable and hash marks on the x-axis indicate lake distribution deciles. Partial
446 dependencies indicate the relationship between predictor and response variables when holding
447 other variables at their mean value. Lakes that experienced no change in either water clarity or
448 density difference between surface and deep waters exhibited little change in deep-water
449 saturation (see also, Fig. 4).

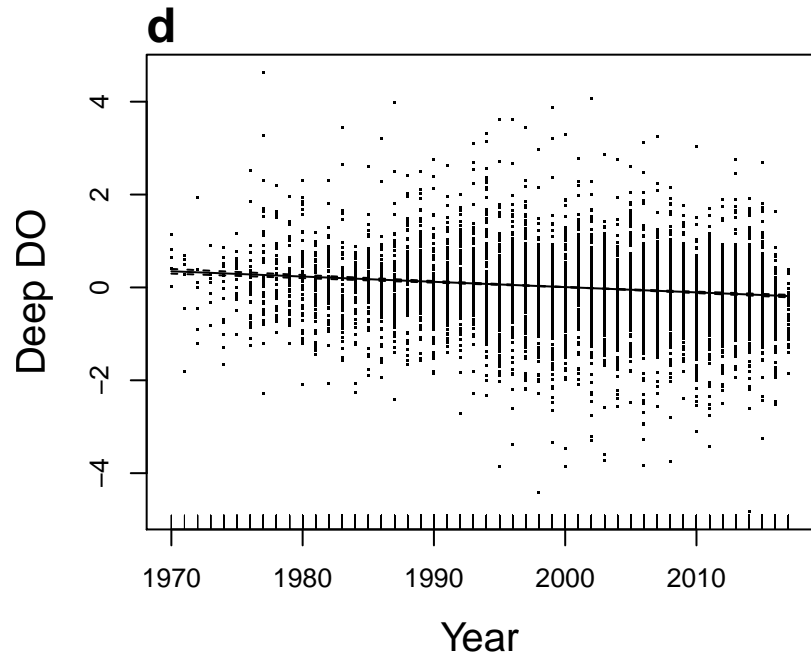
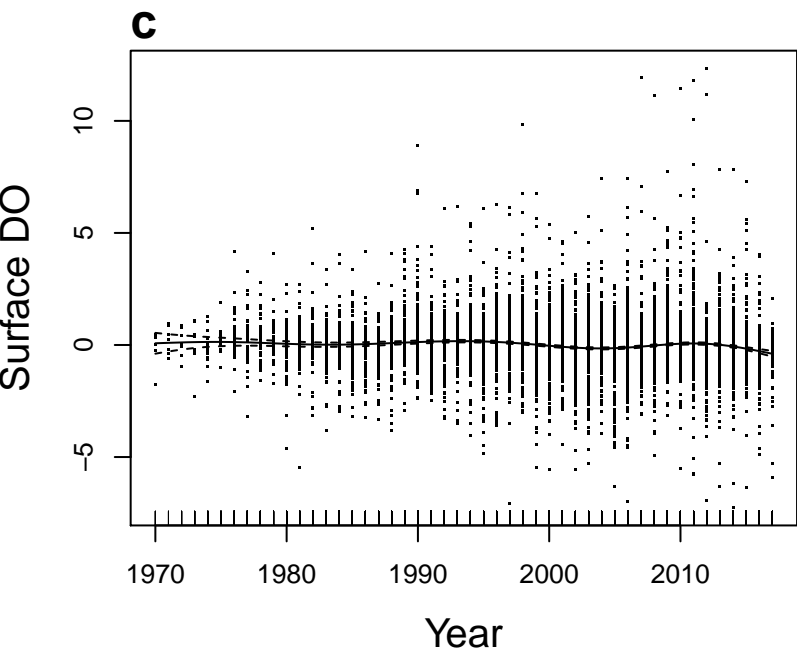
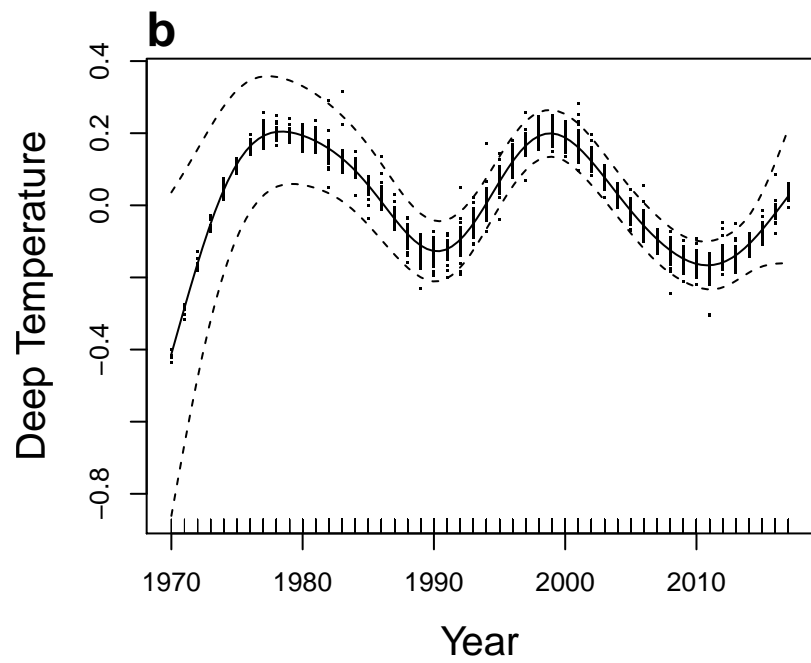
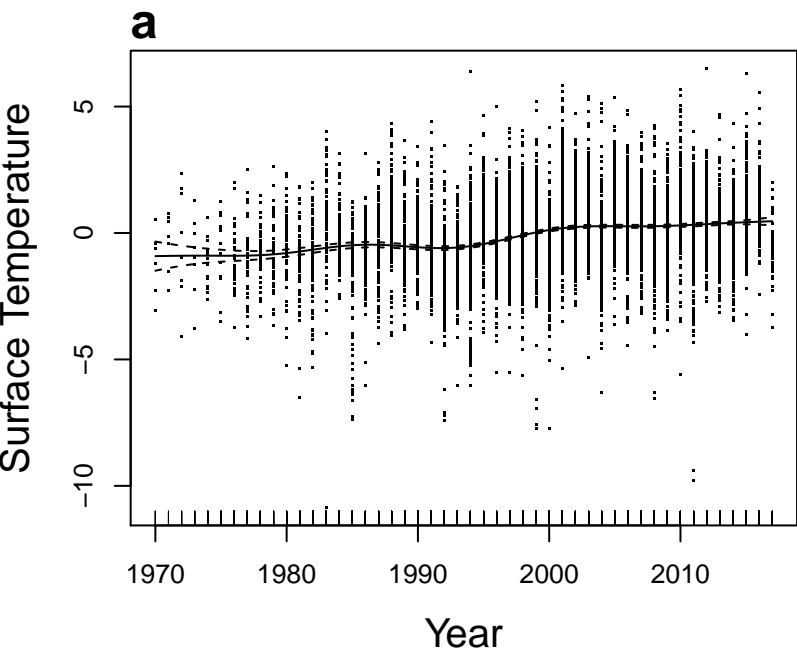
450

451 **Figure S3** | Drivers of the change in density difference between surface and deep waters. **a-f**,
452 Partial dependency plots from a random forest algorithm of deep-water change in water column
453 density difference in the last five years of record relative to the first five years of record for each
454 lake. Plots are ordered by predictor variable importance, decreasing in importance from the
455 upper left to lower right (a to f). Vertical red lines indicate zero values for predictor variable and
456 hash marks on the x-axis indicate lake distribution deciles. Partial dependencies indicate the
457 relationship between predictor and response variables when holding other variables at their mean
458 value.

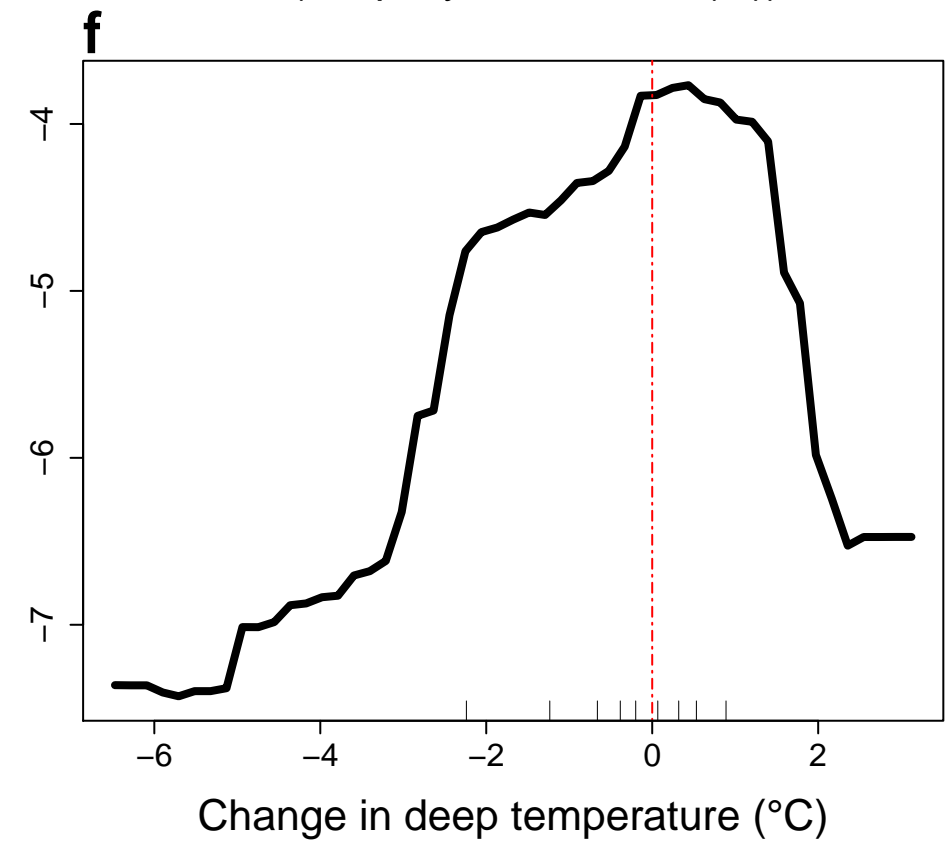
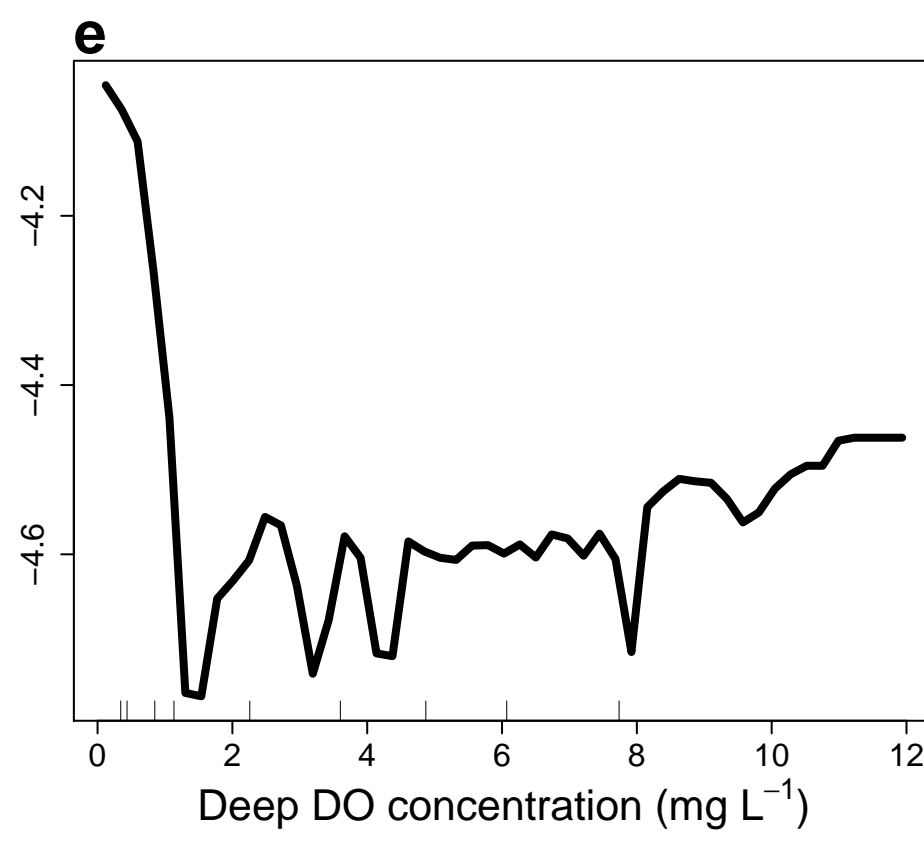
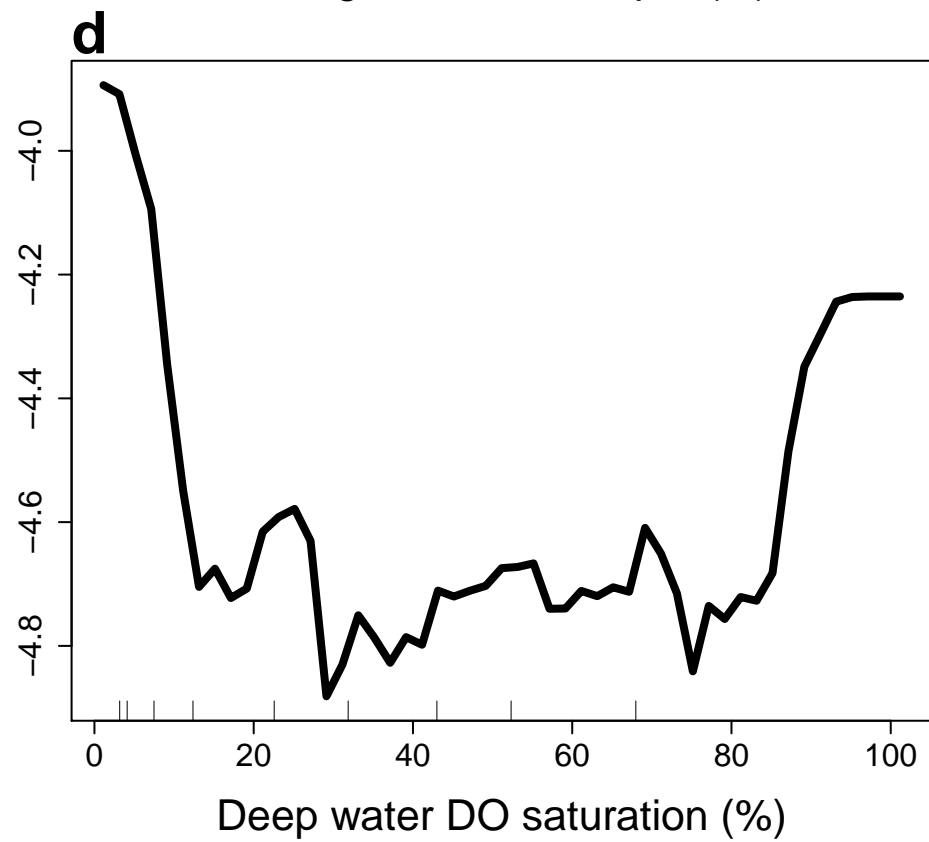
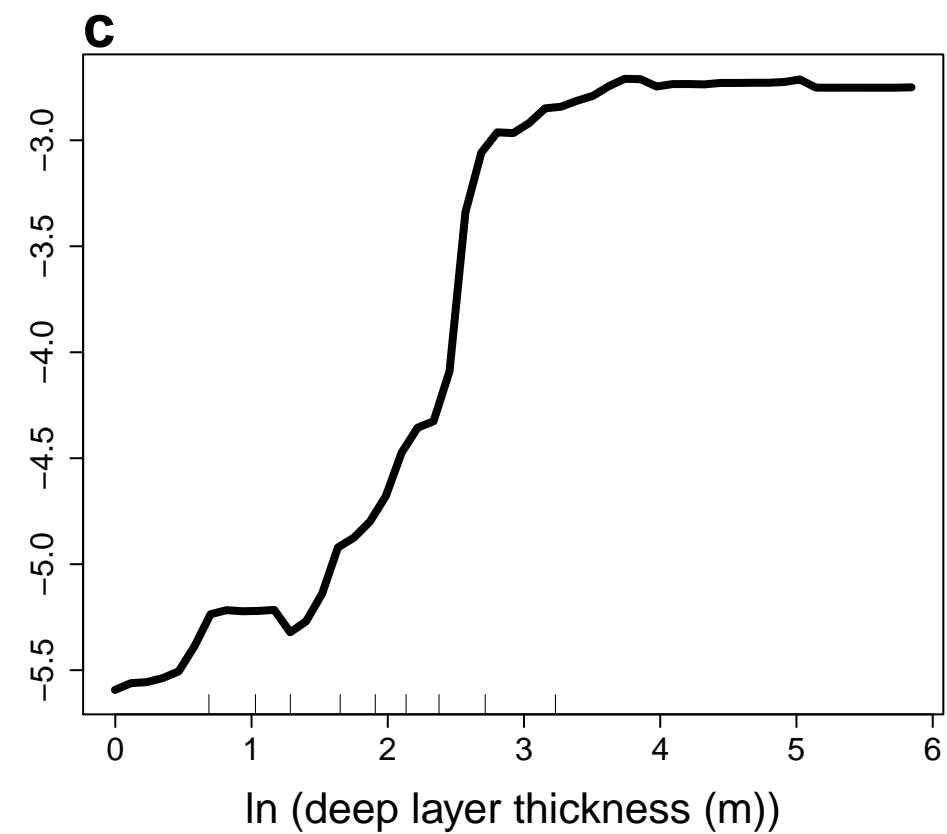
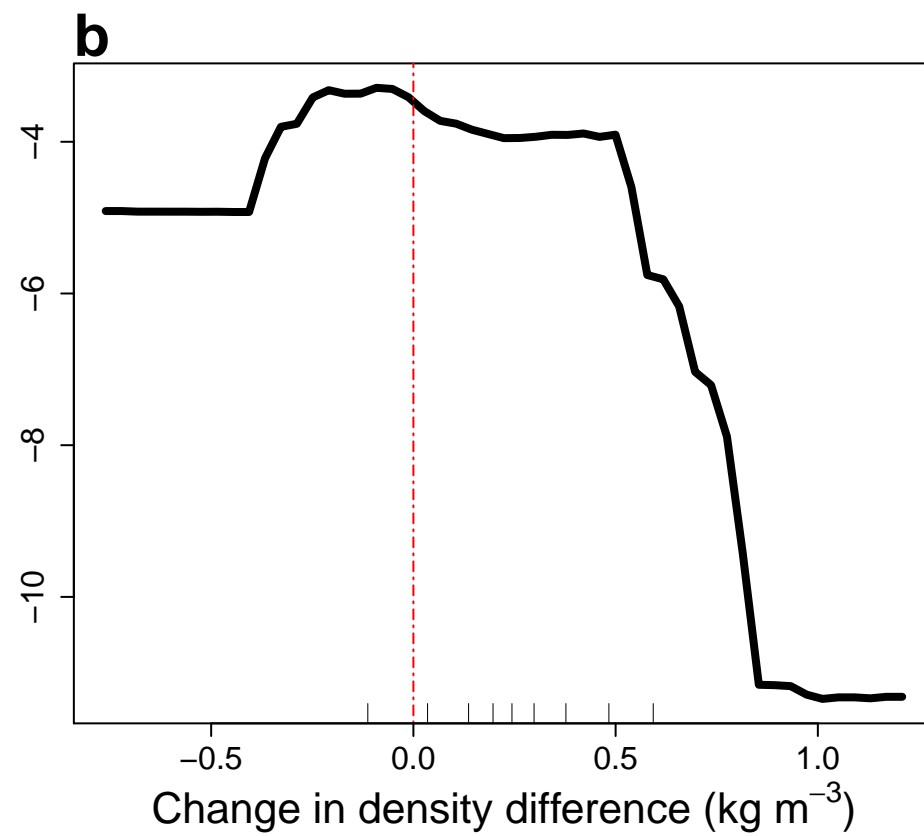
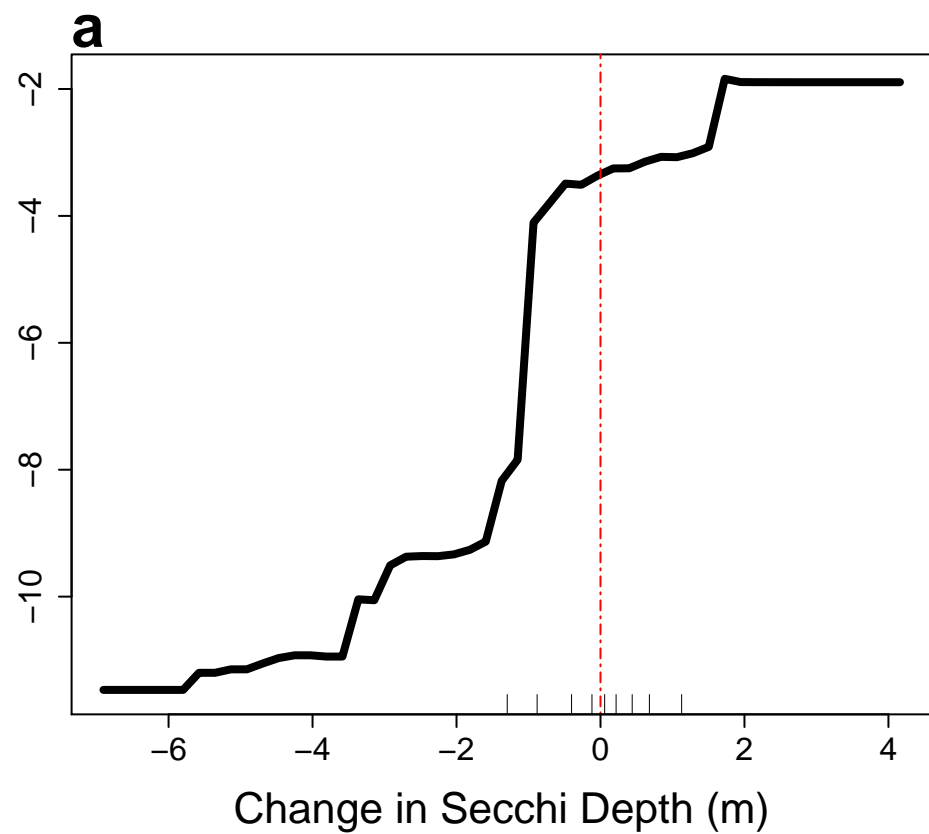
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460 **Fig. S4** | Locations of lakes used in this study (n=393).

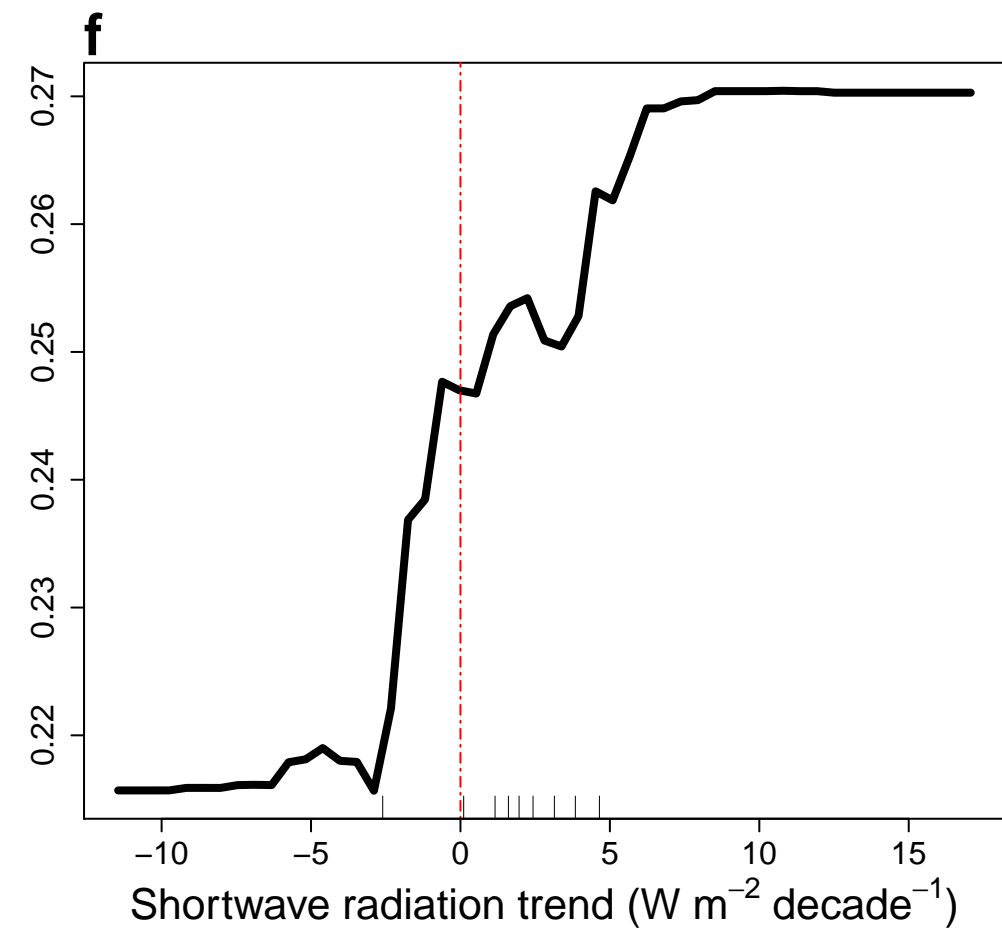
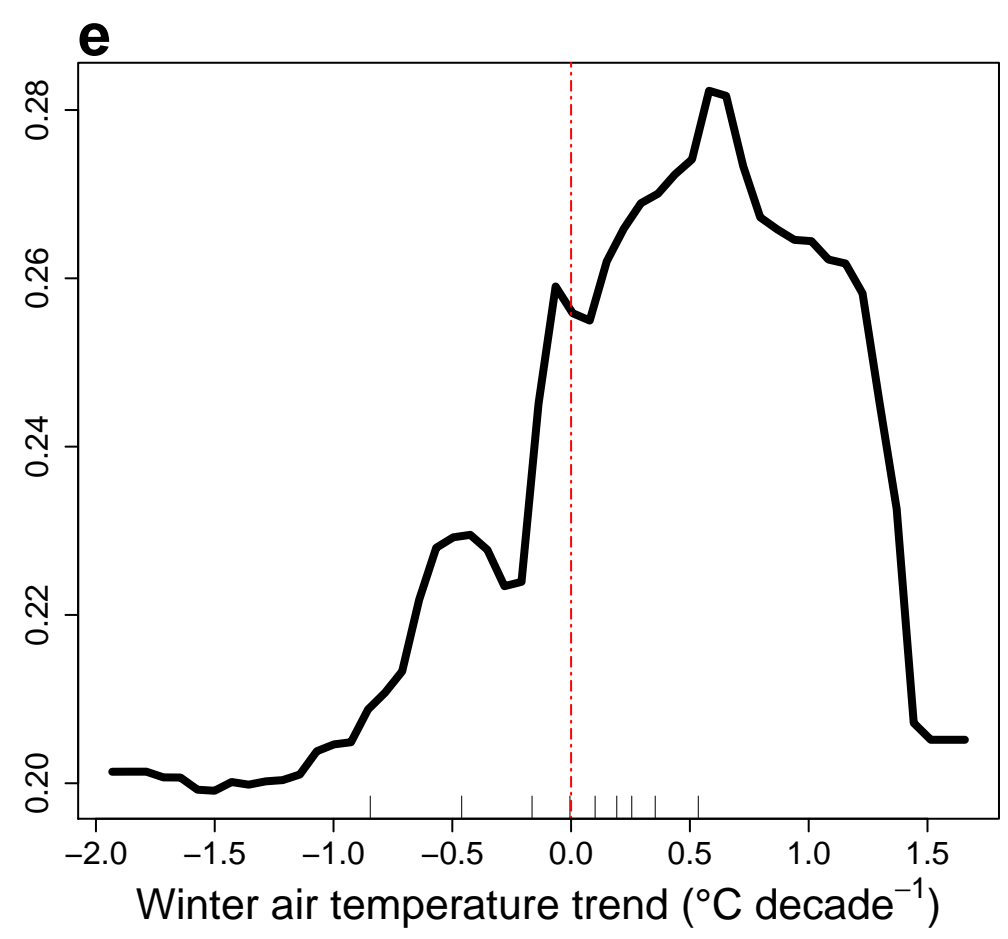
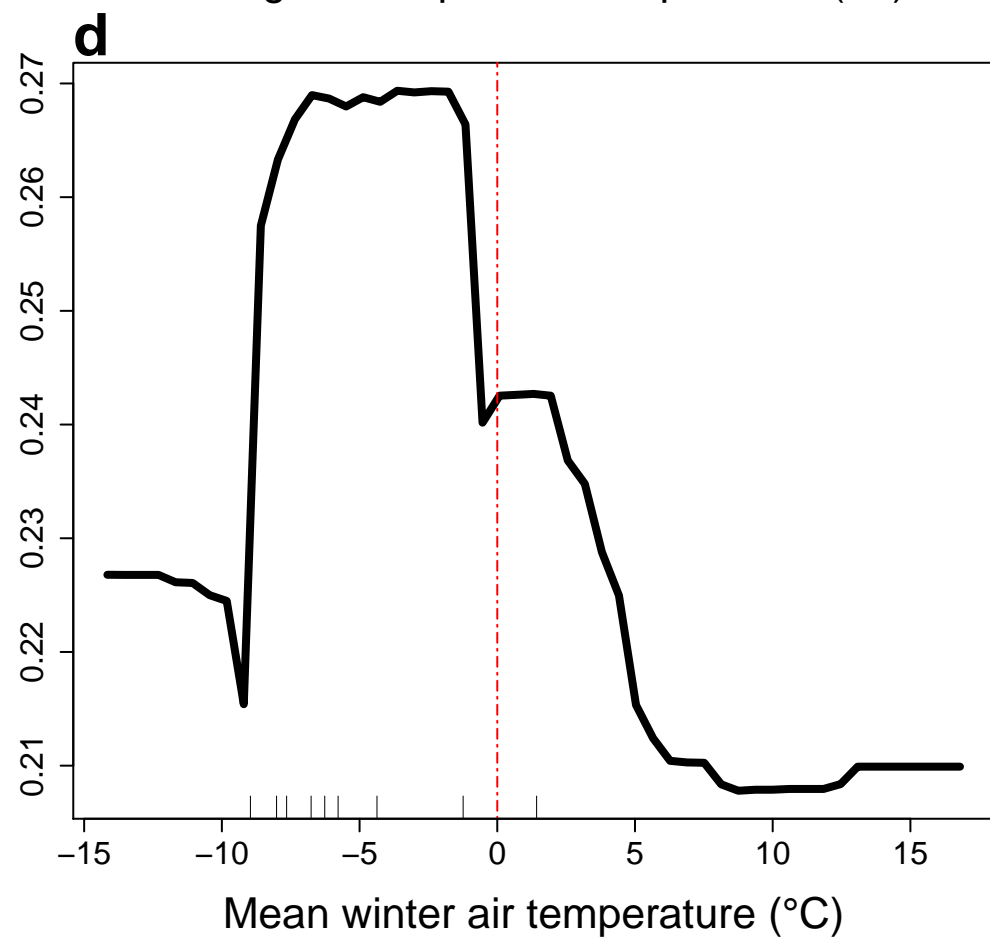
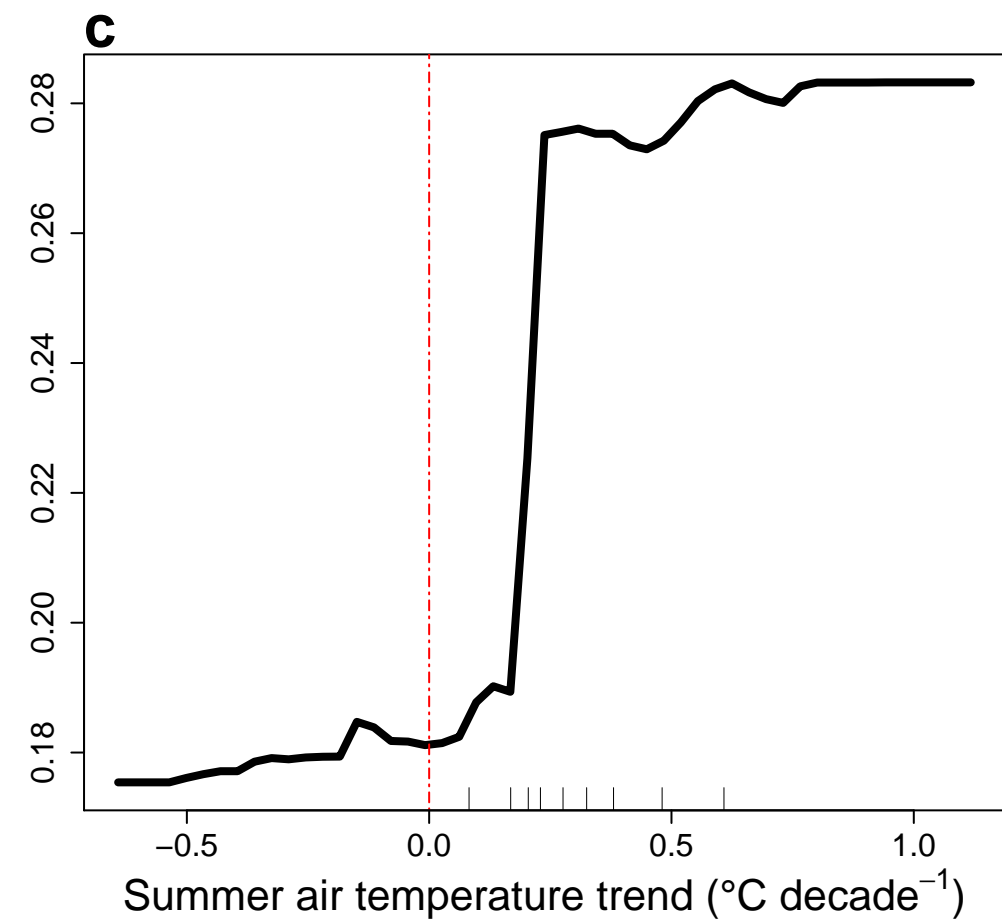
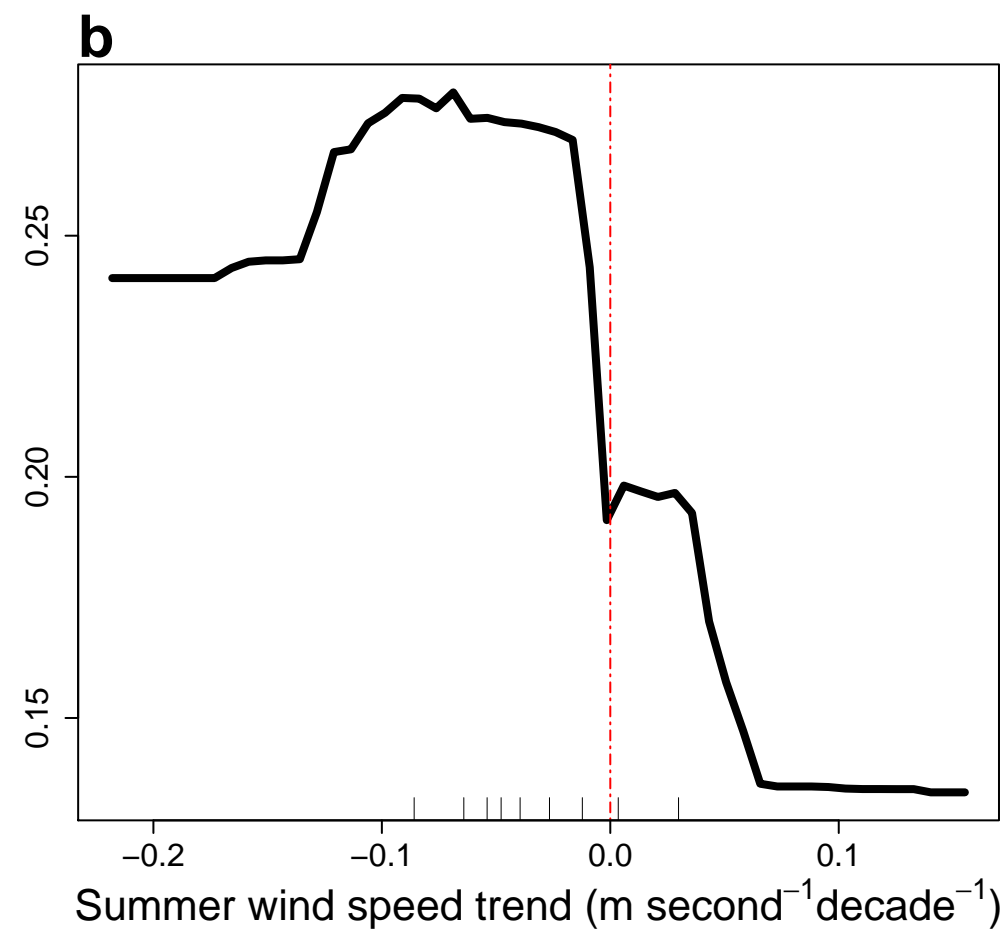
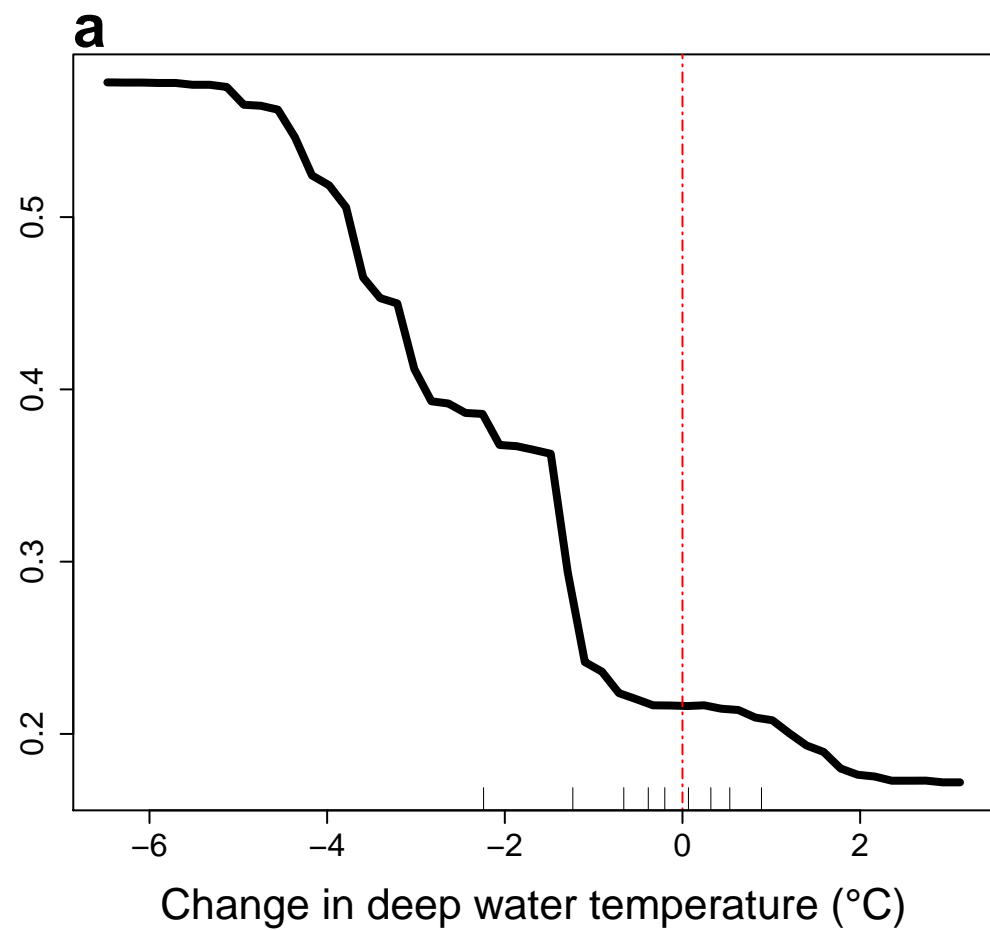
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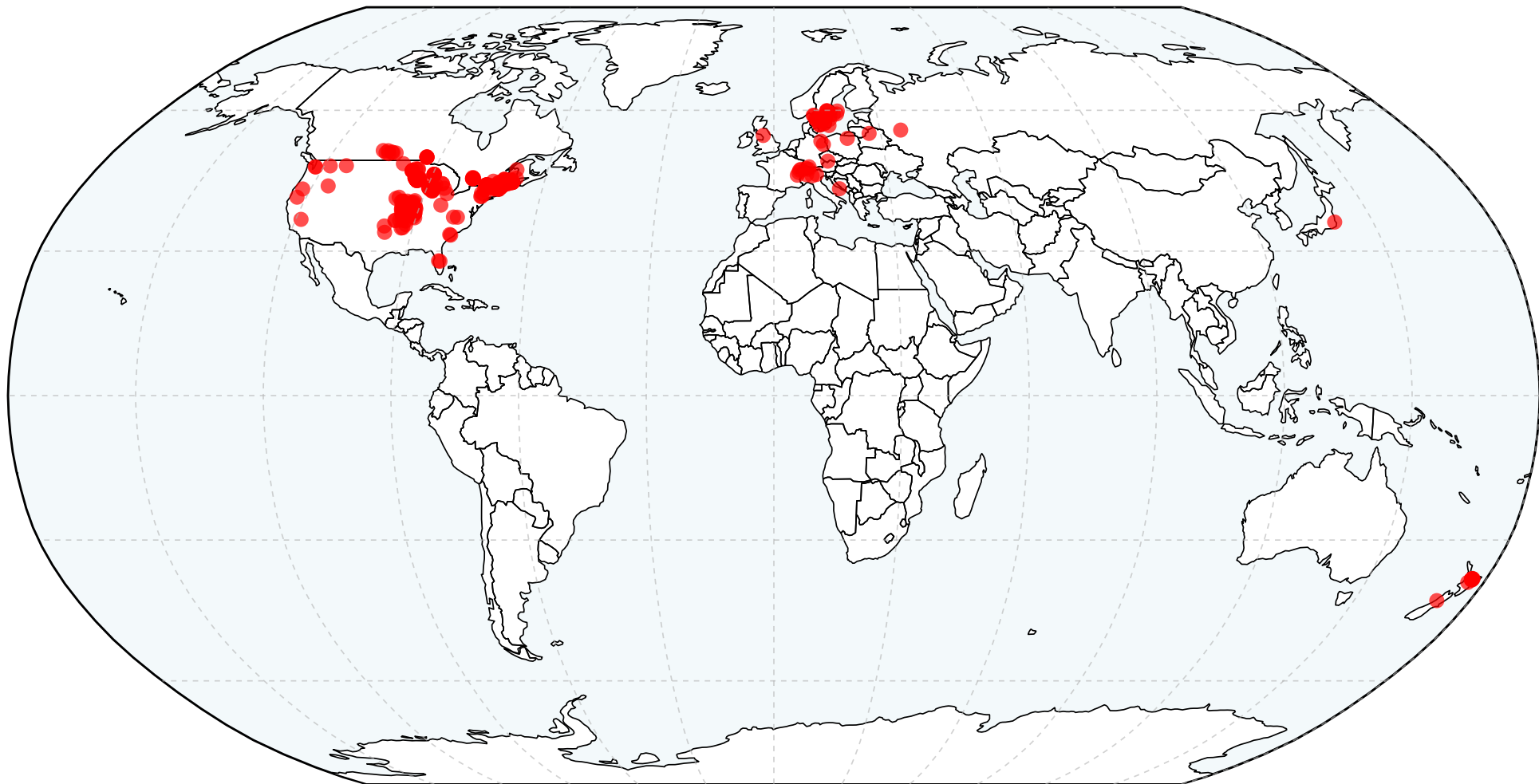


Change in percent saturation (Δ Sat)



Change in density difference (kg m^{-3})





462 **Methods:**

463 **Overview**

464 Our methods here describe how we 1) compiled and quality-checked data, 2) interpolated
465 and delineated water layer strata, and 3) statistically analyzed these data. Our statistical analyses
466 focused on characterizing long-term trends in climate characteristics (air temperature, wind
467 speed, precipitation, and short-wave radiation), DO concentration and saturation, water
468 temperature, and deep-water habitat quality; identifying and characterizing potential non-
469 linearity in DO concentration and water temperature through time; characterizing the relationship
470 between DO concentration changes and solubility, chlorophyll, and land use; identifying the
471 predictors of changes in deep-water DO saturation, and characterizing meteorological drivers of
472 surface temperature trends. These methods are described in detail in the sections below.

473 **Data compilation and quality control**

474 We compiled lake temperature and DO concentration water column measurements from a
475 wide range of government, university, and not-for-profit sources (Fig. S4 and Tables S3 and S4).
476 To assess long-term trends in temperature and DO concentration, we required profiles be made at
477 least once annually during the peak summertime stratification (defined as the late summer
478 period, July 15 - August 31 for northern hemisphere lakes and January 15 - February 28 for
479 southern hemisphere lakes) offshore (e.g., nearest the deepest location in each lake) for at least
480 15 years. In some larger lakes ($n = 6$ lakes), we used profiles from two separate locations if the
481 lake had more than one distinct basin and treated these as separate waterbodies. For some
482 analyses other than long-term trend analyses we included lake time series data less than 15 years
483 long, but always at least 10 years in duration (described below).

484 We conducted quality control on the compiled data as follows. We first removed
485 impossible values, defined as those outside the range 0-40 for both temperature (units: °C) and
486 DO concentration (units: mg L⁻¹). We then removed profiles from consideration if our initial
487 quality control step process removed greater than 95% of the profile or if the profile had less
488 than three distinct depth points. To reduce the potential impacts of DO measurements made
489 when sensors sat on or in sediments, we removed the deepest measurement for individual
490 profiles if the maximum depth for that profile exceeded the maximum depth of 90% of the
491 remaining profiles for a given lake.

492 Not all profiles surveyed the entire water column. Some lakes had some profiles where
493 the shallowest depth was greater than 0 (meaning near-surface measurements were not made),
494 yet temperature measurements showed the nearest surface measurements were within the
495 epilimnion. In these cases, we made the assumption of uniform DO and temperature from the
496 surface to the shallowest measurement and added a 0 m depth point. We did this by either 1)
497 changing the minimum depth in the profile to 0 if it was less than 0.5 m, 2) adding a 0 depth
498 point and assigning temperature and DO values equal to that of the minimum depth point if the
499 minimum depth point was greater than or equal to 0.5 m but less than or equal to 3 m. If the
500 minimum depth was greater than 3 m, we excluded the profile from analyses. If there were
501 multiple values of either temperature or DO for a given depth, the mean value at this depth was
502 used. These operations and all further analyses were conducted in R version 3.4.2²⁹.

503 In total, the above QA steps removed 2,040 profiles out of a total of 25,023 (8.2%). After
504 processing and removing eight non-temperate lakes, we had 22,574 DO profiles with
505 corresponding temperature profiles. There was a median of 2.1 profiles per year (range: 1-38)
506 and 23 years of data per lake (see also, Table S4).

507 **Profile interpolation and strata delineation**

508 In order to generate a dataset with consistent depth resolution within and among lakes,
509 we interpolated each temperature and DO profile from depth 0 m to the deepest depth of each
510 profile at intervals of 0.5 m using the pchip function of the R package pracma³⁰. This
511 interpolation procedure preserves the overall shape of the profile by preventing overshooting of
512 data values³⁰. Following interpolation, we calculated temperature and stability characteristics
513 using the R package rLakeAnalyzer³¹. We delineated the epilimnion and hypolimnion using the
514 meta.depths function (slope = 0.1, seasonal = FALSE), which calculates the top and bottom
515 depths of the metalimnion³¹. If the range of temperatures through the profile is less than 1°C, the
516 meta.depths function does not return values for the metalimnion (i.e., the profile is not
517 considered stratified).

518 Many lakes did not have a well-defined hypolimnion. To identify those with a
519 hypolimnion, we first removed lakes where the meta.depths function failed to calculate a bottom
520 metalimnion depth for more than 10% of profiles. We then calculated the mean of the maximum
521 profile depths across all profiles for each lake, to get a mean profile depth for the lake. If the
522 mean value of the bottom of the metalimnion for a lake was shallower than the calculated mean
523 profile depth for that lake, it was considered to have a hypolimnion. We defined “surface waters”
524 as all depths shallower than or equal to the top metalimnetic depth and “deep waters” as all
525 depths deeper than the bottom depth of the metalimnion.

526 **Characterizing trends in dissolved oxygen and temperature**

527 We calculated the mean surface- or deep-water temperature and DO concentration and
528 percent saturation. For each lake, we calculated the mean of surface- or deep-water DO

529 concentration or temperature for all profiles in a given year (in our defined late-summer period)
530 to obtain a mean annual value. We then calculated the percent DO saturation from temperature,
531 DO concentration, and lake elevation data³². Mean annual surface- and deep-water temperature
532 and DO concentration measurements were then used to calculate long-term trends for surface
533 waters (n = 393 lakes; median number of years per lake: 24) and deep waters (n = 260; median
534 number of years: 24). All trends were calculated using the nonparametric Sen's slope in the R
535 package `openair`³³. For trend analysis, we only used lakes with at least 15 years of data.

536 For deep-water trends, lakes that were essentially anoxic (average hypolimnetic DO < 0.5
537 mg L⁻¹) had trend magnitudes that clustered near 0 relative to other lakes. This was not
538 unexpected as lakes with essentially no hypolimnetic DO have little potential to lose additional
539 DO. When calculating median trends and for graphical depiction of trends (Fig. 1), we removed
540 these lakes (n = 69; difference = 191).

541 We conducted several analyses to examine the potential of variability in lake data
542 through time (i.e., not all lakes sampled all years of observation) or variability in space (i.e.,
543 some regions sampled much more heavily than others) to influence overall population level
544 trends (see following sections and Tables S5-S6).

545 **Spatial autocorrelation and effects of lake clusters**

546 Because the lakes included in this study were not uniformly dispersed over all continental
547 land masses, we examined the potential of large numbers of lakes in relatively concentrated
548 regions to drive overall patterns. To do this, we first examined spatial autocorrelation in trends in
549 lake temperature and dissolved oxygen concentration using Moran's I in the R package `lctools`³⁴.
550 ³⁵. This statistic ranges from -1 for data that are perfectly dispersed to +1 for data that are

551 perfectly autocorrelated. Values near zero suggest randomly distributed data. We observed weak
552 but significant spatial autocorrelation in some variables (Table S5; Moran's I values ranging 0.02
553 to 0.27).

554 Following this analysis, we examined the potential for the large numbers of lakes in some
555 regions to dominate overall trends we reported. We tested for potential bias by examining trends
556 for a subset of lakes. We identified four regions in the US with high numbers of lakes (Maine =
557 113 lakes, New Hampshire = 38 lakes, Missouri = 41 lakes, and Minnesota = 84 lakes). For each
558 of these clustered regions, we randomly subsampled 10% of the lakes. After this random
559 subsetting, we found that the overall trends are similar to the trends obtained from all lakes (see
560 Table S6). These results demonstrate that our observed population-level trends are not driven
561 solely by trends observed in our lake-rich regions. While our analysis focuses on temperate
562 lakes, we obtained data from a small number of non-temperate lakes (n=8). Including these non-
563 temperate lakes in our analysis (Table S6) did not change our overall results.

564 **Uncertainty estimates and temporal variation in trends**

565 We conducted an analysis to compare trends, confidence intervals, and significance of
566 trends over two time periods: 1980-2017 (n = 80) and 1990-2017 (n = 197) to assess whether
567 different lake observation years influenced the overall trends in DO concentration and
568 temperature we observed. For each time period, we used a subset of lakes that had data for at
569 least 80% of years within the defined time period. Following established methods¹⁸, we
570 calculated a yearly anomaly in temperature and dissolved oxygen for each lake as the difference
571 between each year's observation and the long-term mean. We then averaged these anomalies
572 across all lakes and used linear regression to calculate the slope, significance, and confidence
573 intervals of these averaged anomalies (Table S7).

574 **Characterizing trends in climate characteristics**

575 We examined trends in air temperature, total precipitation, wind speed, and shortwave
576 radiation using the ERA-5 reanalysis from the European Centre for Medium-Range Weather
577 Forecasts (ECMWF)³⁶. This data set provides a single gridded global product with a resolution
578 of 0.25° latitude by 0.25° longitude over the period 1979-2019 available as monthly averages (air
579 temperature, wind speed, and shortwave radiation) or totals (precipitation). We used ECMWF
580 time-series data from the gridded location closest to each lake and over the two-month period
581 around when lakes were sampled (July-August for Northern hemisphere lakes, January-February
582 for Southern hemisphere lakes). We calculated temporal trends in mean summer air temperature,
583 mean summer wind speed, summer total precipitation, mean summer shortwave radiation, mean
584 winter air temperature, mean spring air temperature, mean fall air temperature using the same
585 methods we used to examine lake temperature and DO trends (see above). We then conducted a
586 multiple regression analysis to assess which of these predictor variables (trends in air
587 temperature, total precipitation, wind speed, or shortwave radiation) best explained surface-water
588 temperature trends.

589 **Trends in climatic variables over the temperate zone**

590 We delineated gridded latitude and longitudes at 2° intervals across the entire temperate
591 zone over land masses only as well as over large regions, including Asia (defined by longitude \geq
592 29.3°; latitude 23.5° to 60°) Europe and North America (longitude $<$ 29.3°; latitude 23.5° to 60°),
593 South America and western Africa (longitude $<$ 0°; latitude \leq -23.5° to -60°); and southern
594 Africa, Australia, and Oceania (longitude \geq 0°; latitude -23.5° to -60°). We then used data from
595 the ERA-5 reanalysis (see ‘Characterizing trends in climate characteristics’ in Methods for
596 details) to calculate trends in climate variables over each of these regions (Table S1).

597 **Multiple regression analysis of drivers of surface water temperature trends**

598 We conducted a multiple regression analysis of the meteorological drivers of observed
599 surface water temperature trends. Predictors in the analysis included: summer air temperature
600 trend, summer total precipitation trend, summer wind speed trend, summer shortwave radiation
601 trend, winter air temperature trend, spring air temperature trend, fall air temperature trend, and
602 mean winter temperature (as a proxy for ice cover¹⁸). We z-score standardized all variables to
603 facilitate comparison of model coefficients across variables having different units³⁷. We verified
604 that multicollinearity was not a problem by checking that the variance inflation factor was well
605 below ten for all variables³⁸. We used the leaps R package to select subset models including all
606 predictors and two-way interactions, and selected the fitted model having the lowest AIC³⁹.
607 Coefficients and p-values for the selected model appear in Table S2.

608 **Characterizing trends in deep-water habitat quality**

609 We used $T_{\text{DO3}}^{\text{11}}$ to quantify trends in oxythermal habitat relevant for cold-water
610 organisms. T_{DO3} represents the minimum temperature in the water column where DO
611 concentration was greater than or equal to 3 mg L⁻¹ and has been used to describe habitat
612 availability for cold-water fisheries¹¹. To calculate trends in T_{DO3} we excluded lakes where the
613 DO concentration was higher than 3 mg L⁻¹ across all depths in all profiles. For the remaining
614 lakes, we calculated T_{DO3} for each profile. If a given profile did not have DO below 3 mg L⁻¹, we
615 assigned it the minimum temperature in the profile. We then calculated an annual mean T_{DO3} for
616 the late summer period and excluded lakes that had ≤ 15 years of data. This left 369 lakes where
617 DO went below 3 mg L⁻¹ at least once.

618 **Non-linearity in DO and temperature through time**

619 We conducted a generalized additive mixed model (GAMM) analysis to characterize
620 overall response of lake temperature and DO concentration through time and to identify any non-
621 linearity. GAMMs fit a smooth function of the predictor variables showing the relationship of the
622 predictors to the response variable⁴⁰. We conducted separate analyses for four response variables,
623 surface-water temperature, surface-water DO concentration, deep-water temperature, and deep-
624 water DO concentration. For each GAMM, our only predictor variable was the year, resulting in
625 models that show the change in the response variable through time. We used the gamm4 function
626 of the gamm4 package to fit these models using the default thin plate spline for smooth terms⁴¹.
627 Gamm4 uses penalized regression splines of moderate rank for the smooth function. For two of
628 these models we used a normal error distribution. Because residuals for the deep-water
629 temperature analysis were skewed, we used a gamma distribution. Residuals in the deep-water
630 DO analysis were also skewed, but because there were a large number of 0 values we used a
631 Tweedie distribution instead of a gamma distribution. We limited this analysis to data from 1970
632 and later and included all lakes with data in the specified time period (total lake n = 419). To
633 account for the non-independent nature of the repeated measurements through time within each
634 individual lake, the slope and intercept were allowed to vary randomly by lake⁴².

635 We next conducted a GAMM to understand how surface water DO concentration
636 responded to temperature and productivity (n = 419 lakes). We used Secchi disk depth as a
637 surrogate for productivity¹⁹. We included fixed effects of mean summer surface water
638 temperature, mean Secchi depth, and the interaction of these two terms in the model. We
639 included a random intercept and slope by year within each lake and included a corresponding
640 year fixed effect.

641 **Relationship between dissolved oxygen concentration changes and solubility**

642 To determine the relative importance of solubility in explaining changes in DO
643 concentration, we calculated the expected change in DO concentration due to solubility alone
644 and compared this amount to the observed DO change. To do this, we first calculated the
645 difference between the observed mean DO concentration across the last five years and the first
646 five years of record for each lake, requiring a minimum of ten years of data per lake (n = 415
647 lakes for surface (Fig. 2a); n = 259 lakes for deep (Fig 2b)). We then calculated the expected
648 change due solely to solubility and compared observed to expected DO changes. Specifically, we
649 calculated the mean percent saturation in the first five years by first calculating the mean DO
650 saturation for each water column layer (surface or deep waters) and then calculated the mean of
651 all of these values. We then used an analogous approach to calculate mean temperature, DO
652 concentration, and mean DO concentration at 100% saturation in the last five years of record for
653 each lake. Once we calculated these values, we multiplied the mean DO concentration at 100%
654 saturation by the decimal value of percent saturation in the first five years of record. This product
655 represents the expected DO concentration if the percent saturation in the last five years of record
656 remained the same as it was in the first five years of record. In other words, we removed the
657 effect of temperature so that if all changes were due solely to solubility, observed changes in DO
658 concentration would be identical to this value.

659 **Relationship between dissolved oxygen trends and chlorophyll**

660 We used multiple regression to test if chlorophyll concentration and surface-water
661 temperature were predictors of lakes having both increasing surface DO concentration and
662 temperature trends. We first calculated the long-term mean late-summer surface-water
663 (epilimnetic) chlorophyll concentration, which was available for 162 lakes having at least ten
664 years of chlorophyll measurements. We next predicted DO concentration trends using

665 chlorophyll and mean surface-water temperature as independent variables. We first fit the linear
666 regression models, starting with a full model that included the interaction of chlorophyll and
667 temperature. We then fit all subset models and selected the model with the lowest AIC value⁴³.
668 Using this selected model, we predicted DO concentration trends at three different mean
669 epilimnetic temperatures (21, 25, and 28°C) across the observed values for chlorophyll.

670 **Relationship between dissolved oxygen trends and land use**

671 We used logistic regression to better understand the drivers of increasing DO
672 concentration in lakes with increasing surface-water temperatures, using land use/land cover data
673 to model the probability of this phenomenon⁴⁴. Logistic regression predicts the probability of a
674 binary response outcome for different values of predictor variables. Predictors in our logistic
675 regression included the percent of agriculture and developed land cover in the watershed and the
676 mean surface-water temperature over the last ten years of record because these land use
677 characteristics have been associated with increased growth of some phytoplankton taxa in
678 warmer lakes^{5,21}. Our binary response was: either a lake had both increasing surface temperature
679 and DO concentration (1) or it did not (0). We tested for all two-way interactions and all main
680 effects. We used the National Land Cover Database 2011 to derive land cover metrics for US
681 lakes⁴⁵. We considered any land falling into any of the developed classes as developed
682 (Developed – Open Space, Developed – Low Intensity, Developed – Medium Intensity,
683 Developed – High Intensity). We tested the goodness of fit of the final model using the Hosmer-
684 Lemeshow test, available in the ResourceSelection R package (function `hoslem.test`)⁴⁶. This test
685 showed an acceptable goodness of fit ($P = 0.166$). The final number of lakes for analysis that had
686 both land cover data and sufficient data to calculate trends was 326.

687 **Identifying the predictors of changes in deep-water DO saturation**

688 We first used a random forest algorithm to obtain predictors of the observed change in
689 percent saturation (i.e., drivers beyond pure solubility effects) in deep waters⁴⁷. We used the
690 percent increase in mean squared error as a measure of predictor variable importance. We
691 conducted the random forest algorithm analysis using the randomForest package⁴⁸. For each
692 analysis, we only used lakes that had no missing values for any of the predictor variables (n =
693 224 lakes).

694 For the random forest algorithm, the response variable was the change in mean DO
695 percent saturation in the last five years of record relative to the first five years of record for each
696 lake (Δ Sat). A positive Δ Sat indicated an increase in percent saturation while a negative Δ Sat
697 indicated a decrease in percent saturation. Predictor variables included mean hypolimnetic DO
698 percent saturation, DO concentration, temperature, and thickness of the hypolimnion (ln
699 transformed), mean Secchi depth, ln of mean lake depth, log10 of residence time, change in
700 hypolimnetic thickness, change in hypolimnetic temperature, change in Secchi depth, and change
701 in the density difference between surface and deep waters. Mean lake depth and residence time
702 were obtained from the HydroLakes Database⁴⁹. We calculated the density difference across the
703 water column using rLakeAnalyzer to calculate densities for each interpolated depth point in
704 each water column profile³¹. If a given profile was stratified, we then used the mean epilimnetic
705 density and the mean hypolimnetic density and calculated the difference between these densities.
706 If a given profile was not stratified, we took the mean density across the top two meters and the
707 mean density across the bottom two meters and calculated the difference between these densities.
708 We also included trends in the following ERA-5 meteorological variables: summer, fall, and
709 winter air temperature, summer shortwave radiation, and summer wind speed. Finally we
710 included mean winter air temperature as a proxy for ice cover¹⁸.

711 Following the above analysis, change in the density difference between surface and deep
712 waters came out as an important predictor. Although this could be explained by increased surface
713 water temperatures driven by meteorological variables, it is possible that other changes, such as
714 water clarity²⁵, could also explain changes in density difference. To disentangle the drivers of
715 changes in water column density differences, we conducted another RF using the same predictor
716 variables as the above analysis but changing the response variable to the change in the density
717 difference. We did not include the response variable from the first analysis (Δ Sat). The six most
718 important variables are presented in Fig. S3.

719 Based on results of the RF analysis, we conducted a multiple regression analysis to
720 predict change in percent saturation (Δ Sat) for different levels of predictor variables (ln of mean
721 lake depth, change in the density difference across the water column, and change in Secchi
722 depth). We used a subset of lakes where mean deep-water DO concentration exceeded 0.5 mg/L
723 to avoid lakes with little potential to lose DO. Predictor variables were selected because they
724 were the three most important variables identified by RF, except we substituted ln mean lake
725 depth for ln deep layer thickness. This substitution was made because models using ln of deep
726 layer thickness demonstrated substantial non-linearity in plots of residuals against fitted values.
727 Models built with ln mean lake depth greatly improved these patterns and these two variables
728 were correlated ($r = 0.51$). We first fit the multiple regression models starting with a full model
729 that included all predictors and two-way interaction terms. We then fit all subset models and
730 selected the model with the lowest AIC value⁴³. Using this selected model, we predicted Δ Sat at
731 three different values of each of the two predictors change in Secchi depth ($P < 0.001$) and
732 change in water column density difference ($P < 0.001$), with ln mean lake depth held at the
733 median value.

734

735 **Data Availability:**

736 Many of the datasets analyzed during this study are publicly available on-line and associated
737 links can be found in supplementary Table S3. Derived statistics are publicly available via the
738 Environmental Data Initiative (EDI) repository at
739 <https://doi.org/10.6073/pasta/ac8b05bb0da19032b3df3efc21f83874>. Most lakes are included
740 here, but we note that due to the collaborative nature of this project and a wide range of data
741 provenance, it was not possible to include every lake in this repository. Data not otherwise
742 already publicly available are available upon request from the corresponding author pending
743 permission from the appropriate data provider.

744

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