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RESEARCH ARTICLE

# Future warming reshapes inorganic nutrient and plankton dynamics in a temperate lake

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## *Abstract*

Lakes are experiencing high temperatures and frequent phytoplankton blooms. These events threaten the health of lake ecosystems. Phytoplankton respond to lake warming in various ways, making it challenging to predict changes in community composition. Although understanding the effects of lake warming on phytoplankton communities is crucial for lake management, these effects are not clear and have been a matter of debate due to contrasting observations. Here we use a data-informed, trait-based model to disentangle and project, based on future warming scenarios, the effects of temperature on the dynamics of inorganic nutrient (phosphate) and plankton at Greifensee, a medium-size eutrophic lake near Zurich, Switzerland. Assuming identical thermal characteristics among phytoplankton size classes, we find that phosphate concentrations and phytoplankton mean cell size increase with rising lake temperature. This is driven by the interplay between reduced growth and nutrient uptake by all phytoplankton under sub-optimal temperatures, resulting in higher summer nutrients and intensified zooplankton grazing on smaller phytoplankton cells. The small phytoplankton cells typically occurring during winter and spring are replaced by large phytoplankton cells. In addition, peaks of phytoplankton biomass, typically occurring in early summer, emerge earlier, in early spring. The earlier occurrence of these peaks is caused by a shift in the optimal temperature for phytoplankton growth. Although our results are based on various modeling approximations, they highlight the importance of combining observations and trait-based modeling for gaining insights into the future compositions of lake phytoplankton and establish a foundation for examining lake ecosystems in a warming world.

Most lakes on our planet are under threat by climate change and, specifically, by increasing temperatures (O'Reilly et al. 2015; Woolway et al. 2022). The increase in lake water surface temperature, hereafter water temperature, couples with changes in nutrient conditions in the lake to alter the interactions and compositions of lake communities. This may dampen trophic transfer efficiencies, with serious impacts on the stability and productivity of lake food webs (Strecker et al. 2004; Barneche et al. 2021). Increasing occurrences of anomalous algal blooms (dominated, for example, by cyanobacteria) are observed in eutrophic lakes worldwide, especially in connection to rising temperatures (Paerl and Huisman 2008; Ho et al. 2019). However, the mechanisms underlying these blooms remain unclear. Contrary to expectations, clear multidecadal warming trends and reductions in nutrient levels were linked in several temperate lakes (e.g., Pomati et al. 2020) to the dominance of large phytoplankton cells. Hence, a better understanding of the thermal responses of plankton communities is key to managing lake ecosystems in a warming world.

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The effect of temperature on lake phytoplankton communities can be of two types: (1) direct effects can alter metabolic processes of cells and (2) indirect effects can reshape the interactions of biotic and abiotic components (Zohary et al. 2021). Elevated temperatures can indirectly affect phytoplankton nutrient uptake by varying autotrophic metabolic rates and nutrient recycling by varying remineralization rates (Vanni 2002; Dory et al. 2024). Additionally, temperature affects the composition of phytoplankton communities indirectly by enhancing zooplankton grazing, which can favor grazer-resistant phytoplankton species (Sommer and Lewandowska 2011; Lürling 2021). The synergistic direct and indirect effects of temperature can have complex repercussions on phytoplankton communities. These repercussions are frequently observed, but they remain difficult to disentangle and predict.

Warming-induced changes in the seasonal succession of phytoplankton have been modeled and observed in different European lakes over the last two decades (reviewed in Winder and Sommer 2012; Vadadi-Fülöp and Hufnagel 2014). Phenological shifts in planktonic communities impact key lake ecosystem functions such as productivity, diversity, and trophic transfer efficiency (Strecker et al. 2004; Woolway et al. 2022). Minimal predator–prey models proposed that earlier onsets can be caused by warming-induced shifts or decoupling of plankton dynamics (Scheffer et al. 2001; De Senerpont Domis et al. 2007a). A competition model based on several phytoplankton species found that warming-induced shifts observed in phytoplankton succession were driven by species-specific responses to temperature change (De Senerpont Domis et al. 2007b). Another way temperature can influence key ecosystem functions is by altering the size composition of phytoplankton, often with opposing effects, especially in the context of temperate lakes. Some mesocosm experiments found that warming favors small phytoplankton cells (Yvon-Durocher et al. 2011; Rasconi et al. 2015), whereas others observed a shift toward large cells (Rüger and Sommer 2012; Yvon-Durocher et al. 2015). Long-term field studies also showed similar contrasting results: high water temperatures fostered both large (Pomati et al. 2020; Dory et al. 2024) and small phytoplankton (Zohary et al. 2017).

The major effects of warming on phytoplankton sizes appear to be driven by temperature-mediated trophic interactions and resource availability (Murphy et al. 2020; Zohary et al. 2021). However, these two drivers are confounded in natural environments and that limits our ability to make sound predictions on the compositions and dynamics of planktonic communities in lake ecosystems. Mathematical models are useful tools for disentangling the interacting effects of temperature on lake plankton. Recent modeling investigations included more comprehensive ecological interactions between plankton communities and the environment. By considering seasonal variations in light, water temperature, mixed layer depth, and nutrients in a plankton ecosystem model, Cagle and Roelke (2021) and To et al. (2024) found that grazing characteristics of zooplankton regulate the succession of different phytoplankton species and their community composition in temperate lakes. However, such modeling investigations have not been implemented in combination with a high degree of biotic and abiotic data inputs. A data-informed model that is verifiable by in-situ observations can strengthen our understanding of the effects that lake warming can have on the composition of phytoplankton communities.

Building on our previous modeling study (To et al. 2024), we present here an updated data-informed trait-based model to explain plankton dynamics in a specific temperate lake and to explore lake ecosystem responses under different warming scenarios. Greifensee is a medium-size eutrophic lake near Zurich (Switzerland). Multi-decadal observations show that Greifensee is phosphorus-limited (Eyring et al. 2025, plotted in Supporting Information Fig. S10) and has experienced multi-decadal warming and re-oligotrophication trends (Pomati et al. 2020; Merz et al. 2023). The composition of the phytoplankton community in the lake was found to be sensitive to long-term changes in thermal and nutrient conditions (Bürgi et al. 2003; Monchamp et al. 2017), making Greifensee an ideal lake for studying the impacts of changing temperature on the abundance and community composition of lake plankton. This new model version includes additional physiological details on the thermal dependence of the plankton communities (presented in Methods) and assumes that temperature impacts phytoplankton growth and zooplankton grazing through data-derived relationships. The physical processes in the model are driven by observed environmental data and the model outputs are calibrated against averaged nutrient concentration, phytoplankton and zooplankton biomasses, and size data collected at Greifensee. The calibrated model is then run into the future to predict the evolution of the ecosystem under projected climate change scenarios. We considered three Representative Concentration Pathways (RCPs), RCP 2.6, RCP 6.0, and RCP 8.5, reflecting low, medium, and high emission scenarios, respectively. We aim to understand the effect of increased water temperature on future nutrient concentrations, plankton biomasses, size composition of the phytoplankton community, and timing of the peaks in phytoplankton biomass.

## Methods

### Size-based plankton ecosystem model

Building on a previous modeling study (To et al. 2024), we apply a size-based plankton model to a real lake, Greifensee. The model consists of: (1) an inorganic nutrient, $P$ (i.e., phosphate, $PO_4^{3-}$), (2) a community of phytoplankton $A_i$, subdivided into ten size classes ($i = 1, \ldots, 10$), covering the phytoplankton size range typically observed at Greifensee (1–200 $\mu$m ESD), (3) a community of herbivorous zooplankton $Z_j$ subdivided into two size classes ($j = 1, 2$), and (4) a detritus

pool, $D$ (Fig. 1). The phytoplankton community ($A_i$) exploits nutrients and light for growth. Water temperature affects both the growth of phytoplankton and the grazing of zooplankton. Since phosphate is considered the most limiting inorganic nutrient for most lakes (Schindler 1978), all state variables are expressed in units of $\mu$M P. A detailed model description, including equations and formulation of processes, is reported in Supporting Information Text S1. In the following, we present the novel features of the model, which include the temperature dependence of phytoplankton growth and zooplankton grazing and the ecological projections under the different warming scenarios.

### Temperature dependences

The temperature dependences of phytoplankton growth and zooplankton grazing represent key extensions of the model introduced by To et al. (2024) (*see* Supporting Information Text S1 for the full model formulation). The temperature-regulated growth of phytoplankton is described by the following function (Norberg 2004):

$$E(T) = e^{0.063T} \cdot \left[1 - \left(\frac{T - T_{opt}}{\sigma_T}\right)^2\right] \quad (1)$$

with $T$ representing temperature (°C). $T_{opt}$ and $\sigma_T$ representing, respectively, thermal optima and thermal tolerance. The curve is set to reflect the observed range of temperatures, between 3 and 23°C (Eq. 1 and Fig. 2e). Zooplankton grazing is regulated by temperature through the following function (Fig. 2f):

$$\psi(T) = Q_{10}^{\frac{T - T_{ref}}{10}} \quad (2)$$

This function represents how grazing scales with environmental temperature, $T$, through the $Q_{10}$ coefficient (Supporting Information Table S1) and the reference temperature, $T_{ref}$,

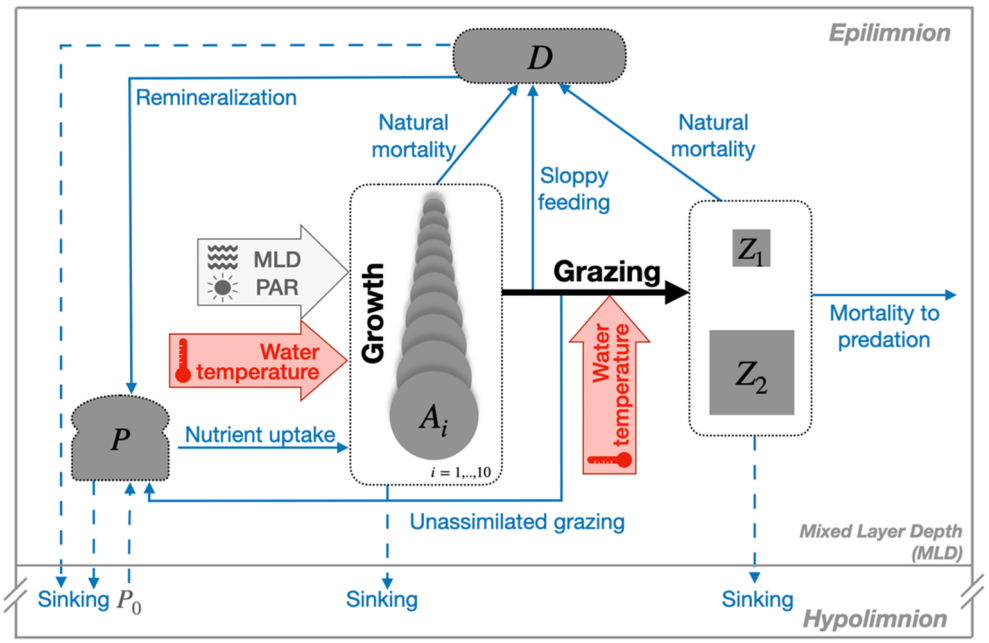


**Fig. 1.** Schematic of the size-based planktonic model. The general structure and the various model components are based on our previous work (To et al. 2024). The new features of this model are highlighted in red. These are the temperature dependences of phytoplankton growth and zooplankton grazing. The model assumes a zero-dimensional spatial configuration, the so-called slab physics approximation (Anderson et al. 2015; Post et al. 2024). The epilimnion contains a plankton ecosystem consisting of four components, inorganic phosphate ($P$), phytoplankton, ($A_i$), zooplankton, ($Z_j$), and detritus, ($D$). Phytoplankton, ($A_i$), is subdivided into $i$ size classes (with $i = 1, \ldots, 10$) and zooplankton, $Z_j$ (with $j = 1, 2$), is subdivided into 2 size classes, $Z_1$ and $Z_2$. Phytoplankton growth and zooplankton grazing are size-dependent. The depth of the epilimnion reflects the Mixed Layer Depth (MLD). The blue arrows indicate ecological and biogeochemical processes (solid lines) and physical processes (dashed lines). Environmental forcing to this model is provided by in-situ observations of photosynthetically active radiations (PAR), mixed layer depth (MLD—an indicator of lake mixing), and water temperature. To approximate real-world grazing, the grazed material is split into: (1) a portion that is not ingested (due to sloppy feeding) and is immediately lost into detritus, (2) a portion that is ingested and assimilated by zooplankton, and (3) an additional portion that is not assimilated after being ingested and is excreted and quickly remineralized into inorganic nutrients. The loss of zooplankton to higher order predation is density-dependent and formulated as a quadratic function. We assume that the loss of phosphate from the epilimnion is recharged through changes in MLD by a constant source, $P_0$, from the hypolimnion. We determined the value $P_0$ based on average winter concentrations of phosphate, when the entire water column is well mixed and phosphate is homogeneously distributed throughout it. The detailed model configuration and all equations describing the processes shown in the schematic are reported in Supporting Information Text S1.

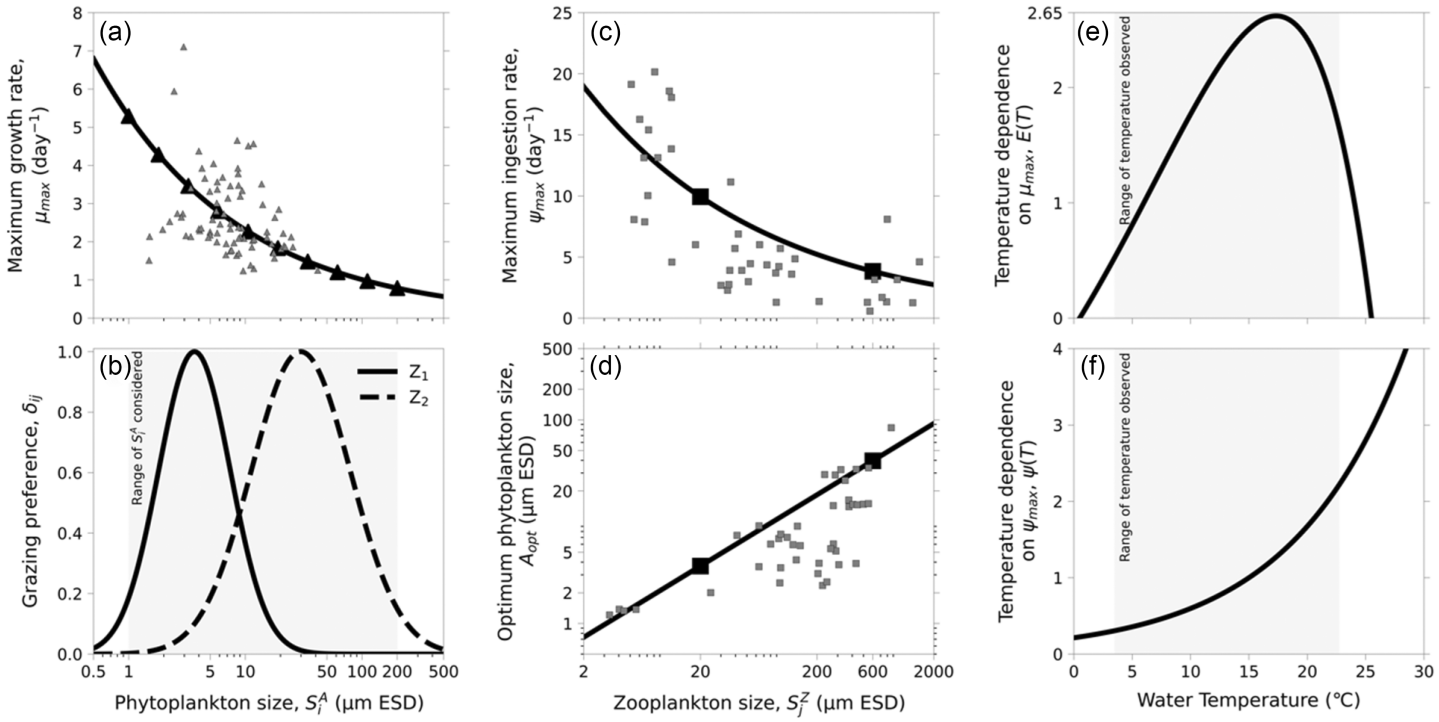


**Fig. 2.** Model assumptions related to phytoplankton growth and zooplankton grazing. (**a**) Allometric relationship defining maximum growth rates, $\mu_{max}$, for a given phytoplankton size $S_i^A$. (**b**) Size-grazing breadth of the two zooplankton over a range of phytoplankton size classes. Allometric relationships defining (**c**) maximum ingestion rates, $\psi_{max}$, and (**d**) optimal phytoplankton size, $A_{opt}$, for a given zooplankton size $S_j^Z$. The community-wide temperature dependence on (**e**) phytoplankton growth, $E(T)$, and (**f**) zooplankton grazing, $\psi(T)$. The gray triangles and squares are the data points obtained from literature compilations by Edwards et al. (2012), (a); Hansen et al. (1994), (c); and Hansen et al. (1997), (d). Black triangles and squares represent the specific size values considered in this study for, respectively, phytoplankton and zooplankton. Shaded areas in panel (b) represent the range of phytoplankton sizes considered in this study, whereas in panels (e) and (f) represent the present observed range of water temperatures at Greifensee.

representing the temperature at which no factorial change in maximum ingestion rate of zooplankton occurs (set to 15°C, Supporting Information Table S1). The value of the $Q_{10}$ coefficient was determined from a range of values observed by Hansen et al. (1997) for the maximum ingestion rate of Flagellates, Ciliates, and Copepods (functional groups abundant at Greifensee). In our model, the thermal optima ($T_{opt}$) and the thermal tolerance ($\sigma_T$) for phytoplankton growth and the $Q_{10}$ coefficient for zooplankton grazing are assumed constant. This assumption implies that different phytoplankton and zooplankton size classes have identical thermal responses in relation to, respectively, growth and grazing. These temperature dependencies allow us to examine the effects of temperature on phytoplankton growth and zooplankton grazing and to investigate possible changes to lake ecosystem components when temperature increases.

### Ecological projections based on climate change scenarios

The model parameterization obtained from the community-integrated outputs of the standard model run produces model results that reflect current average annual conditions (in terms of nutrient concentrations, total phytoplankton and zooplankton biomasses and aggregated phytoplankton size structures) at Greifensee. The details regarding model calibration, including the data for calibration and the conversion procedures of data, and the parameter table are reported in Supporting Information Text S3. With this parameter configuration, we forced the model with new temperatures, representing three climate change scenarios, based on three Representative Concentration Pathways (RCPs), Supporting Information Table S4, expected by the end of this century (i.e., year 2099) in the region covering Greifensee, between 40°N and 60°N. We considered average and seasonally uniform increases in water temperature by 1.4°C (RCP 2.6), 2.5°C (RCP 6.0), and 4.2°C (RCP 8.5). However, our future projections did not include physical feedback that could be induced by increasing temperatures, like changes in lake stratification (but *see* Supporting Information Text S5 for a sensitivity run exploring the impact of this omission on our results under scenario RCP 8.5). Also, for these climate change scenarios, we run the model to steady-state for 10 years, using the same annual forcing for every year, and considering only the final year for analyses. In our analyses, annual seasons are defined as follows: winter, from December to February; spring, from March to May; summer, from June to August; and autumn, from September to November.

### Sensitivity analyses on phytoplankton thermal traits

For each temperature scenario, we undertook a series of sensitivity analyses on the thermal optima and the thermal tolerance of the phytoplankton community. These sensitivity analyses examine the effects on the model results (annual medians) under variations of ± 15% from standard values (Fig. 3). These thermal traits play a key role in regulating phytoplankton responses to temperature change but are difficult to measure in natural systems and their values can vary within and between species (Thomas et al. 2016). The range of variability we considered for these sensitivity analyses covers the values of thermal optima and thermal tolerance observed in freshwater species (Thomas et al. 2016).

## Results

### Current status in the seasonal dynamics of lake ecosystem components

We focus on the seasonal dynamics of four major variables: (1) phosphate concentration, (2) phytoplankton biomass, (3) zooplankton biomass, and (4) phytoplankton (biomass-weighted) mean biovolume. Biomasses are total community aggregates, whereas mean biovolume is a total community average. Biomass and biovolume reflect magnitude and structure of the phytoplankton and zooplankton communities, providing useful macroecological insights (Acevedo-Trejos et al. 2018; To et al. 2024). The simulated inorganic nutrient dynamics capture the average annual cycle of epilimnetic phosphorus observed at Greifensee (Fig. 4a). The nutrient concentration is characterized by a steady decline, starting at the beginning of the year and lasting for about 3 months; it remains low throughout summer and for part of autumn, and it restocks by the end of the year (Fig. 4a).

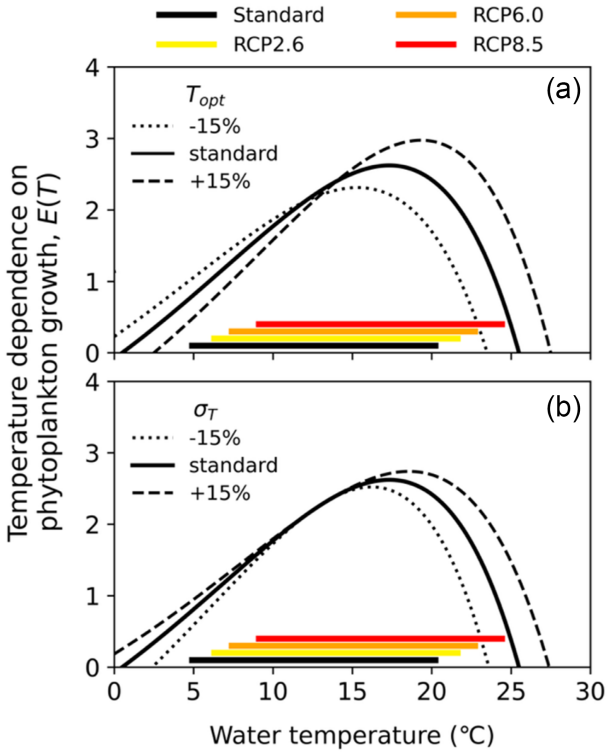


**Fig. 3.** Temperature dependence curves tested in the sensitivity analyses. These curves result from changes of ± 15% from standard values in (**a**) thermal optima, $T_{opt}$, and (**b**) thermal tolerance, $\sigma_T$, for phytoplankton growth. The standard values for $T_{opt}$ and $\sigma_T$ are, respectively, 13°C and 12.5°C (black curves). The colored bars represent the annual ranges of water temperatures for various warming scenarios: dark (current average state); yellow (RCP 2.6); orange (RCP 6.0); and red (RCP 8.5).

The simulated plankton dynamics also capture the observed community-integrated biomass qualitatively well (Fig. 4b). The model captures the biomass accumulation of phytoplankton during spring, summer, and autumn, and reproduces correctly the low phytoplankton biomass levels after the summer and autumn peaks (Fig. 4b). However, the model produces a first winter peak that is not shown by the data, underestimates the spring biomass, and overestimates the summer biomass (Fig. 4b). The simulated zooplankton biomass matches well with the autumn and winter observations, despite a slight overestimation for the spring peak (Fig. 4c). A mismatch is noticeable in June and July, when the simulated zooplankton biomass declines due to the dominance of large and less grazable phytoplankton (Fig. 4c,d). In summary, despite being an approximation of the real lake in terms of physics and ecology, the model captures several general features of the phytoplankton and zooplankton seasonal cycles; namely, the spring, summer, and autumn biomass accumulations of phytoplankton and the spring biomass peaks of zooplankton.

A good match is also obtained between the simulated and observed seasonal patterns in the community-mean biovolume of phytoplankton. In general, both model and data show small mean biovolume in late winter and beginning of spring (Fig. 4d), when smaller cells outcompete larger cells due to weaker grazing on smaller cells (Fig. 4c). Relatively larger phytoplankton cells are present during summer and autumn (Fig. 4d), when zooplankton grazing on smaller cells increases and the larger, less grazable cells gain dominance. Additionally, we find that the phytoplankton size composition is strongly controlled by grazing characteristics, namely, the allometric scaling of grazing (i.e., maximum ingestion rate and optimal phytoplankton size) and the size-grazing breadth of zooplankton (Supporting Information Figs. S4A and S6I,J,L).

### Expected future seasonal dynamics of major variables

#### *Alterations in nutrient dynamics*

We find seasonal changes in the nutrient dynamics under the warming scenarios, with the strongest alteration occurring under RCP 8.5 (water temperature increased by 4.2°C with respect to the current average). The most prominent change in the nutrient concentration occurs in summer and autumn, that is, from July to October, when there are excessive

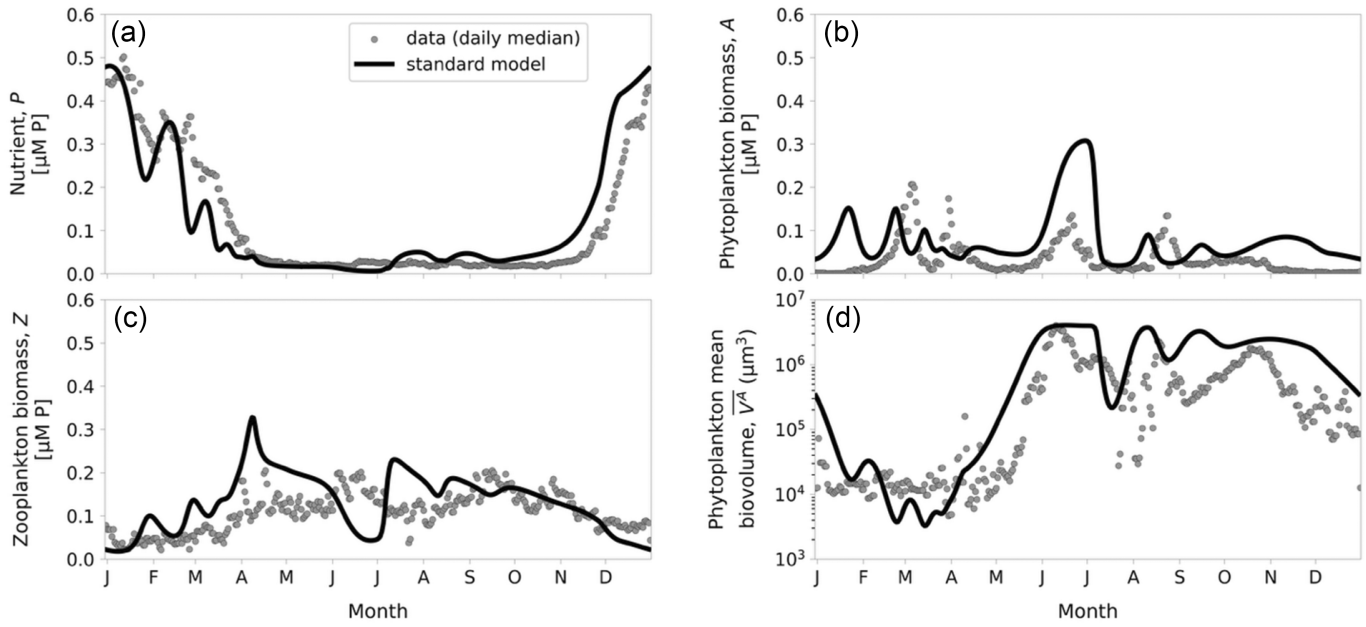


**Fig. 4.** Results of the standard run showing temporal dynamics of (**a**) nutrient concentration, (**b**) phytoplankton community biomass concentration, (**c**) zooplankton community biomass concentration, and (**d**) phytoplankton mean biovolume. The gray dots represent the observational data collected in the epilimnion by the underwater imaging device (*see* details about data transformation in Supporting Information Text S3) and the black lines represent the model outputs. The model is run to steady-state over 10 years and we show here the results of the 10$^{th}$ year. The observations are median daily values over 3 years of data (from March 2019 to December 2022).

nutrient accumulations in the lake, and accumulation intensifies with the warming scenarios (Fig. 5b). Under RCP 8.5, the nutrient accumulation in summer reaches an annual maximum, a pattern that contrasts sharply with the current status (standard run) when the highest nutrient level occurs in winter (Fig. 5b). This summer nutrient peak coincides with a decline in phytoplankton biomass, caused by the unfavorable temperature conditions for growth experienced by the system under RCP 8.5 (Supporting Information Figs. S7A and S8). Warming also causes an increase in the overall annual nutrient concentration in the epilimnion. Under RCP 8.5, the annual median nutrient concentration is about four times higher than that under the current status, that is, 0.2 $\mu$M P (RCP 8.5) vs. 0.05 $\mu$M P (current status), Fig. 5c. In summary, our model projections suggest that as the lake warms up, phosphorus redistributes from the phytoplankton pool to the dissolved nutrient pool, particularly in summer, leading to elevated phosphate concentration in the epilimnion.

### *Alterations in plankton phenology*

As the lake warms up, the model shows lower winter peaks and earlier summer peaks of phytoplankton (Fig. 5d). The timing of the summer peaks depends on the timing of thermal optima, which shifts with the warming scenarios (Supporting Information Fig. S7C). Under RCP 8.5, the summer phytoplankton peak advances by about 2 months, from July to May. The earlier arrival of the summer peaks shortens the corresponding period of low phytoplankton biomass after the spring peaks. We also notice an increased number of minor phytoplankton peaks during the year as warming intensifies, with small reductions in annual median phytoplankton biomass concentrations (Fig. 5e). In summary, the increase in water temperature advances the timing of the major phytoplankton peaks and increases the number of minor peaks occurring throughout the year.

The model results also show phenological shifts for zooplankton. The timing of the first zooplankton peak in April remains the same in all climate scenarios, but the second peak moves earlier with the severity of the RCP scenarios (Fig. 5f). Consequently, the period between the first and the second zooplankton peaks shortens by 2 months under RCP 8.5. Also, the zooplankton biomass in late summer decreases noticeably under RCP 8.5 compared to other scenarios, due to the decline in phytoplankton growth (Supporting Information Fig. S8). The annual median zooplankton biomass is lower in RCP 8.5 compared to other scenarios (Fig. 5g). In summary, major alterations in the phenology of zooplankton include a reduction in the period between the first and the second peak and a reduction in the summer biomass.

### *Alterations in phytoplankton mean biovolume*

An elevated water temperature increases the mean biovolume of phytoplankton and reduces the range of size variations during the year. As the lake warms up from winter to spring, relatively smaller cells, such as *Rhodomonas* and *Chlorophytes* (Supporting Information Table S5), are replaced by larger cells like *Dinobryon* and *centric Diatom*, resulting in

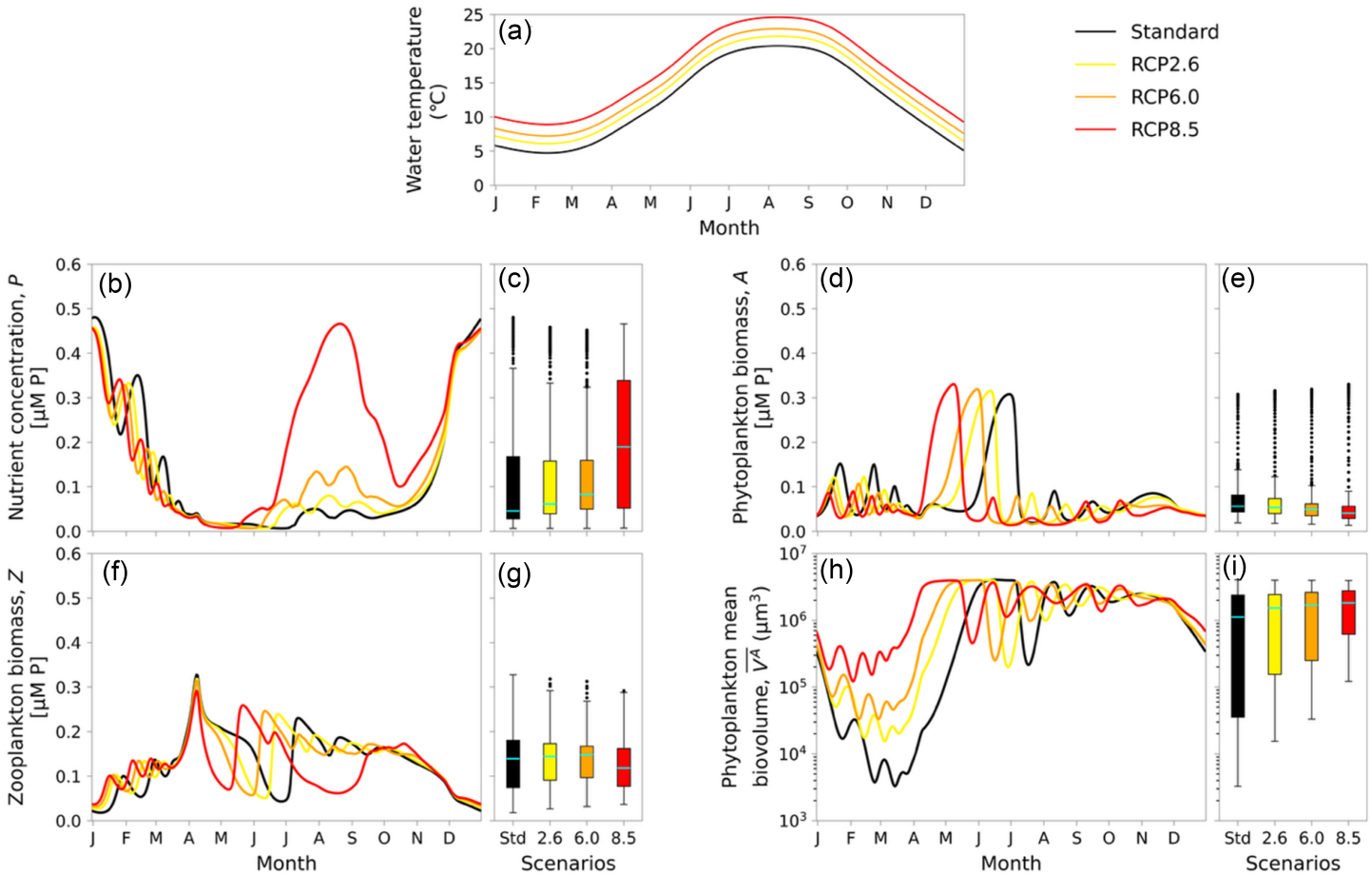


**Fig. 5.** Results of climate change scenarios compared to the current average status of the lake (standard run, black lines and Fig. 4). The climate change scenarios, RCP 2.6, RCP 6.0, and RCP 8.5 simulate an average and seasonally uniform increase in water temperature by, respectively, 1.4°C, 2.5°C, and 4.2°C (**a**). The results show temporal dynamics of (**b**) nutrient concentration in the epilimnion, (**d**) phytoplankton biomass, (**f**) zooplankton biomass, and (**h**) phytoplankton mean biovolume. Boxplots (panels **c**, **e**, **g**, and **i**) show the overall seasonal variability (width) and median (cyan lines) of the corresponding variables. The model is run to a steady annual cycle over a period of 10 years with repeated annual forcing, the results shown are those of the 10$^{th}$ year.

increasing mean biovolume (Fig. 5h). Under RCP 8.5, the dominance of relatively larger phytoplankton like *Uroglena* (Supporting Information Table S5) appears already in April, 2 months earlier than in the current status (red vs. black line, Fig. 6h). In summary, a warmer lake fosters a narrower size diversity of phytoplankton and reduces seasonal variations in mean biovolumes (Fig. 5i).

### Sensitivity analysis on phytoplankton thermal traits under future scenarios

We examined the sensitivity of the model results by varying the values of thermal traits related to phytoplankton growth—these are thermal optima ($T_{opt}$) and thermal tolerance ($\sigma_T$)—by $\pm 15\%$ from standard values. The results show that, under future warming scenarios, the nutrient concentration, among other variables, is most sensitive to changes in the thermal traits. A reduction in either of the thermal traits leads to a higher median nutrient concentration, whereas an increase in either of the thermal traits leads to a lower median nutrient concentration (Fig. 6). These changes are exacerbated by the severity of the warming scenarios. Under RCP 8.5 (Fig. 6c), the median nutrient concentration increases by at least 200% when the phytoplankton community is characterized by lower values of thermal traits (i.e., lower tolerance to higher temperatures, Fig. 3). Such higher nutrient concentrations are caused by reduced growth of phytoplankton, from spring to autumn, due to a less suitable temperature for growth (Supporting Information Fig. S9G,I). Additionally, lower $T_{opt}$ (or $\sigma_T$) for phytoplankton growth leads to pronounced reductions in phytoplankton and zooplankton biomasses and in phytoplankton mean biovolume, particularly under RCP 8.5 (Fig. 6c). A higher $T_{opt}$ (or $\sigma_T$) for phytoplankton growth does not induce as many variations to the model variables; even under RCP 8.5, the greatest relative change is less than 50%. That is because higher thermal trait values produce a more heat-tolerant phytoplankton community (Fig. 3).

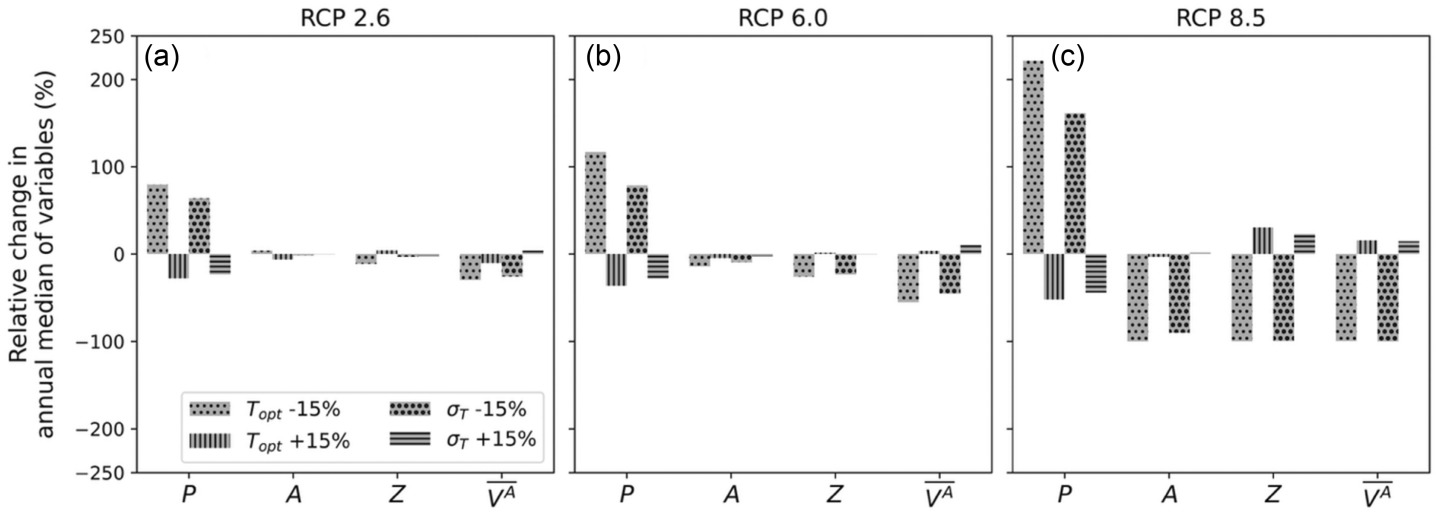


**Fig. 6.** Sensitivity of model variables (annual medians) caused by ± 15% changes from standard values of thermal optima ($T_{opt}$) and thermal tolerance ($\sigma_T$) for phytoplankton growth, in different climate change scenarios: (**a**) RCP 2.6, (**b**) RCP 6.0, and (**c**) RCP 8.5. The model variables are nutrient concentration, *P*; phytoplankton biomass, *A*; zooplankton biomass, *Z*; and phytoplankton mean biovolume, $\overline{V^A}$.

## Discussion

Mounting evidence over the last two decades shows rising lake temperatures on a planetary scale, with European temperate lakes expected to experience the fastest warming trend (Woolway et al. 2022). The consequences of rising temperatures on the physiology and ecology of plankton are far from clear. Under future climate change scenarios, our model predicts increased epilimnetic phosphate concentrations, advancements in phytoplankton biomass peaks, and dominance of relatively larger phytoplankton at Greifensee. We also find that a phytoplankton community with lower thermal optima or narrower thermal tolerance leads to even higher accumulation of phosphate due to the less favorable temperature ranges for phytoplankton growth and, thus, lower nutrient uptake.

### Current seasonal patterns of nutrients and phytoplankton concentrations

With respect to the current average state of Greifensee, the seasonal pattern of phosphorus dynamics produced by the model matches well with the observational data and reflects the typical nutrient dynamics of temperate lakes, which are characterized by high nutrient concentrations in winter and low in summer (Sommer et al. 2012). In temperate lakes, relatively high phosphorus concentrations at the beginning and the end of the year coincide with limited light and sub-optimal temperatures, resulting in reduced phytoplankton growth and nutrient uptake rates (Staehr and Sand-Jensen 2007; Sommer et al. 2012). The June–July peaks in the observed phytoplankton and zooplankton biomasses coincide, whereas the model results show a slight temporal shift, with zooplankton peaking shortly after phytoplankton. This small delay, typical of predator–prey systems, is an expected feature given the general resource-prey–predator structure of our model. We find that annual variations in mean phytoplankton biovolume are characterized by higher abundances of smaller phytoplankton (e.g., *Rhodomonas*, *centric Diatom*) in spring, larger phytoplankton (e.g., *Dinobryon*, *Uroglena*) in summer, and intermediate-size phytoplankton (e.g., *Cryptophytes*) in autumn. These patterns are consistent with the general phytoplankton dynamics expected to occur when interactions between inorganic nutrient limitation and grazing pressure are primary driving factors of lake ecosystems (Vanni and Temte 1990; Sommer et al. 2012). Our results are consistent with previous size-based models (Banas 2011; Taniguchi et al. 2023; To et al. 2024) showing that the biomass of phytoplankton is regulated by variations in resources like light and nutrients, whereas the annual variations in the phytoplankton size composition are strongly controlled by grazing characteristics like the size-feeding breadth of zooplankton. By using appropriate zooplankton size-feeding characteristics under the influence of major physical factors in lakes, we capture and elucidate the phenology of phytoplankton biomass and size composition at Greifensee.

### Drivers of future increase in phosphate concentration

Our model projections show that epilimnetic phosphate concentrations increase with the severity of global warming. This increase is driven by a mechanism of internal nutrient loading. A shift in phytoplankton phenology, due to sub-optimal temperature conditions for phytoplankton growth, reduces phosphate uptake and phytoplankton biomass during summer times, accumulating unused phosphate in the epilimnion. As the world warms up, this internal accumulation of phosphorus adds up to the expected increase of nitrogen and phosphorus runoff from agricultural catchments to freshwater systems (Ockenden et al. 2017), a synergy that can

potentially lead to rampant eutrophication (Moss 2011; Meerhoff et al. 2022). While part of the summer phosphate retention in our model depends on the uniform thermal characteristics we considered for the different phytoplankton size classes, responses to temperature in lakes may be species-specific (Thomas et al. 2016; Bestion et al. 2018). In some temperate lakes (such as Greifensee), elevated summer temperatures may favor cyanobacteria, which can, in turn, influence phosphate dynamics in the epilimnion through biological feedbacks, including cyanobacterial senescence, nitrogen co-limitation, and internal recycling processes (Cottingham et al. 2015). In addition, higher temperatures lead to stronger lake stratification, altering nutrient and light availability, with possible impacts on competition, community composition, and phytoplankton dynamics (Tilzer and Goldman 1978; Donis et al. 2021). Stronger and longer stratification events (Winder and Sommer 2012; Woolway et al. 2021) can also disrupt the nutrient exchanges between epilimnion and hypolimnion, potentially contributing to epilimnetic phosphate retention (Supporting Information Text S5 and Supporting Information Fig. S5B). In summary, under warming conditions, epilimnetic phosphate dynamics can be shaped by a combination of several physical and biological factors. Our model provides a first-order approximation of these effects. Detailed quantifications of temperature-driven nutrient feedback would require explicit representation of species-specific thermal traits and lake-specific nutrient recycling mechanisms.

### Earlier accumulation of phytoplankton biomass driven by thermal optima

Our climate change scenarios produce earlier accumulations of summer phytoplankton biomass. Earlier formation of spring blooms in temperate lakes was detected by previous studies based on simulations and observations. For example, a dynamic diatom-daphnia model showed that under lake warming, a high phosphorus supply leads to earlier diatom spring blooms (Huber et al. 2008). A depth-resolved hydrodynamic model coupled to a simple phytoplankton growth model showed that earlier spring blooms can be triggered by changes in lake stratification patterns (Peeters et al. 2007). In our model, the earlier peaks of large phytoplankton are produced by a warmer winter that advances the timing of optimal temperature for the growth of all phytoplankton size classes but intensifies the grazing of zooplankton on small phytoplankton size classes. Thermal characteristics, like optimal temperature for growth, are important factors for driving seasonal succession in culture experiments comprising marine diatoms (Anderson and Rynearson 2020). Although our projections are largely consistent with these studies, a long-term observation conducted in a large Norwegian lake revealed delayed phytoplankton peaks (Moe et al. 2022). Their observation considered taxonomic details of the phytoplankton community and showed that the phenological changes of phytoplankton are contingent to the different succession patterns exhibited by individual taxa. Therefore, taxonomic details related to the different thermal responses in a community are important for understanding specific changes in the phenological patterns of phytoplankton (Thackeray et al. 2008; Segura et al. 2018). This shows the importance of considering size or taxonomic differences in thermal traits for capturing specific phenological trends.

### Changes in phytoplankton mean biovolume under increasing temperature

Changes in phytoplankton mean biovolume are driven, in our model, by thermally-regulated bottom-up (nutrient uptake by phytoplankton) and top-down (zooplankton grazing) processes. As temperature increases, the optimal temperature for phytoplankton growth occurs earlier and the summer temperatures become sub-optimal (Supporting Information Fig. S7C); whereas zooplankton grazing, which targets smaller phytoplankton, intensifies (Supporting Information Fig. S7B). These aspects interact not only to favor intermediate-sized phytoplankton cells (*Dinobryon*, *centric diatoms*; Supporting Information Table S5) over small-sized cells (*Rhodomonas*, *Chlorophytes*), but also to foster an earlier appearance of large-sized phytoplankton like *Uroglena*. Intensified grazing on smaller phytoplankton was observed in warmer freshwater environments (Winder and Sommer 2012). Analyses of time-series from eight Swiss lakes revealed a rising proportion of larger mixotrophic phytoplankton in summer than in winter, in association with higher temperatures, higher zooplankton abundances, and lower nutrient levels (Pomati et al. 2020). However, lakes characterized by weak zooplankton grazing may exhibit different responses. In Lake Kinneret (Israel), the prevalence of cyanobacteria in stratified summer waters (based on an eight-year observation) resulted from a strong selection by sinking processes on the better-suspended small phytoplankton (Zohary et al. 2017). Sinking was not included in our model because Greifensee has a relatively shallow mean depth (18 m), but this loss process can influence the size composition of phytoplankton communities (Zohary et al. 2017). While our results underscore the influence of enhanced grazing on phytoplankton community composition in a warmer Greifensee, they also suggest that temperature-driven community shifts depend strongly on the specific physical and biological characteristics of a lake.

### Thermal traits affect future nutrient concentrations

Temperature-driven changes in phytoplankton performance are mediated by species-specific traits such as optimal temperature for growth and thermal tolerance. Our sensitivity analyses suggest that future projections of lake nutrient dynamics strongly depend on these traits, which control phytoplankton growth and nutrient uptake efficiencies under varying temperature conditions. Previous modeling studies also showed that the thermal traits of phytoplankton regulate community responses. An ecosystem model resolving biogeochemical processes, for example, showed that alterations of the $Q_{10}$ factor can markedly change the community

composition of phytoplankton under the most severe climate change scenario (Anderson et al. 2024). An NPZ model driven by seasonal variations of temperature showed that accounting for species differences, especially in thermal optima, is important for accurately estimating the thermal sensitivities of phytoplankton (Chen 2022). In addition, optimal temperatures for phytoplankton growth may co-vary with nutrient and light availabilities (Edwards et al. 2016; Bestion et al. 2018) in ways that are not captured by our model. We suggest that measuring size-specific thermal trait values would be a crucial asset for modeling studies such as this study. These data would facilitate the formalization of a robust functional relationship between thermal traits and plankton sizes, a fundamental assumption for investigating the effects of temperature on plankton communities and the corresponding ecosystem feedback under climate change scenarios.

**Limitations and future directions**

Our results are based on a relatively idealized lake physics, which does not specify vertical stratification and lateral transport processes. We consider this choice appropriate for Greifensee, a relatively shallow lake that is typically fully mixed in winter and stratified into two distinct and homogenously mixed layers in summer (Mieleitner et al. 2008; Huntscha et al. 2018). Many studies (e.g., Livingstone 2003; Rempfer et al. 2010; Winder and Sommer 2012; Woolway et al. 2021) also show that, in a warming world, lakes will experience weaker mixing, with higher temperatures potentially structuring the water column into two stable layers, making our simplified physical scheme an appropriate first-order approximation. Our model assumes a biologically inactive hypolimnion with a constant reservoir of inorganic phosphate. This assumption may oversimplify internal nutrient recycling and loading processes. Future model applications—especially those that, in contrast to our focus, will target short-term transient dynamics—could incorporate hypolimnetic microbial and sedimentary processes to capture internal nutrient dynamics and microbial feedbacks in greater temporal and spatial detail. Additionally, several temperature-dependent processes, such as phytoplankton respiration (Robarts and Zohary 1987) and nutrient remineralization rates (Boscolo-Galazzo et al. 2018), were not considered in this study. Moreover, the absence of size-specific temperature dependencies in our model prevents niche differentiation with respect to thermal traits (Chen 2022). As a result, some phytoplankton size classes disappear during the simulations, limiting the model's ability to maintain all 10 size classes over time due to competitive exclusion (Hardin 1960), a common outcome in plankton models (e.g., To et al. 2025) but rarely observed in nature (the "paradox of the plankton", Hutchinson 1961).

Building on these limitations, future studies could examine size-specific thermal responses, incorporate more diverse zooplankton communities in relation to body size, or include additional temperature-dependent processes, such as phytoplankton respiration (Robarts and Zohary 1987) and nutrient remineralization (Boscolo-Galazzo et al. 2018). Spatially explicit hydrodynamic modeling and analysis of interannual variability would further improve our understanding of lake ecosystem dynamics under warming scenarios. Real-world, size-scaling relationships for optimal growth temperature and thermal tolerance remain scarce, although they are crucial for mechanistic investigations of size-based models, particularly in relation to synergistic effects of temperature, nutrients, and zooplankton grazing (Chen 2022; Litchman 2023; Pomati et al. 2020; Dory et al. 2024).

Our study provides a first-order assessment of how warming may influence phosphate concentrations, phytoplankton and zooplankton biomasses, and phytoplankton community composition in a temperate lake. Our model predicts three potential consequences in a warmer lake: increased epilimnetic nutrient retention, earlier onset of phytoplankton blooms, and a shift toward larger cells, resulting in higher mean biovolume. While our model parameters and forcing are site-specific and mostly relevant to Greifensee, the mechanisms identified are likely relevant to other temperate lakes exhibiting marked stratification. These findings highlight the importance of combining long-term monitoring programs, like those undertaken at Greifensee, with trait-based modeling to improve projections of lake ecosystem responses to climate change. Extending this framework to lakes with different nutrient regimes or capturing additional physical and ecological processes will help refine predictions and unravel implications for lake management under warming scenarios.

## Author Contributions

Sze-Wing To: Conceptualization (equal); Formal analysis (lead); Methodology and software (lead); Writing—original draft (lead); Writing—review and editing (supporting). Subhendu Chakraborty: Methodology and software (supporting); Supervision (equal); Writing—original draft (supporting); Writing—review and editing (supporting). Esteban Acevedo-Trejos: Methodology and software (supporting); Supervision (supporting); Writing—review and editing (supporting). Francesco Pomati: Funding Acquisition (equal); Project administration (equal); Writing—review and editing (supporting). Agostino Merico: Conceptualization (equal); Funding Acquisition (equal); Project administration (equal); Supervision (equal); Writing—original draft (supporting); Writing—review and editing (lead).

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## Conflicts of Interest

None declared.

## Data Availability Statement

The code, lake data, and model outputs associated with this study are available on Zenodo at https://doi.org/10.5281/zenodo.11390344.

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## Supporting Information

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

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