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Increasing air temperature relative to water temperature makes the mixed layer shallower, reducing phytoplankton biomass in a stratified lake

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Abstract

1. The depth of the mixed layer is a major determinant of nutrient and light availability for phytoplankton in stratified waterbodies. Ongoing climate change influences surface waters through meteorological forcing, which modifies the physical structure of fresh waters including the mixed layer, but effects on phytoplankton biomass are poorly known.
2. To determine the responses of phytoplankton biomass to the depth of the mixed layer, light availability and associated meteorological forcing, we followed daily changes in weather and water column properties in a boreal lake over the first half of a summer stratification period.
3. Phytoplankton biomass increased with the deepening of the mixed layer associated with high wind speeds and low air temperature relative to the temperature of the mixed layer ($T_{air}–T_{mix} < 0$), whereas heatwave conditions—shallow mixed layer driven by high $T_{air}–T_{mix}$ value and low wind speed—reduced the biomass.
4. Improving light availability from low to moderate light conditions increased the phytoplankton biomass, while the highest light availability was associated with low phytoplankton biomass.
5. Our study demonstrates that the climatic impact-drivers wind speed and $T_{air}–T_{mix}$ are major drivers of mixed layer depth, which controlled phytoplankton biomass during the early summer stratification period. Our study suggests that increasing air temperature relative to water temperature and declining wind speeds have potential to lead to reduced phytoplankton biomass due to a shallower mixed layer during the first half of the stratification period in non-eutrophic lakes with sufficient light availability.

KEYWORDS
algal biomass, climate warming, heatwave, lake mixing, thermal stratification

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1 | INTRODUCTION

Phytoplankton are essential for primary production and secondary production in aquatic food webs (Field et al., 1998). In stratified water bodies, actively photosynthesising phytoplankton often reside in the surface mixed layer, which refers to a turbulently mixed and relatively homogenous layer above a diurnal thermocline (Imberger, 1985; MacIntyre, 1993; Monismith & MacIntyre, 2009; Figure 1). Climatic and weather conditions as well as lake morphometry and water transparency are the major controllers of the lake mixing regimes (Hutchinson & Löffler, 1956; Imberger, 1985; Kirillin & Shatwell, 2016). The depth of the mixed layer (Z_{mix}) is determined by the balance between the rate at which turbulence is produced due to wind action and convection, and the buoyancy created by surface heat flux towards the waterbody (Imberger, 1985; Imboden & Wuest, 1995; Spigel & Imberger, 1987).

The depth of the mixed layer affects light availability, nutrient supply, grazing pressure and sedimentation losses of phytoplankton (Diehl, 2002; Huisman et al., 1999; Winder & Sommer, 2012). The shallowing of Z_{mix} relative to the depth of the euphotic layer (Z_{eu})—the depth at which the photosynthetically active radiation (PAR) attenuates to 1% of the surface values (Wetzel, 2001)—enhances light conditions for phytoplankton in the mixed layer (Huisman et al., 1999). At the same time, the reservoir of nutrients in the mixed layer decreases and the sinking losses of phytoplankton out of the mixed layer increases (Berger et al., 2006; Ptacnik et al., 2003; Weithoff et al., 2000; Yang et al., 2016). In contrast, deepening of Z_{mix} reduces light availability for phytoplankton but leads to entrainment of colder, typically nutrient rich water into the mixed layer. Moreover, deepening of Z_{mix} dilutes phytoplankton and zooplankton densities and reduces their encounter rates, whereas a shallow mixed layer may allow effective grazing by zooplankton (Berger et al., 2006).

The physical structure of a water column depends on external meteorological forcing such as solar radiation, wind speed, and air temperature (T_{air}) acting on the surface of the water body (Imberger & Parker, 1985; Macintyre et al., 1999; Persson & Jones, 2008). After the onset of spring turnover in lakes, an increase in solar radiation and air temperature relative to water temperature (T_{mix}) enhances the strength of stratification in the water column up to late summer when surface water reaches its maximum seasonal temperature (Boehrer & Schultze, 2008; Persson & Jones, 2008). The climate change-driven increase in summertime T_{air} further enhances the strength of stratification and reduces Z_{mix} (e.g., during heatwaves, which have become more frequent and severe; Coumou & Rahmstorf, 2012; Stetler et al., 2021; Woolway, Jennings, et al., 2021). Climate change has also reduced average wind speeds over continents (Woolway et al., 2019). This, also called as atmospheric stilling, tends to strengthen thermal stratification (Magee & Wu, 2017; Stetler et al., 2021; Woolway et al., 2019). Furthermore, climatic warming has advanced the timing of the onset of thermal stratification and prolonged the stratification season (Shatwell et al., 2019; Stetler et al., 2021; Woolway, Sharma, et al., 2021). The advanced onset of summer stratification increases a temporal mismatch between spring phytoplankton blooms (during high nutrient availability after spring overturn) and the highest seasonal light availability, which occurs around the solstice (Gronchi et al., 2021).

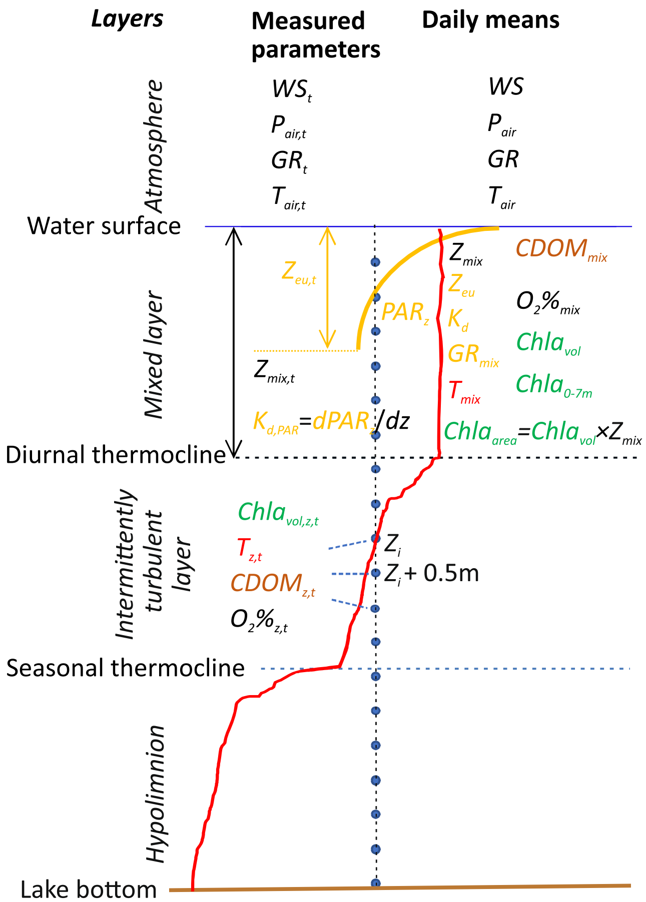


FIGURE 1 A schematic figure of the layers examined (left), the measured parameters (middle) and their daily means (right). Meteorological parameters were wind speed (WS_t, m/s), atmospheric pressure ($P_{air,t}$, mbar), global radiation (GR_t, kW m^{-2}), and air temperature ($T_{air,t}$, °C) recorded at 1-min intervals on Lake Jyväsjärvi. The corresponding daily means were WS, P_{air}, GR, and T_{air}. Vertical light attenuation coefficient ($K_{d,t}$, m^{-1}) and euphotic layer ($Z_{eu,t}$, m) refer to weekly measurements, which were interpolated to daily values (K_d, Z_{eu}). Water temperature ($T_{z,t}$, °C), CDOM fluorescence ($CDOM_{z,t}$, RFU), Chl-*a* concentration ($Chla_{vol,z,t}$, mg/m^3) converted from in situ Chl-*a* fluorescence (RFU), and oxygen saturation ($O_2\%_{z,t}$) were measured at 0.5 m depth (*z*) intervals from water-column profiles once in 1 hr. Mixed-layer depth ($Z_{mix,t}$) was determined from each temperature profiles and the daily means were reported as Z_{mix}. Daily mean water qualities within the mixed layer were reported as T_{mix}, $CDOM_{mix}$, $O_2\%_{mix}$, GR_{mix}, $Chla_{vol}$, $Chla_{area}$, and $Chla_{0\text{–}7m}$.

The climate change-driven increase in stratification strength has reduced the transport of nutrients from the deeper layers to the ocean surface and reduced phytoplankton biomass in the global ocean (Behrenfeld et al., 2006; Mishra et al., 2022; Siemer et al., 2021). Evidence for similar trends in lakes is not as clear, and both positive and negative responses by phytoplankton biomass to warming and reduced mixing have been reported, highlighting the system-specificity of lakes (Gray et al., 2019; Lepori et al., 2018;

Straile et al., 2003). Phytoplankton biomass can nevertheless correlate negatively with the surface water temperature in non-eutrophic lakes, where an increase in stratification possibly reduces phytoplankton biomass (as in the ocean) (Kraemer et al., 2017). In eutrophic lakes, the response of phytoplankton might be the opposite (Kraemer et al., 2017). The latter can be explained by improved light availability, nutrient supplies from the catchment and N_2-fixing cyanobacteria, which favour higher temperature and can retrieve nutrients from hypolimnion via vertical migrations (Kraemer et al., 2017; O'Neil et al., 2012).

In this study, we hypothesise that climate change-driven shallowing of the mixed layer would have a negative impact on freshwater phytoplankton biomass in a stratified mesotrophic lake, where compensatory nutrient supplies from external sources are low. More precisely, an increase in summertime T_{air} relative to T_{mix} and reduced wind speeds are expected to reduce the depth of Z_{mix} during the first half of the summer stratification period when the water column is becoming more stable. A shallower Z_{mix} increases grazing and sedimentary losses of phytoplankton and reduces nutrient transport from the bottom of the mixed layer. To test these predictions, we monitored day-to-day variability in the meteorological forcing on the lake surface, the water column profiles and phytoplankton biomass in the mixed layer in a boreal lake over 2.5 months during the first half of the summer stratification period. Our study period included several cold spells and warm periods, one associated with a record-breaking heatwave in Europe (Vautard et al., 2020).

2 | MATERIAL AND METHODS

2.1 | Study lake

Our study lake is a boreal dimictic Lake Jyväsjärvi (area 3.3 km^2; mean depth 7.0 m; maximum depth 25 m; mean total phosphorus concentration 20 mg/m^3), ice-covered in winter and thermally stratified typically from May to October (Kuha, Arvola, et al., 2016; Kuha, Palomäki, et al., 2016). We examined the lake during the first half of the stratification period from May 15 to July 31 2019 (Supporting Information 1.1.1). An automated floating monitoring station profiled the water column and measured weather parameters continuously at the deepest point of the lake at 62°14′11.671″N 25°46′2.868″E (Kuha, Arvola, et al., 2016; Kuha, Palomäki, et al., 2016; Figure S1). Manual measurements and water samples were collected from the monitoring station.

2.2 | Water quality and meteorological variables

Our aim was to analyse day-to-day variability in phytoplankton biomass in the mixed layer and explain its variability using the corresponding variability in lake physics and meteorological forcing acting on the lake. The cell division of phytoplankton occurs typically once a day (Nelson & Brand, 1979), and thus our analyses focused on daily changes (Supporting Information 1.1.2). The primary measurements of phytoplankton biomass, lake physics, and weather conditions were averaged over 1 day and water quality was averaged over the mixed layer for statistical analyses (as explained below).

A weather station (Campbell Scientific Research Grade Weather Station) measured continuously air temperature ($T_{air,t}$, °C), atmospheric pressure ($P_{air,t}$, mbar), global radiation (GR_t, kW m^{-2}) and wind speed (WS_t, m s^{-1}) 2 m above the lake surface and recorded the data at 1-min intervals (Figure 1). The daily means of the meteorological variables were calculated as the averages of 1,440 measurements from midnight to the following midnight (T_{air}, P_{air}, GR, and WS; Figure 1).

The water quality monitoring covered four conceptual layers: euphotic, mixed, and an intermittently turbulent layer as well as the hypolimnion below the seasonal thermocline (Figure 1, details in Supporting Information 1.2). Daily depths of euphotic layer (Z_{eu}) were linearly interpolated from the manual weekly determinations of a vertical light attenuation coefficient (K_d [PAR], m^{-1}). The K_d values were determined as the slope of a line fitted on the relationship between depth z and $\log_e$ transformed downwelling irradiance, E_d (PAR, W m^{-2}), measured with TriOS Ramses ACC-UV/VIS sensors (Rastede, Germany) from approximately 15 depths (Figure 1, Supporting Information 1.3 for details).

An automated EXO2 Multiparameter Sonde (YSI Inc. Yellow Springs, OH, USA) profiled the water column at 0.5 m depth z intervals about once in 1 hr (t) and measured water temperature ($T_{z,t}$, °C), fluorescence of chromophoric dissolved organic matter (CDOM; $CDOM_{z,t}$, RFU), oxygen saturation ($O_2\%_{z,t}$), and in vivo chlorophyll-*a* (Chl-*a*) fluorescence (RFU; Figure 1; the monitoring station in Figure S1). The relative fluorescence units of Chl-*a* were converted to concentration ($Chla_{vol,z,t}$, mg m^{-3}, Figure 1) based on a calibration of the fluorometer with concentration of Chl-*a* measured in laboratory from water samples collected manually (see details in Supporting Information 1.4). The depth of the mixed layer (i.e., diurnal thermocline, $Z_{mix,t}$, m) was defined as the depth at which $T_{z,t}$ decreased 0.3°C from the surface temperature (details in Supporting Information 1.2). The depth of a seasonal thermocline was defined as the deepest density gradient found in the profile according to the R package rLakeAnalyzer (Winslow et al., 2019). Daily mean water quality in the mixed layer (Z_{mix}, T_{mix}, $Chla_{vol}$, $O_2\%_{mix}$, and $CDOM_{mix}$) was calculated as the averages from the measurements across the depths z from the surface to $Z_{mix,t}$ and over the *c*. 24 profiles per day (Figure 1). Daily mean global radiation in the mixed layer (GR_{mix}) was determined by combining daily values of Z_{mix}, K_d and GR as (Minor et al., 2016):

$$GR_{mix} = \left(Z_{mix} K_d\right)^{-1} \times \left(1 - e^{-Z_{mix} K_d}\right)$$

2.3 | Phytoplankton biomass in the mixed-layer and its specific rate of change

On each day, phytoplankton biomass was quantified in the mixed layer as the concentration of Chl-*a* expressed per volume ($Chla_{vol}$, mg m^{-3}) and per area integrated from the surface to the diurnal thermocline ($Chla_{area}$, mg m^{-2}). A lake bathymetry correction was also tested for the $Chla_{area}$ values (equations 3 and 6 in Johansson et al., 2007) but omitted due to its minor effect on the statistical tests (see Supporting Information 1.4.1). Additionally, phytoplankton biomass was expressed per area integrated over the mixed and the intermittently turbulent layer ($Chla_{0-7m}$, mg m^{-2}). $Chla_{area}$ was chosen as the main response variable in the statistical analyses. $Chla_{vol}$ describes the volumetric phytoplankton biomass in the mixed layer and is proportional to the primary production rate in the euphotic layer but sensitive to dilution by deepening Z_{mix} (Behrenfeld & Boss, 2014; Kuha, Arvola, et al., 2016; Kuha, Palomäki, et al., 2016). $Chla_{area}$ expresses collectively the biomass of phytoplankton, which is responsible for the primary production over the entire water column (Behrenfeld & Boss, 2014). Additionally, $Chla_{area}$ is sensitive to the changes in Z_{mix} and acts as the ultimate source of phytoplankton biomass to the secondary consumers in the water column and in the sediment surface too (details in Supporting Information 1.4).

The daily values of $Chla_{vol}$ were calculated from a calibration equation between a spectrophotometrically measured Chl-*a* concentration (Shimadzu UV-1800 spectrophotometer, Shimadzu Co., Kyoto, Japan) from weekly collected composite water samples between 0–2 m and a mean in situ Chl-*a* fluorescence measurements (RFU) in the mixed layer at corresponding times (see the calibration curve in Figure S2, details in Supporting Information 1.4). $Chla_{area}$ was calculated as a multiplication of the daily mean volumetric Chl-*a* concentration ($Chla_{vol}$, mg m^{-3}) and the Z_{mix} (Figure 1, see details in Supporting Information 1.4). $Chla_{0-7m}$ was an integral of $Chla_{vol,z}$ from water surface to 7 m depth (methodological details in Supporting Information 1.4).

A daily specific rate of change in $Chla_{area}$ (r_d, d^{-1}) was determined as

$$r_d = \ln\left(\frac{Chla_{area,di+1}}{Chla_{area,di}}\right)$$

where $Chla_{area,di}$ and $Chla_{area,di+1}$ refer to $Chla_{area}$ on day *i* and the following day $i+1$, respectively (Behrenfeld & Boss, 2014). A positive value of r_d indicates an increase and negative value a decrease in phytoplankton biomass.

2.4 | Data analysis

Statistical analyses assessed how the phytoplankton biomass ($Chla_{area}$, $Chla_{vol}$, and $Chla_{0-7m}$) and its change (r_d) depended on water quality parameters (Z_{mix}, Z_{eu}, K_d, T_{mix}, $O_2\%_{mix}$, $CDOM_{mix}$, and GR_{mix}, Figure 1) and associated external meteorological forcing parameters (T_{air}, P_{air}, *GR*, and *WS*, Figure 1). Z_{eu} was also related to Z_{mix} (Z_{eu}:Z_{mix}) to further characterise underwater light availability. Air temperature minus water temperature in the mixed layer ($T_{air} - T_{mix}$) acted also as an explanatory variable because climatic warming (i.e., an increase in T_{air}) affects Z_{mix} through this difference (see details in Supporting Information 1.3.2).

We used several statistical approaches to investigate the dependence of phytoplankton biomass on environmental variables. Firstly, a Pearson correlation matrix addressed the relationships between the meteorological and water quality parameters. Secondly, the dependence of phytoplankton biomass (on day *i*) and its change (from day *i* to *i* + 1) on individual meteorological and lake physical parameters (on day *i*) were assessed with regression analysis using two competing models (a linear model $y = \beta_1 x + \beta_0$; a quadratic model $y = \beta_2 x^2 + \beta_1 x + \beta_0$). The quadratic model approximated non-linear dependencies common to phytoplankton such as the dependence of photosynthesis on light. The most parsimonious model was selected based on an adjusted R^2 value. Thirdly, we used principal component analysis (PCA) to reduce the dimensionality of the external meteorological and lake physical parameters into two independent principal components. The interpretation of the principal components is based on the loadings of explanatory variables on the components. Finally, the dependence of phytoplankton biomass (on day *i*) and its change (from day *i* to *i* + 1) on the principal components (on day *i*) were analysed with regression analysis as described above. Statistical testing was done with R studio (version 3.6.1) using the Base Package, and RColorBrewer package was used in figure making.

3 | RESULTS

3.1 | Dynamics of the mixed layer depth and phytoplankton biomass

During the first half of the summer stratification period in Lake Jyväsjärvi, the daily mean of mixed layer depth (Z_{mix}) ranged from 2.7 to 7.2 m and was on average shallower than the seasonal thermocline (Figures 2 and 3h). Chl-*a* concentration ($Chla_{vol,z,t}$), O_2 saturation ($O_2\%_{z,t}$) and the CDOM content ($CDOM_{z,t}$) were approximately homogenous within the mixed layer and followed its dynamics (Figure 2). $Chla_{vol,z,t}$ values decreased steeply below the diurnal thermocline without a deep Chl-*a* maximum (Figure 2a). Daily mean phytoplankton biomass in the mixed layer ($Chla_{area}$) ranged from 21 to 115 mg m^{-2} (Figures 1 and 3a; see Figure S3 for the corresponding $Chla_{vol}$ and $Chla_{0-7m}$ range). The daily specific rate of changes in $Chla_{area}$ (r_d) varied between −0.5 and 0.4 d^{-1} (Figure 3b). The lowest $Chla_{area}$ values and the longest period of negative r_d co-occurred when Z_{mix} became shallower and during the warmest air temperatures at the end of July, when a record-breaking heatwave advected hot air from North Africa across western Europe to our study lake (Vautard et al., 2020; Figures 2 and 3, Figure S3).

3.2 | The relationships between meteorological and lake physical parameters

Z_{mix} on day *i* correlated significantly with many daily mean meteorological parameters on the same day *i* (Figure 4). The correlation was positive with wind speed (*WS*) and negative with air pressure (P_{air})

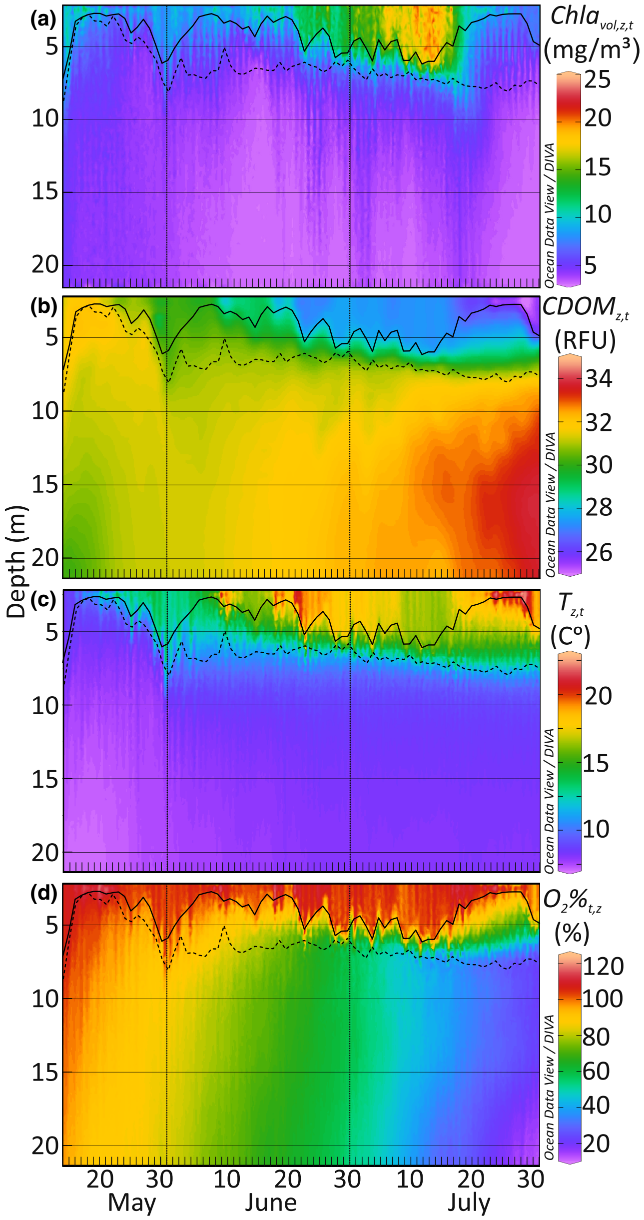


FIGURE 2 (a) Chlorophyll-*a* concentration ($Chla_{vol,z,t}$), (b) CDOM fluorescence ($CDOM_{z,t}$), (c) water temperature ($T_{z,t}$), and (d) oxygen saturation ($O_2\%_{z,t}$) along the study period. Black solid line is the daily mean mixed-layer depth (Z_{mix}) and the dashed line the seasonal thermocline.

and the difference between air temperature and water temperature ($T_{air}-T_{mix}$; Figure 4). Thus, Z_{mix} was deep during high wind speeds, low air pressures and when air was colder than water ($T_{air}-T_{mix}<0$), which favoured convective mixing (Figures 3 and 4).

Light availability for the phytoplankton in the mixed layer was characterised by the global radiation received by the lake (*GR*), the vertical attenuation coefficient of light (K_d), CDOM content in the mixed layer ($CDOM_{mix}$), the ratio of euphotic layer depth to Z_{mix} (Z_{eu}:Z_{mix}) and mean global radiation in the mixed layer (GR_{mix}; Figure 3c,g,j,k,l). *GR* varied from 0.08 to 0.37 kW/m^2 without a temporal trend during the study period (Figure 3c). High *GR* values (i.e., sunny days) correlated positively with high atmospheric pressures (Figure 4). The values of K_d varied from 1.6 to 2.2 m^{-1}, a higher value meaning a faster light attenuation with depth (Figure 3j). The values of K_d correlated positively with $CDOM_{mix}$ but negatively with *GR* (Figure 4). The $CDOM_{mix}$ values had a decreasing trend associated with the photobleaching of CDOM in the mixed layer (Figures 2b and 3l). The euphotic layer was typically shallower than the mixed layer (Z_{eu}:Z_{mix} was 0.39–1.0, Figure 3g). The Z_{eu}:Z_{mix} correlated negatively with *WS* and K_d and positively with $T_{air}-T_{mix}$, P_{air}, and *GR* (Figure 4). Thus, light availability in terms of Z_{eu}:Z_{mix} was highest on calm, sunny and warm days with low K_d-values (Figures 3 and 4).

3.3 | The dependence of phytoplankton biomass on individual environmental variables

$Chla_{area}$ was high on days with deep Z_{mix}, which explained 69% of the daily variability in $Chla_{area}$ (Figure 5a; Table S2). $Chla_{area}$ was low on days with high Z_{eu}:Z_{mix} values (Figure 5b; Table S2). Similarly, $Chla_{area}$ was low on days with high values of GR_{mix}, P_{air}, and $O_2\%_{mix}$ as well as when air temperature was higher than water temperature ($T_{air}-T_{mix}>0$; Figure 5c,f,g,j; Table S2). $Chla_{area}$ had a non-linear dependence on $CDOM_{mix}$ but no significant dependence on K_d, *WS* or *GR* (Figure 5d,e,h,i; Table S2). The same regression analyses with $Chla_{vol}$ and $Chla_{0-7m}$ as response variables gave similar results as those done with $Chla_{area}$ (Figures S4 and S5, Table S3).

Individual explanatory variables on day *i* explained up to 9% of the variation in r_d, i.e., a change in $Chla_{area}$ from day *i* to day *i*+1 (Figure S6, Table S4). The value of r_d had significant positive dependencies on *WS* and K_d (Figure S6, Table S4), and significant negative dependencies on Z_{mix}, $T_{air}-T_{mix}$, *GR* and $O_2\%_{mix}$ (Figure S6, Table S4). Thus, a net increase in $Chla_{area}$ took place after cold days with high wind speed and low solar radiation (Figure S6, Table S4).

3.4 | Dependence of phytoplankton biomass on the principal components of environmental variability

The PCA simplified and reduced the multiple and complex relationships between the meteorological and lake physical factors into two principal components (Figure 6). The first two principal components (PC1 and PC2) of the PCA explained 61% of variation in the environmental parameters on the study days (Figure 6). PC1 explained 43% of the variation and received high loadings from Z_{mix} and related variables such as $T_{air}-T_{mix}$, GR_{mix}, Z_{eu}:Z_{mix} and *WS* (Figure 6). High scores of PC1 indicated deep Z_{mix} on windy days when air (T_{air}) was cooler than the mixed layer (T_{mix}), whereas low PC1 scores indicated shallow Z_{mix} on calm days when air (T_{air}) was warmer than the mixed layer (T_{mix}). PC2 explained 18% of the variation and had high loading from variables associated with light availability ($CDOM_{mix}$, K_d, *GR* and GR_{mix}; Figure 6). Increasing score of PC2 indicated higher light availability.

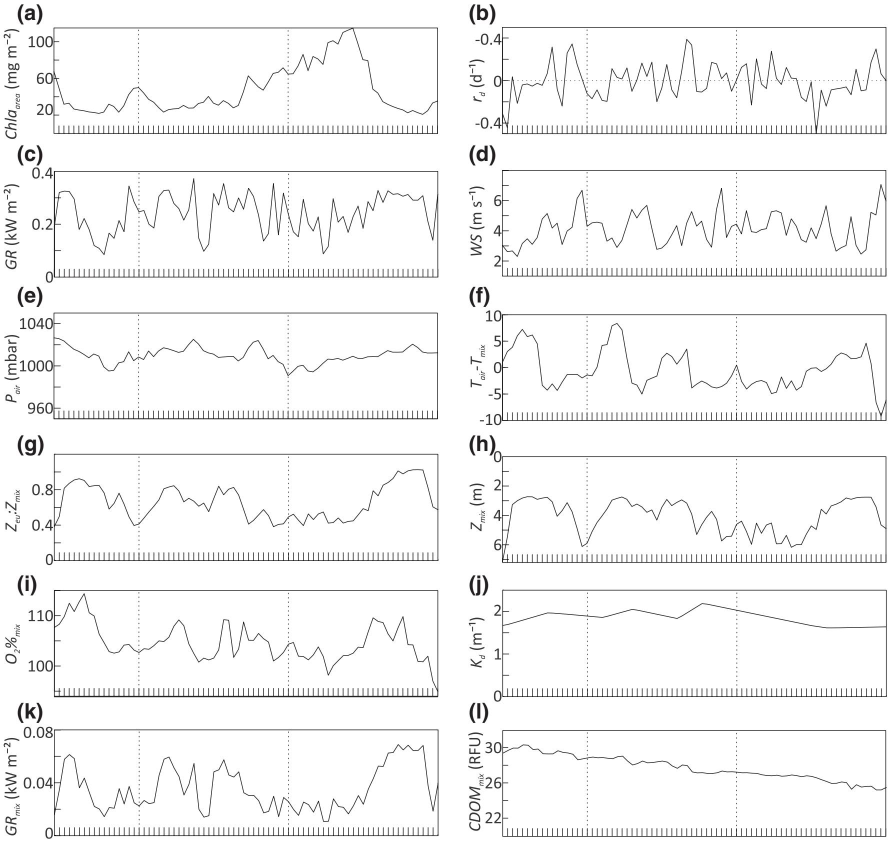
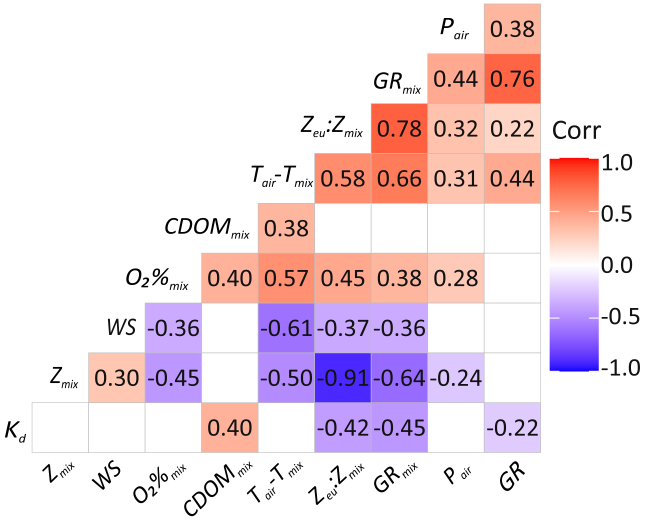


FIGURE 3 Time series of daily mean values of the response (a, b) and explanatory (c–l) parameters used in statistical analyses. Figure 1 explains the parameters and Figure S5 shows the values for T_{air}, T_{mix}, and Z_{eu}.



	Z_{mix}	WS	$O_2\%_{mix}$	$CDOM_{mix}$	T_{air}-T_{mix}	Z_{eu}:Z_{mix}	GR_{mix}	P_{air}	GR
P_{air}									0.38
GR_{mix}								0.44	0.76
Z_{eu}:Z_{mix}							0.78	0.32	0.22
T_{air}-T_{mix}						0.58	0.66	0.31	0.44
$CDOM_{mix}$					0.38				
$O_2\%_{mix}$				0.40	0.57	0.45	0.38	0.28	
WS			-0.36		-0.61	-0.37	-0.36		
Z_{mix}		0.30	-0.45		-0.50	-0.91	-0.64	-0.24	
K_d				0.40		-0.42	-0.45		-0.22

FIGURE 4 Correlation matrix of the meteorological and water quality parameters reported in Figure 3c–l. blue and red colours highlight the values of significant ($p < 0.05$) negative and positive correlation coefficients, respectively.

$Chla_{area}$ on day i was significantly dependent on both principal components on the same day i (Figure 7; Table S5a). The PC1 scores explained 43% of the variability in $Chla_{area}$ according to the non-linear model (Figure 7a; Table S5a) indicating that $Chla_{area}$ was high on days with deep mixed layer characterised by high winds and air temperatures colder than those in water. The PC2 scores explained 25% of the variability in $Chla_{area}$ (Figure 7b; Table S5a) indicating higher $Chla_{area}$ with improving light availability when light levels were low but low $Chla_{area}$ with the highest light availabilities. The dependencies of $Chla_{vol}$ and $Chla_{0\text{–}7m}$ on the PC1 and PC2 scores were similar as found for $Chla_{area}$ (Figure S6, Table S6). The r_d values concerning the changes of $Chla_{area}$ from day i to following day $i+1$ did not show significant dependencies either on the PC1 or PC2 score on day i (Figure 7c,d; Table S5b).

4 | DISCUSSION

Our study shows that during the first half of the summer stratification period in a boreal mesotrophic lake, external meteorological variables (wind speed and $T_{air} - T_{mix}$) are most strongly associated with the depth of the mixed layer, Z_{mix}. Moreover, the variability in phytoplankton biomass depends primarily on the Z_{mix}. In our study, phytoplankton biomass increased with deepening of the mixed layer, caused by higher winds and lower air than water temperature. Instead, phytoplankton biomass decreases when the mixed layer becomes shallower on calm sunny days when air pressure is high and air temperature is warmer than water temperature (e.g. during a heatwave). Light availability showed only a modest influence on phytoplankton biomass.

4.1 | Mixed layer and phytoplankton biomass

The high positive dependence of $Chla_{area}$ on Z_{mix} found in this study is generally consistent with models that predict an increase

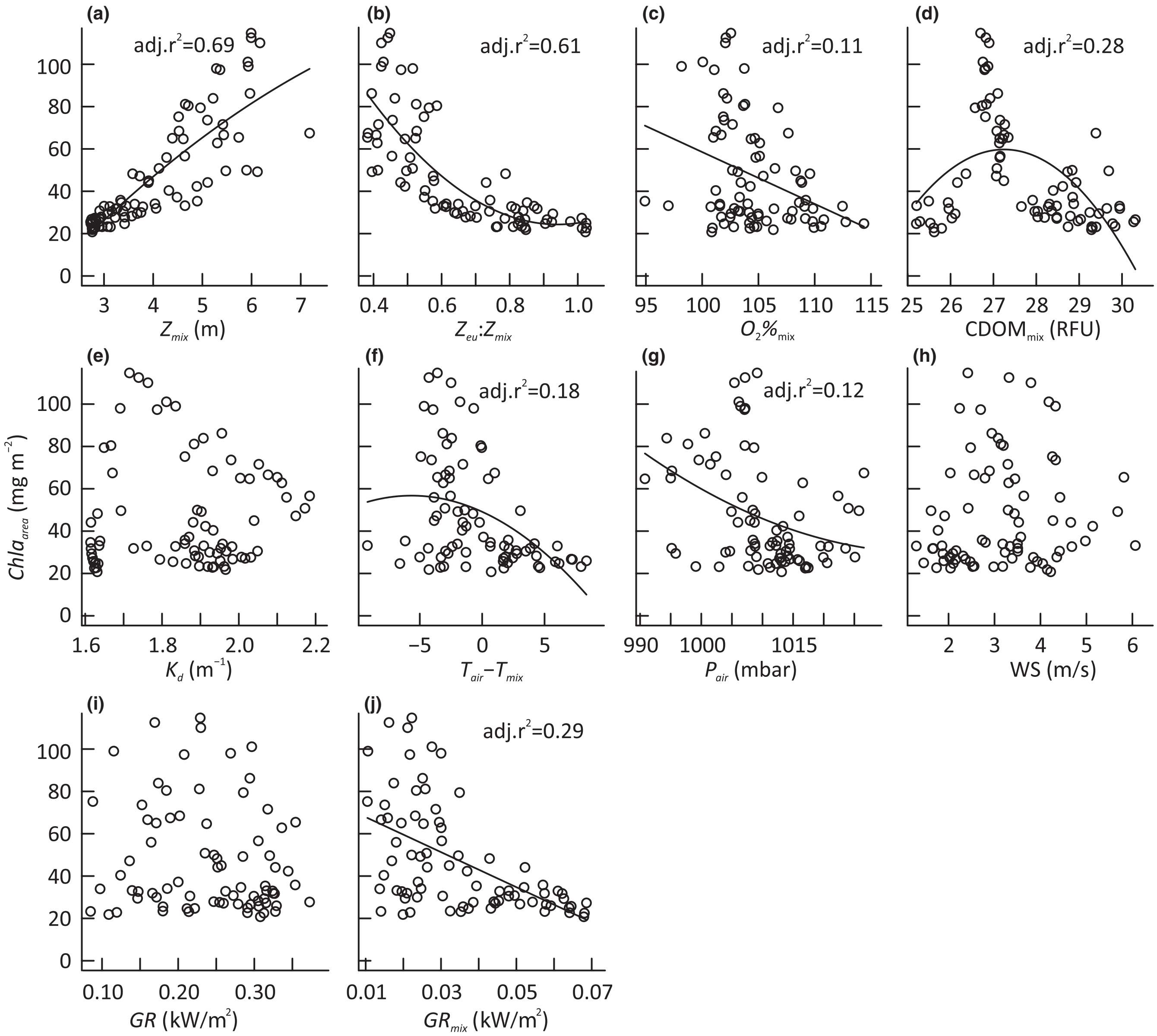


FIGURE 5 The dependence of $Chla_{area}$ on individual explanatory parameters (Figure 3). The lines and curves show significant linear or non-linear, respectively, dependences, which are reported also in Table S2.

in phytoplankton biomass with a deepening mixed layer (Berger et al., 2006; Diehl, 2002; Mesman et al., 2022). These findings are supported by results from enclosure experiments, where artificial deepening of the mixed layer typically increases phytoplankton growth and biomass (Cantin et al., 2011; Diehl et al., 2002; Giling et al., 2017). Similarly, in 65 European lakes, $Chla_{area}$ increases with Z_{mix} in most (*c.* 85%) lakes, where Z_{mix} is <8 m like in our study (Berger et al., 2006). In our study, the positive dependence on Z_{mix} was also found for volumetric Chl-*a* concentration ($Chla_{vol}$) and areal Chl-*a* concentration at 0–7 m depth ($Chla_{0\text{–}7m}$), which do not include Z_{mix} as a multiplier by their definitions, and thereby verify the real dependencies between the phytoplankton biomass and the Z_{mix}. Our study shows that the positive relationship between $Chla_{area}$ and Z_{mix} found in earlier studies concerns also natural day-to-day dynamics in a stratified lake driven by meteorological forcing.

The dependence of $Chla_{area}$ on Z_{mix} can be explained primarily by an improved availability of nutrients from the bottom of (deepening) mixed layer (Diehl, 2002; Giling et al., 2017; Weithoff et al., 2000). Phytoplankton require nutrients to gain in biomass (Falkowski & Raven, 2014). Deep Z_{mix} also reduces sinking losses of phytoplankton out of the mixed layer (Cantin et al., 2011; Ptacnik et al., 2003). In addition, deep Z_{mix} decreases the encounter rate between phytoplankton and grazers and may reduce grazing losses of phytoplankton in the mixed layer (Berger et al., 2006).

4.2 | Light availability and phytoplankton biomass

During the first half of the summer stratification period in our study lake, the PC2 component, which expresses light availability,

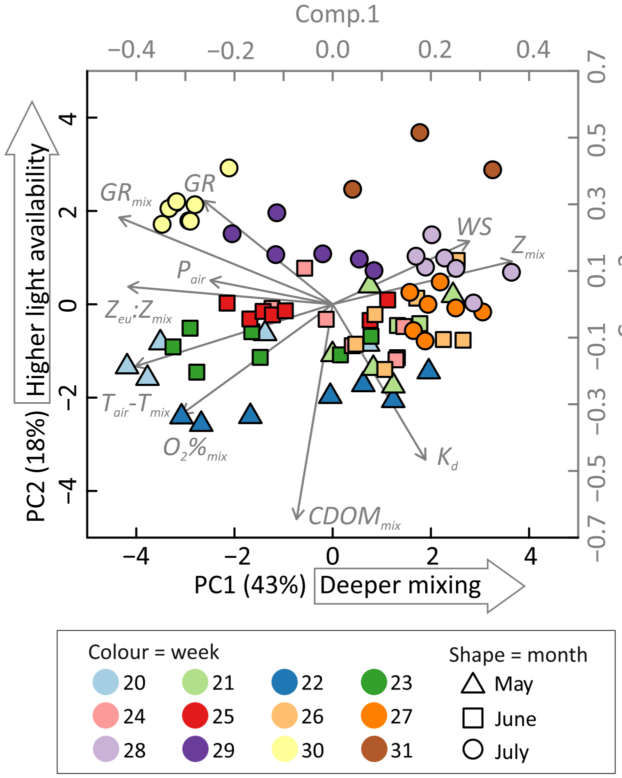


FIGURE 6 Principal component analysis of variability in the environmental parameters (Figure 3c–l) on the study days. The first (PC1) and second (PC2) principal components explain 43% and 18% of variability in the environmental parameters on the study days shown as symbols highlighting month by shape and week by colour. The Comp1 and Comp2 axes quantify the loadings of environmental parameters (arrows) on PC1 and PC2.

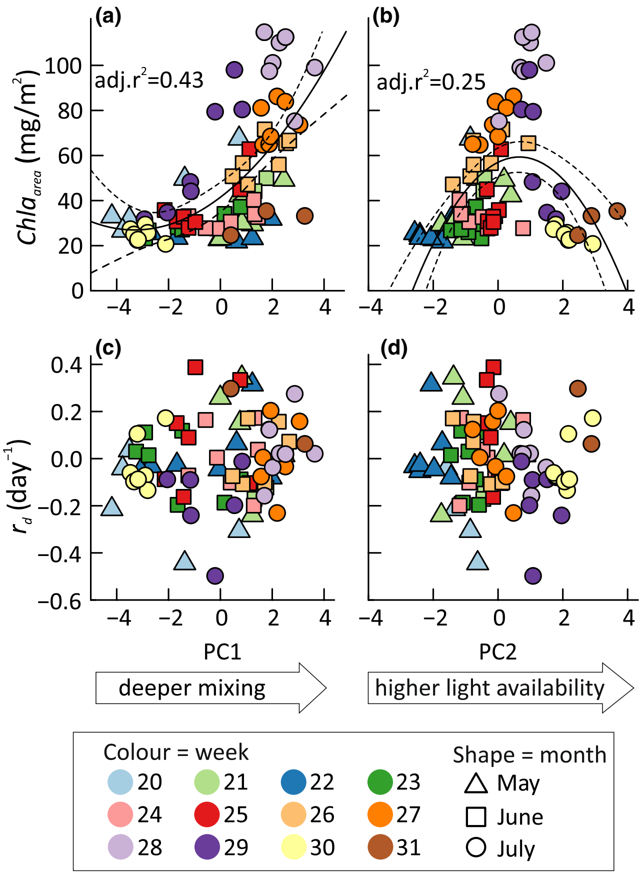


FIGURE 7 The dependence of $Chla_{area}$ on day i (Figure 3a) and r_d (i.e., change in $Chla_{area}$ from day i to day $i+1$, Figure 3b) on the PC1 and PC2 scores on day i (Figure 6). The solid and dashed curves show non-linear dependencies and their 95% confidence intervals reported also in Table S5. The symbols are explained in Figure 6.

was not related to the changes in $Chla_{area}$ (i.e. to the values of r_d). Nevertheless, phytoplankton biomass shows a non-linear dependence on PC2 score, where the $Chla_{area}$ has a tendency to increase with improving light availability when light level is poor, characterised by low global radiation (i.e., cloudy days), and high $CDOM_{mix}$ and K_d values. Under the highest light availability, however, $Chla_{area}$ values are also low, creating the overall non-linear shape of the dependency.

The ratio Z_{eu}:Z_{mix} provides essential information about the underwater light conditions for phytoplankton within the mixed layer. In our study lake, the Z_{eu}:Z_{mix} values (*c.* 0.4–1.0) are larger than *c.* 0.2, which is a critical value for supporting a net growth of $Chla_{area}$ in various aquatic environments (estuaries, ocean, lakes) according to theoretical models (Diehl, 2002), observations from field (Berger et al., 2006; Cloern, 1987; Sverdrup, 1953) and experiments (Diehl, 2002). When our results are combined with those from earlier studies, they indicate that an increase in Z_{mix} primarily increases $Chla_{area}$ in aquatic ecosystems where the Z_{eu}:Z_{mix} is ≥ *c.* 0.37 like in our study lake (Cantin et al., 2011; Diehl, 2002; Diehl et al., 2002). When Z_{eu}:Z_{mix} values fall from *c.* 0.37 towards *c.* 0.2, light availability becomes a major limiting factor of $Chla_{area}$. In such light limited aquatic ecosystems with Z_{eu}:$Z_{mix} < c.\ 0.2$, a shallowing of Z_{mix} can increase the light availability above a critical threshold and increase $Chla_{area}$ (Cloern, 1987; Diehl et al., 2002; Sverdrup, 1953). Overall, our results and older findings (e.g., Cantin et al., 2011; Diehl et al., 2002) suggest that light availability is not the major controlling factor of phytoplankton biomass in mesotrophic lakes like our study lake in the first half of the summer stratification period.

4.3 | Responses of phytoplankton biomass to warming climate

Our study shows that climatic impact-drivers, wind speed and $T_{air}-T_{mix}$, influence the depth of the mixed layer, which is then strongly associated with phytoplankton biomass during the first half of the summer stratification period in a mesotrophic lake. Our lake is non-eutrophic like most global oceans and lakes, where phytoplankton have been shown to respond negatively to increased surface water temperatures as an indicator of stratification strength (Behrenfeld et al., 2006; Kraemer et al., 2017; Mesman et al., 2021; Mishra et al., 2022; Siemer et al., 2021). This common response indicates that the strengthening of stratification and shallowing of Z_{mix} can reduce nutrient supply to phytoplankton and primarily act on non-eutrophic stratified waters.

We limited our study to the first half of the summer stratification period, when sedimentation of particles reduces the nutrient content of mixed layer and ongoing strengthening of seasonal stratification diminishes upward transport of nutrients. Under these circumstances, heatwaves and atmospheric stilling can reduce Z_{mix} and further diminish upward transport of nutrients to the mixed layer with a negative impact on phytoplankton (Coumou & Rahmstorf, 2012; Deng et al., 2021; Perkins-Kirkpatrick & Lewis, 2020; Woolway et al., 2019; Woolway, Sharma, et al., 2021). These findings suggest that climate change-driven increase in summertime T_{air} and reduced wind speed has an overall tendency to reduce the depth of mixed layer and phytoplankton biomass in non-eutrophic lakes during the first half of the stratification period.

The impact of climatic drivers on phytoplankton may be different or absent during the second half of the stratification season, when the seasonal cooling of T_{air} and reduced solar irradiance increase Z_{mix} towards the autumn turnover. For example, warmer air can lengthen the growth season of phytoplankton and increase phytoplankton biomass in the second part of the stratification period (Kraemer et al., 2017; Wasmund et al., 2019; Yang et al., 2016). Thus, the impact of weather variables altered by climatic change on phytoplankton may be different between the first and second half of the same summer stratification season.

5 | CONCLUSIONS

In this study, we observed a negative response of phytoplankton biomass associated with the mixed layer becoming shallower, caused by increasing air temperature relative to water temperature and declining wind speed; the drivers of climate change. These drivers of climatic change (e.g. experienced as heat waves) can cause oligotrophication during the first half of the stratification period in many boreal lakes without deep chlorophyll maxima, which are non-eutrophic and not limited by light availability like our study lake. Earlier works have shown that elevated surface water temperatures can increase phytoplankton biomass in lakes with extensive external sources of nutrients from a catchment, the atmosphere, N_2 fixing, or hypolimnion through vertical migrations of plankton. Our work highlights a contrasting response by a lake to climate change. These preliminary results are based on observations over one first half of a summer stratification period in one lake. Thus, further work is needed to understand how the characteristics of lakes regulate the responses of lakes to climate change at different phases in the annual cycles of lakes.

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods: S.A.A., A.V.V., J.S. Conducting the research: S.A.A., A.V.V., J.S.K., J.K. Data analysis: S.A.A., A.V.V. Preparation of figures and tables: S.A.A. Data interpretation, writing: S.A.A., A.V.V., J.S., J.S.K., J.K.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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