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LETTER

Aquatic heatwaves increase surface chlorophyll concentrations in experimental and reference lakes

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Scientific Significance Statement

Aquatic heatwaves are projected to increase in frequency, intensity, and duration worldwide. While their effects on marine phytoplankton have received much attention, less work has been done on heatwave effects on lake phytoplankton outside of mesocosm and modeling studies. In particular, the dominant mechanisms driving lake phytoplankton response to heatwaves at an ecosystem scale remain unknown. We used daily observations of chlorophyll during a decade of whole-lake nutrient and food web experiments to investigate phytoplankton response to heatwaves across a range of environmental conditions. Surface chlorophyll concentrations increased during most heatwaves. The effects of whole-lake experiments were varied but may have depended on heatwave timing and seasonality.

Abstract

Aquatic heatwaves are increasing in frequency, intensity, and duration worldwide. While increases in mean water temperatures are linked to enhanced phytoplankton biomass, it is unclear how heatwaves alter phytoplankton dynamics in lakes at an ecosystem scale. We investigated changes in surface chlorophyll during 29 summer heatwaves between 2008 and 2019 in 3 north temperate lakes. These lakes vary in staining and were either references or manipulated with nutrients and top predator additions. The manipulations provided a variety of nutrient, grazing, and light conditions during heatwave and non-heatwave conditions. Surface chlorophyll concentrations increased during 24 out of 29 heatwaves. In the low-nutrient reference lake the mean increase in chlorophyll was 57% while in the two experimental lakes the mean increases were 127% and 183%. Overall, the effects of the whole-lake experiments were variable but still provided context for possible patterns amid a diverse set of food web and nutrient conditions.

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Data Availability Statement: Data and metadata are available in the Environmental Data Initiative repository at https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-ntl&identifier=438&revision=1. Code used to perform the analysis is available at Zenodo: https://doi.org/10.5281/zenodo.14968815.

Heatwaves are increasing in intensity, frequency, and duration worldwide, and like other extremes may lead to unexpected biological responses (de Eyto et al. 2016; Oliver et al. 2018; Tassone et al. 2022; Wang et al. 2023). In lakes, field studies of phytoplankton response to heatwaves have often considered a single heatwave or several heatwaves occurring within a single year (Bergkemper and Weisse 2017; Donis et al. 2021; Wilk-Woźniak et al. 2024). Studying multiple heatwaves for multiple lakes over many years offers the potential to assess variation in phytoplankton response resulting from differing heatwave duration, intensity, or timing. Remote sensing studies can meet this goal of relating heatwave dynamics to phytoplankton responses but often lack the temporal resolution to determine the timing of effects, and frequently do not have the in situ data needed to investigate mechanism (Free et al. 2022; Li et al. 2023). Because of the small number of field studies and the resolution of remote sensing approaches, questions remain about the timing, direction, and magnitude of heatwave effects on phytoplankton as they interact with other drivers like eutrophication and grazing pressure.

There are many well-grounded hypotheses that increases in heatwaves will exacerbate algal growth in lakes and lead to harmful blooms (Jöhnk et al. 2008; Paerl and Huisman 2009; Brookes and Carey 2011). However, phytoplankton response to temperature is tied to multiple mechanisms which can either enhance or diminish biomass, making the overall effect of heatwaves uncertain (O'Neil et al. 2012). Heatwaves may increase phytoplankton biomass by pushing some species such as cyanobacteria closer to their thermal optimum, but growth may also depend on nutrient availability (Robarts and Zohary 1987; Paerl and Huisman 2009; Weisse et al. 2016). While nutrients from dissolved organic matter (DOM) may stimulate phytoplankton growth, higher concentrations of dissolved organic matter could also block light, limiting photosynthesis (Graham and Vinebrooke 2009; Olson et al. 2020). Finally, top-down control by zooplankton may weaken if heatwaves increase grazer mortality or change inter-zooplankton predation (Huỳnh et al. 2024).

We addressed these questions by investigating the effects of heatwaves on surface chlorophyll concentrations in three north temperate lakes over a decade of whole-lake experiments. These lakes vary in light availability due to dissolved organic matter, and two of the lakes were experimentally enriched with nutrients in some years or underwent food web manipulations, allowing us to study the effects of heatwaves under a variety of nutrient, light, and grazing conditions (Carpenter et al. 2011; Wilkinson et al. 2018; Buelo et al. 2022b). We expected heatwaves to have stronger, positive effects on chlorophyll under higher nutrient conditions, as observed in marine ecosystems (Hayashida et al. 2020). We also anticipated that chlorophyll response would be dampened in lake-years with higher water color due to decreased light availability (M. L. Pace et al. 2019; Carpenter and Pace 2018). Extreme events like heatwaves can be difficult to study because they are, by definition, rare (Turner et al. 1998). Datasets that include multiple heatwaves and information on possible drivers of phytoplankton response are even rarer. Our decade of daily summertime observations combined with whole-lake experiments offered an exceptional opportunity to investigate heatwave effects on surface chlorophyll concentrations across a range of heatwaves and environmental conditions.

Methods

Study lakes and manipulations

We investigated the response of chlorophyll *a* concentrations to heatwaves in Peter, Paul and Tuesday Lakes in Gogebic County, Michigan, USA (46°250N, 89°500W). Peter and Paul Lakes are oligotrophic, and Tuesday Lake is dystrophic. All three lakes are relatively small (Paul Lake is 1.9 ha, Peter Lake is 2.5 ha, and Tuesday Lake is 0.9 ha), but deep (max depth of Paul Lake is 12 m, Peter Lake is 18 m, and Tuesday Lake is 15 m). Their watersheds are comprised of temperate forest and fringing bog. Water color (measured by light absorption at 440 nm) varies from year-to-year due to changes in precipitation (Carpenter and Pace 2018).

Conditions in Peter and Tuesday Lakes were manipulated by top predator and nutrient additions that varied among years and lakes, while Paul was an unmanipulated reference system. Peter Lake received largemouth bass (*Micropterus salmoides*) additions between 2008 and 2011 to shift the food web from planktivore-dominated to piscivore-dominated, inducing a trophic cascade and increasing zooplankton grazing (Carpenter et al. 2011). Subsequently, nutrients were added to Peter and Tuesday Lakes in 2013–2015 as part of a study on early warning indicators (Wilkinson et al. 2018). Nutrient additions were ramped (rates increased weekly) in 2013, which was one of the darkest water color years on record, but held constant at 3 mg P m^{-2} d^{-1}in 2014 and 2015 (M. L. Pace et al. 2019). Nutrients were also added to Peter Lake in 2019 using a weekly ramp to investigate spatial and temporal early warning statistics (Buelo et al. 2022b).

Data collection

Water temperature was recorded using a combination of HydroLab hydrosondes (OTT Hydromet) and EXO 3 sondes (YSI, Inc) suspended from surface floats at 0.75 m depth at the deepest point in each lake (Pace et al. 2022; Carpenter, Pace, Cole, Batt, et al. 2022). We collected daily water samples for chlorophyll *a* concentration from a single surface grab from each lake, filtered onto Whatman 47-mm GF/F filters, froze, extracted in methanol, and measured using a Turner Trilogy fluorometer (Holm-Hansen and Riemann 1978; Buelo et al. 2022a, 2022b; Carpenter, Pace, Cole, Kitchell, et al. 2022; Szydlowski et al. 2025). Chlorophyll concentrations vary little within the epilimnion of each lake, down to 10% of surface irradiance and into the top of the metalimnion (Carpenter, Kitchell, et al. 2022; Supporting Information S1). Daily sampling of chlorophyll provided resolution of phytoplankton dynamics at a timescale commensurate with their likely response to disturbance (Padisák 1993, Stockwell et al. 2020).

Identifying heatwaves

Historical climatologies used to define heatwaves are seasonally-varying average temperatures calculated from long-term data, ideally at least 30 yr, though 10 yr of data may be sufficient (Fig. 1; Schlegel et al. 2019). However, Peter and Paul Lakes only have 9 yr of daily temperature data available, and Tuesday Lake only has 3 yr. To increase the climatology baseline, we followed an approach used by Tassone and Pace (2023) modeling past water temperature using air temperature from a nearby weather station and a long-term record of water temperature from a nearby lake (Supporting Information S2). Air temperature was measured at Woodruff Airport (−89.734, 45.925), located 40 km from our study lakes (Magnuson et al. 2024). Long-term water temperature was measured in Sparkling Lake (46.008, −89.700), located 31 km from our study lakes (Magnuson et al. 2023). The long-term air and water temperature data included 23 complete years between 1989 and 2022.

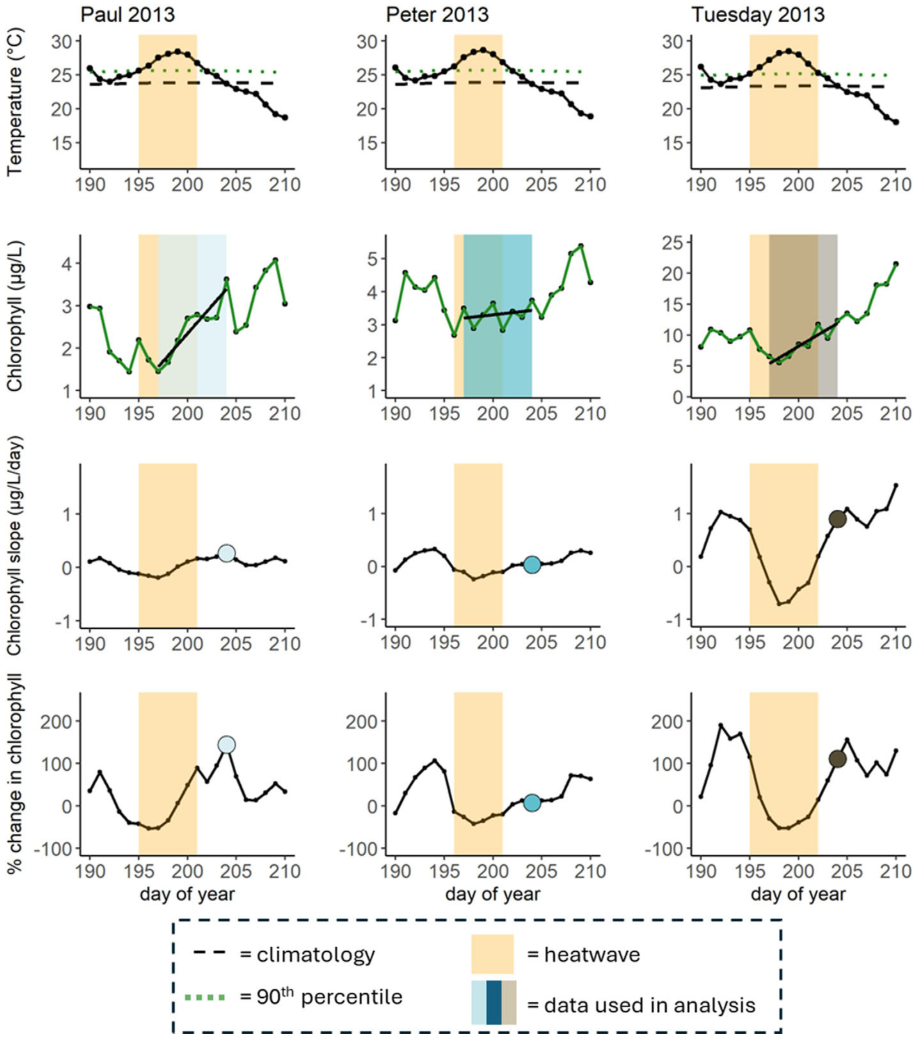

Fig. 1. Sequence of analysis of chlorophyll concentration response to heatwaves using one heatwave in July 2013 as an example. Across all panels, orange highlights the period when the heatwave occurred. The 1st row is temperature in each lake, with the seasonal climatology shown as the dashed black line and the 90th percentile threshold shown as a dotted green line. The 2nd row shows the chlorophyll time series over time (in green), with single example rolling windows of 8 d over which the change in chlorophyll was calculated. The rolling window for Peter Lake is dark blue, the rolling window for Paul Lake is light blue, and Tuesday Lake's window is brown to represent its staining by high concentrations of DOC. Slopes are shown as solid black lines. The 3rd row shows the slope of chlorophyll over time, with the colored points highlighting the slopes we used for analysis. The 4th row shows the slopes converted to a percent change in chlorophyll, with blue or brown points showing what percent changes were included in distributions of heatwave effects.

We constructed a linear mixed effects model between existing temperature data in the three study lakes and the longer-term air and water temperature data from Woodruff Airport and Sparkling Lake. Strong linear relationships between temperature in the study lakes and both Sparkling Lake ($R^2 = 0.9$) and Woodruff Airport air temperature ($R^2 = 0.76$) supported their inclusion in the model (Tassone and Pace 2023). We included lake as a random effect to account for variation in temperature among lakes and day of year as a fixed effect to account for seasonal changes in temperature. We used 75% of daily temperature values from Sparkling Lake and Woodruff Airport in model building ($n = 1649$) and validated the model against the remaining 25% of values using linear regression ($n = 412$; $R^2 = 0.95$; Supporting Information S2; Tassone and Pace 2023). We then used our model to predict water temperatures for our three study lakes between 1989 and 2022, expanding our seasonally varying climatology baseline to 23 yr (Supporting Information S2). Given the strong seasonality of the north temperate region, we used measured sonde temperatures in the *heatwaveR* package to identify heatwaves as periods of time lasting 5 d or more above the 90th percentile of our seasonally varying, modeled climatology (Schlegel and Smit 2018; Hobday et al. 2016; Supporting Information S3, S4). All analyses were done in R version 4.3.0. (R Core Team 2023).

Response of chlorophyll to heatwaves

To assess chlorophyll responses and compare dynamics among lakes and years, we calculated percent change in chlorophyll using linear models fit to daily data with an 8-d rolling window. The 8-d window matched the average length of heatwaves observed (Fig. 1; Supporting Information S3). Estimated slopes from these models were relatively insensitive to the window width (Supporting Information S4). We multiplied the slope from each linear model (μg of chlorophyll d^{-1}) by length of slope (8 d) to get an absolute change in chlorophyll in the window then converted to a percentage change following Eq. 1.

$$\text{Percent change in chlorophyll} = 100 \times \frac{\text{slope} \times \text{length of slope}}{\text{chlorophyll on } 1^{\text{st}} \text{ day of slope}} \quad (1)$$

To assess the magnitude of change in chlorophyll during and immediately following a heatwave, the rolling window with the highest percent change during the heatwave event was compared to all other non-heatwave rolling windows in the same lake, during years when heatwaves were identified. We compared to all other days so that we could better evaluate whether changes in chlorophyll following heatwaves were different from changes caused by normal dynamics or experimental conditions. To assess if there were consistent lag effects in the chlorophyll response, the rolling window percent change was aligned by the last day of the heatwave when we expected the cumulative effects to be highest and averaged across time for all events within a given lake.

Finally, we used measures of lake variables related to phytoplankton community size and growth to test for associations with variation in chlorophyll percent change. Phytoplankton community size is determined by a balance of growth, sinking, and grazing (Reynolds and Wiseman 1982; Carpenter et al. 1998). Growth, in turn, is affected by temperature, light, and nutrients (Staehr and Sand-Jensen 2005, Striebel et al. 2008). We investigated heatwave intensity, water color, and total phosphorus concentrations as measures of temperature, light, and nutrients that might mediate changes in phytoplankton growth processes during heatwaves. Heatwave intensity is defined as the mean temperature anomaly during the heatwave period relative to our 90th percentile threshold (Schlegel et al. 2018). Water color (hereafter g440) was measured weekly from integrated surface water samples filtered through a 25-mm GF/F filter using a spectrophotometer at an absorbance of 440 nm (Cuthbert and del Giorgio 1992; Carpenter, Kitchell, et al. 2025). Total phosphorus concentrations were measured from integrated weekly epilimnion samples using an Astoria-Pacific nutrient analyzer (Carpenter et al. 2024a).

We also considered factors associated with phytoplankton loss, including both grazing and sinking. Grazing was investigated as *Daphnia* biomass during the heatwave, which was measured weekly by counting and measuring the length of zooplankton from daytime vertical net tows using an 80-μm mesh net (Carpenter et al. 2024b). Grazing could be affected by heatwaves if they alter inter-zooplankton predation rates and community composition (e.g., Huỳnh et al. 2024). Losses due to sinking could be affected by increases in stratification during heatwaves, which may decrease sinking of buoyant species such as cyanobacteria and increase their exposure to surface irradiance (Paerl and Huisman 2009). Alternatively, larger diatoms which lack buoyancy regulation might experience increased sinking under more stratified conditions (Winder et al. 2008). To investigate the effects of stratification, we related changes in chlorophyll to Schmidt stability during each heatwave calculated using *rLakeAnalyzer* (Winslow et al. 2019; Carpenter, Pace, et al. 2025). In addition to these predictors, we also tested over 40 total predictors to explore variation in chlorophyll response and considered other potential factors affecting chlorophyll concentrations (Supporting Information S1, S5). When covariate data were not available during the heatwave, we used values from the week preceding the heatwave.

Results

A total of 34 heatwaves occurred from 2008 to 2019, of which 29 were usable in our analysis because they occurred at times with daily chlorophyll data before and after the heatwave. By these criteria, there were 11 heatwaves in Paul Lake, 13 in Peter Lake, and 5 in Tuesday Lake. Each year had at least one heatwave except for 2008. Heatwaves ranged in duration from 5 to 16 d, with a median length of 7 d. Heatwaves were relatively synchronous between Peter and Paul lakes, which shared 11 of 13 events (Fig. 2). In dystrophic Tuesday Lake, one of the five heatwaves only occurred in that lake.

On average, heatwaves increased chlorophyll concentrations by 57% in Paul Lake, 127% in Peter Lake, and 183% in Tuesday Lake over an 8-d period (Fig. 2). Comparatively, mean changes in chlorophyll for non-heatwave periods in the dataset were 4% in Paul Lake, 17% in Peter Lake, and 13% in Tuesday Lake. Chlorophyll response across the lakes was relatively synchronous and the percent change in chlorophyll was highest when slopes included both the final 5 d of heatwave events and 2 or 3 d following the heatwave (Fig. 2).

Chlorophyll increased during 24 out of 29 heatwaves, though the strength of response was highly variable (Fig. 3). Peter Lake had stronger responses of chlorophyll relative to Paul Lake in 2009 and early 2010, and weaker responses at the end of 2010 and 2011. In 2015, the heatwave occurred in August when nutrient additions had ceased in Peter Lake but were ongoing in Tuesday Lake. The response of chlorophyll in August 2015 was negative in Peter Lake, but positive in Paul and Tuesday. The heatwaves in 2019 were less severe compared to other events. There was a strong response of chlorophyll to the July 2019 heatwave in Peter Lake, but a comparatively weak response in Paul. During the August 2019 heatwave, there was a similar, positive response of chlorophyll in Peter and Paul lakes. Finally, we observed strong responses of chlorophyll to early season heatwaves during May of 2014 and 2018.

While heatwaves had stronger mean effects on chlorophyll concentrations in the manipulated lakes (Peter Lake, Tuesday Lake) than the reference lake (Paul; Fig. 1), there were no strong linear relationships between chlorophyll response and heatwave intensity, water color, total phosphorus, *Daphnia* biomass, or Schmidt stability (Fig. 4), nor with any of the other 40 predictors we tested (Supporting Information S5). Heatwaves were associated with increases in chlorophyll concentrations during 18 out of 22 events when nutrients were not actively being added (including in the reference lake).

Discussion

Chlorophyll concentrations temporarily increased during 24 out of 29 heatwaves, including in both experimental and reference lakes (Fig. 3). The timing of phytoplankton response was synchronous across lakes, with effects on chlorophyll persisting for several days after each event (Fig. 2). The mean response was stronger in experimental lakes, demonstrating

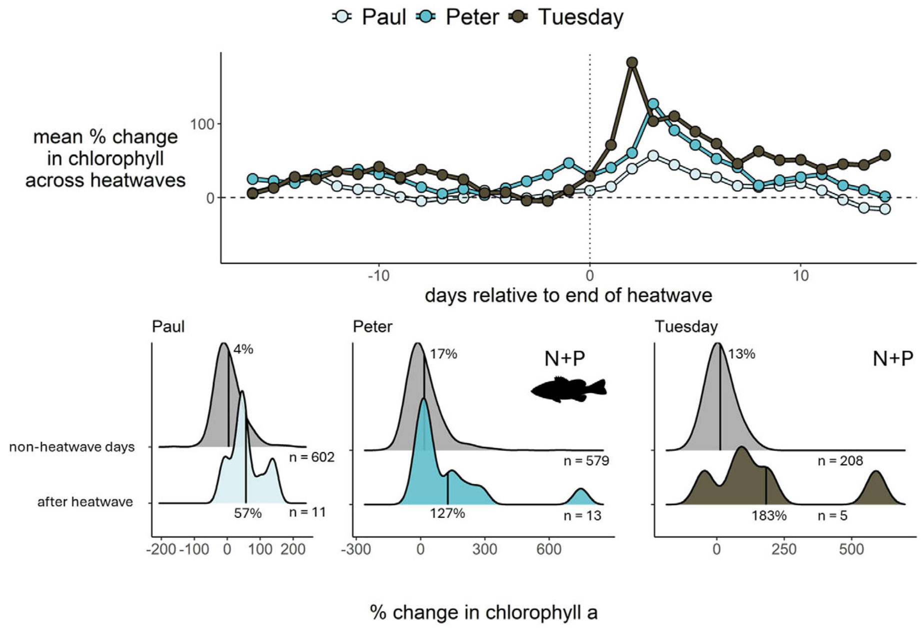

Fig. 2. The top plot shows average percent change in chlorophyll over time relative to the end of all heatwaves. Paul Lake is light blue, Peter Lake is dark blue, and Tuesday Lake is brown to represent its staining by high concentrations of DOC. Each point represents a smoothed percent change over the previous 8 d of chlorophyll concentrations. The bottom row shows density distributions of the percent change in surface chlorophyll *a* concentration at their peak following heatwaves compared to non-heatwave days of the dataset. Distribution means are shown as vertical lines and labeled. The number of days included in each distribution (*n*) is shown on each plot. "N + P" indicates lakes where nutrient additions occur, and the fish outline represents largemouth bass (*Micropterus salmoides*) additions in Peter Lake. Largemouth bass outline is from phylopic.org.

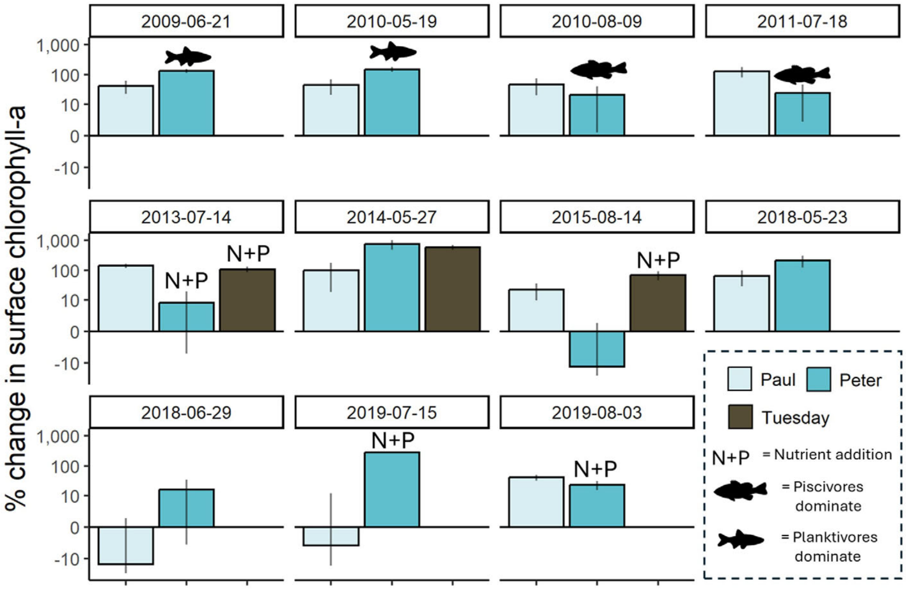

Fig. 3. Percent change in surface chlorophyll *a* during heatwaves grouped by average start date of each individual heatwave event. Peter Lake is dark blue, Paul Lake is light blue, and Tuesday Lake is brown to represent its staining by high concentrations of DOC. Heatwaves detected in only one of the three study lakes were excluded to simplify the visualization. Daily chlorophyll concentrations for Tuesday were only measured in the years 2013–2015, limiting analyses for that lake. Error bars represent standard error of each slope estimate, transformed using the same methods used to estimate percent change in chlorophyll. Largemouth bass outline is from phylopic.org.

that heatwaves may interact with other drivers like top-down pressure or eutrophication to cause changes in surface chlorophyll concentrations. We even observed a positive response of chlorophyll to heatwaves in Tuesday Lake in 2013, the darkest water year on record for our study lakes, suggesting that nutrients may be more important than light attenuation in mediating phytoplankton response to heat events (Fig. 3; Hamdan et al. 2021).

The increases in surface chlorophyll concentrations are consistent with remote sensing studies and marine research showing positive effects of heatwaves on phytoplankton (Woolway et al. 2021; Duan et al. 2024; Hayashida et al. 2020). Simulated heatwaves have also enhanced phytoplankton production in mesocosm and modeling experiments, with responses influenced by factors such as nutrient availability and strength of stratification (Jöhnk et al. 2008; Hamdan et al. 2021; Graham and Vinebrooke 2009; Weisse et al. 2016). Because heatwaves are rare, even a study with a decade of data like ours has limited statistical power (Fig. 4; Supporting Information S5). However, our whole-lake experiments provided context for possible patterns, a diverse set of food web and nutrient conditions, and potential to identify mechanisms driving phytoplankton response.

Food web experiments in our lakes suggest that the strength of phytoplankton response to heatwaves is influenced by top-down pressure. Chlorophyll increased more strongly in Peter Lake in 2009 and 2010, when there was documented instability of the food web and planktivores were dominant, than in late 2010 and 2011 when largemouth bass additions suppressed grazing through a trophic cascade (Carpenter et al. 2011). Other changes in zooplankton community composition could also be important drivers of chlorophyll concentrations during heatwaves. For example, heatwaves could lower top-down effects by affecting interzooplankton predation rates, such as favoring omnivorous copepods over rotifers (Huỳnh et al. 2024).

The effect of nutrient additions on phytoplankton response was likely influenced by heatwave timing and intensity. Nutrient additions in Peter Lake in July 2019 coincided with a strong response of phytoplankton to heatwaves. In contrast, 1 month later, phytoplankton response to a 2$^{\text{nd}}$ heatwave in Peter Lake was similar to the response in unmanipulated Paul Lake. Both heatwaves were not as severe compared to other events. The responses observed could have instead been dominated by the trajectory of algal conditions at the time of the heatwave. Similarly, in August of 2015, surface chlorophyll in Peter Lake responded negatively to heatwaves while chlorophyll in Paul and Tuesday increased. The decline in Peter Lake was likely the result of an ongoing decline in chlorophyll caused by the cessation of nutrient additions (Wilkinson et al. 2018). While nutrients play a role in driving phytoplankton response to heatwaves, the timing and intensity of heatwaves relative to ongoing algal dynamics is seemingly important in determining phytoplankton response.

The seasonal timing of heatwaves and species-specific responses could shape overall phytoplankton response (e.g., Weisse et al. 2016). Some of the strongest responses of phytoplankton to heatwaves occurred in May 2014, before

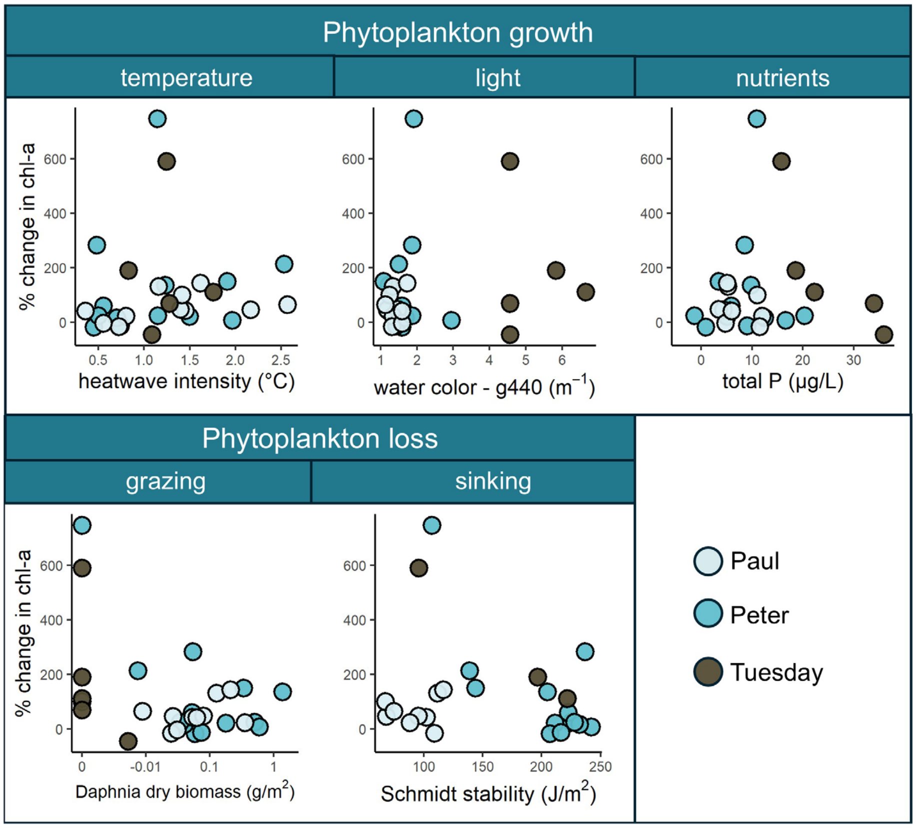

Fig. 4. Average percent change in chlorophyll during each heatwave event related to factors influencing the growth of phytoplankton (temperature, light, and nutrients), as well as factors influencing the loss of phytoplankton (grazing, sinking). Heatwave intensity is the mean temperature anomaly during the heatwave relative to the 90th percentile threshold. Water color, total phosphorus (P), and *Daphnia* biomass (dry g m^{-2}) were measured during each heatwave as part of weekly summer sampling. If no sampling occurred during a heatwave, values were taken from the closest preceding sampling event to the heatwave. Heatwaves without covariate data available were excluded from the plot.

nutrient additions, and we observed similarly strong early-season responses in 2018, a year of no nutrient additions. Early in the season, heatwaves may serve as a trigger for seasonal blooms (Sommer et al. 2012). Later in the summer, lower water viscosity during heatwaves could increase sedimentation of diatoms, while modeling shows that increased thermal stratification may bolster buoyant groups of phytoplankton such as cyanobacteria (Walsby et al. 1997; Jöhnk et al. 2008; Paerl and Huisman 2009; Huber et al. 2012). Heatwave effects may consequently be tied to the phenology and seasonal succession of phytoplankton, zooplankton, or fish communities (Huber et al. 2010; Feiner et al. 2022).

Increases in chlorophyll concentrations following heatwaves could indicate changes in phytoplankton biomass, but may also be influenced by changes in phytoplankton community composition or cellular chlorophyll concentration (Supporting Information S1; Yoder 1979; Thompson et al. 1992). For example, chlorophyll concentrations might have increased if heatwaves triggered a shift toward chlorophyll-rich chlorophytes from diatoms or cyanobacteria (Reynolds 2006). At the cell level, higher temperatures can cause individual phytoplankton to increase chlorophyll content (Thompson et al. 1992). Finally, while our samples were representative of the epilimnion of each lake, changes in the vertical position of phytoplankton because of the effects of heatwaves on water column stability could also affect surface concentrations (Longhi and Beisner 2009; Supporting Information S1). Overall, phytoplankton adaptation to and recovery from heat stress occurs on the order of hours (Hemme et al. 2014), while our estimates of changes in chlorophyll span the mean length of heatwaves (8 d). While these factors are undoubtedly at play, the observed magnitude of increase in chlorophyll concentrations cannot be fully explained by these non-biomass increasing mechanisms.

Our study investigated the effects of multiple heatwaves on epilimnetic chlorophyll throughout a series of whole-lake experiments. We manipulated factors thought to influence phytoplankton and their response to heatwaves (Carpenter et al. 2011; Wilkinson et al. 2018; Buelo et al. 2022b). We documented temporary increases in surface chlorophyll in 24 out of 29 cases, providing strong evidence that heatwaves increase chlorophyll across a range of conditions. Chlorophyll concentrations even increased in our unmanipulated reference lake. Increased growth due to higher temperatures is one possible reason for the responses we observed. Another is reduced mortality due to lower grazing because of zooplankton community change during heatwaves. Increased stratification during heatwaves could also change phytoplankton sinking rates. Focused research on phytoplankton growth and loss processes embedded within long term observations will help discern among hypotheses.

Author Contributions

Daniel K. Szydlowski led the manuscript and was advised by Grace M. Wilkinson. All authors came up with the research questions. Daniel K. Szydlowski and Katie A. Bollini conducted the statistical analyses. Grace M. Wilkinson and Michael L. Pace led the field data collection. Daniel K. Szydlowski wrote the paper with input from all authors.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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