Warming combined with experimental eutrophication intensifies lake phytoplankton blooms

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Abstract
Phytoplankton blooms are a global water quality issue, and successful management depends on understanding their responses to multiple and interacting drivers, including nutrient loading and climate change. Here, we examine a long-term dataset from Lake 227, a site subject to a fertilization experiment (1969–present) with changing nitrogen:phosphorus (N:P) ratios. We applied a process-oriented model, MyLake, and updated the model structure with nutrient uptake kinetics that incorporated shifting N:P and competition among phytoplankton functional groups. We also tested different temperature and P-loading scenarios to examine the interacting effects of climate change and nutrient loading on phytoplankton blooms. The model successfully reproduced lake physics over 48 yr and the timing, overall magnitude, and shifting community structure (diazotrophs vs. non-diazotrophs) of phytoplankton blooms. Intra- and interannual variability was captured more accurately for the P-only fertilization period than for the high N:P and low N:P fertilization periods, highlighting the difficulty of modeling complex blooms even in well-studied systems. A model scenario was also run which removed climate-driven temperature trends, allowing us to disentangle concurrent drivers of blooms. Results showed that increases in water temperature in the spring led to earlier and larger phytoplankton blooms under climate change than under the effects of nutrient fertilization alone. These findings suggest that successful lake management efforts should incorporate the effects of climate change in addition to nutrient reductions, including intensifying and/or expanding monitoring periods and incorporating climate change into uncertainty estimates around future conditions.

Eutrophication and harmful algal blooms (HABs) are global water quality issues, increasing in occurrence and intensity in lakes worldwide (Paerl et al. 2018; Ho et al. 2019). Anthropogenic nutrient loading is the major driver of excess phytoplankton growth (Carpenter et al. 1998). Climate-related drivers including temperature and precipitation are additional influencing factors, with higher peak temperatures nearing phytoplankton growth optima, longer growing seasons leading to earlier blooms, and more extreme precipitation patterns driving alternating patterns of enhanced watershed nutrient loading during storm events and longer hydraulic residence times during drought periods (Peeters et al. 2007; Paerl et al. 2011; Prein et al. 2017; Sinha et al. 2017). Changes in nutrient and climate drivers can induce shifts from clear water- to phytoplankton-dominated state or from one dominant phytoplankton group to another, which often occur abruptly (Ratajczak et al. 2018). Most efforts to manage eutrophication in lakes focus on nutrients (Huo et al. 2018), but moving forward it is unlikely that the impacts of nutrients will occur independently from the impacts of climate change. Mitigating the negative effects of eutrophication and HABs requires a nuanced understanding of the interacting effects of external drivers (Elliott 2012).

Phosphorus (P) has been identified as the primary limiting nutrient in many lakes (Carpenter 2008), whereas nitrogen (N) is often a secondary or co-limiting nutrient (Sterner 2008). Importantly, low N supplies can trigger a shift in the phytoplankton community to favor N-fixing (diazotrophic) cyanobacteria (Hendzel et al. 1994; Gobler et al. 2016). Lake 227 at the IISD-Experimental Lakes Area (Ontario, Canada) is the site of a well-known whole ecosystem experiment, where...
experimental nutrient loading has provided insights into phytoplankton nutrient limitation, phytoplankton community succession, and the impacts of changing N:P stoichiometry. Lake 227 has been fertilized with P and N over the course of five decades (1969–present). Annual P loads to the lake have remained constant over the course of the experiment, and N loads have varied to produce three stoichiometric regimes of varying N:P ratio (molar ratios of 27:1 from 1969–1974, 9:1 from 1975–1989, and 0:1 from 1990–present). In response to a decrease in N loading, diazotrophic cyanobacteria came to dominate mid-summer phytoplankton blooms (Schindler et al. 2008; Paterson et al. 2011; Higgins et al. 2018). Lake 227 offers an opportunity to leverage a long-term fertilization experiment to characterize drivers of phytoplankton blooms, including not only experimentally manipulated nutrient stoichiometry but also independently co-varying environmental factors.

The response of lakes to concurrent drivers of eutrophication can be explored using process-oriented models, also known as mechanistic models (Couture et al. 2018; Page et al. 2018; Janssen et al. 2019). A variety of lake ecosystem models include physical processes and nutrient dynamics, varying in modeling approach, spatial dimensions, and complexity of process representation (Robson 2014). Models using a one-dimensional (1D) physical driver allow for the simulation of vertical stratification and mixing but assume horizontally homogeneous conditions across the lake (Saloranta and Andersen 2007). Small, seasonally stratified lakes with rapid horizontal mixing such as Lake 227 are ideally suited for 1D models, enabling relevant physical processes to be simulated while taking advantage of shorter runtimes and calibration demands relative to 3D models.

Here, we explore phytoplankton bloom dynamics using statistical approaches and process-oriented modeling to integrate climatic variables and fertilization as drivers of phytoplankton growth. Specifically, we aim to (1) characterize the long-term trends in in-lake and climatic conditions across the five-decade fertilization experiment, (2) assess the ability for a process-oriented model to capture the magnitude and composition of phytoplankton blooms under shifting N and P loading, and (3) disentangle the concurrent effects of climate and nutrient loading on phytoplankton blooms to inform management under multiple stressors.

**Methods**

**Study site and aim 1: Historical trends**

Lake 227 is a small (5 ha) headwater lake in northwestern Ontario, Canada. The hydrology of Lake 227 is relatively simple, with a bowl-shaped morphometry (mean depth 4.4 m, maximum depth 10 m) and negligible groundwater inputs. Lake 227 is dimictic with seasonal ice cover and experiences rapid horizontal mixing, so its mixing regime in addition to its small size and bowl-shaped morphometry makes it an ideal candidate for a 1D process-oriented model.

The five-decade experiment added artificial N and P loadings in molar ratios of 27:1 (“High N:P”; 1969–1974), 9:1 (“Low N:P”; 1975–1989), and 0:1 (“P-only,” 1990–present), with the magnitude of P loading held constant across fertilization regimes and N loading decreasing as N:P ratios decreased. From 1969–present, physical, chemical, and biological data were typically collected biweekly in Lake 227 during the ice-free season and 2–4 times during the ice-covered period. Daily meteorological data, including air temperature, wind speed, precipitation, and radiation, were collected at a station jointly operated with Environment and Climate Change Canada, located 4.1 km from Lake 227. Nutrient loads from the Lake 227 watershed were estimated using data from streams flowing into a nearby first-order (headwater) reference lake, Lake 239, which were monitored continuously for flow and weekly for nutrient chemistry during the ice-free season.

Measurements of wind speed, radiation, ice phenology, and inflow volume and temperature were scaled to the conditions at Lake 227. Wind speeds measured at the ELA meteorological station were scaled by an empirically determined factor of 0.527 to account for the wind sheltering effect of small lake size (Solinske 1982). Photosynthetically active radiation (PAR) measurements from the meteorological site were scaled by a factor of 2.22 to convert to total radiation (Meek et al. 1984). Gaps in PAR measurements were filled with the average value across the dataset for each Julian day. Inflow temperature was estimated according to the empirical relationship presented by (Erickson and Stefan (2000) for streams from the adjacent US state of Minnesota, 14 out of 39 of which were located in the same level III ecoregion as Lake 227:

\[
\text{Water temperature} (^\circ \text{C}) = 0.82 \times \text{Air temperature} (^\circ \text{C}) + 4.18
\]

(1)

Inflow volume and chemistry from the Lake 239 catchment (335 ha) were scaled by the catchment size of Lake 227 (49 ha) following previous examples (Higgins et al. 2018). Experimental P and N loadings to Lake 227 were added to the natural loads from inflowing streams to construct total nutrient loads. For variables with seasonal trends, gaps between measurements were filled via linear interpolation. For variables with no evident seasonal trends, gaps between measurements were filled with the mean value across the dataset. Dates of ice break-up and freezing were estimated from direct observations from Lake 239 each year, corrected for differences in lake size based on empirical relationships between lake size and ice phenology assessed during 2016 and 2017. The corrected ice break dates for Lake 227 ranged from 3 to 5 d earlier and corrected ice freeze dates ranged from 9 to 18 d earlier than dates observed for Lake 239.

We conducted statistical analyses of climate, nutrient, and phytoplankton data to determine trends in environmental conditions over time. Time series datasets included year-round measurements for meteorology, and measurements only from...
Salk et al. Phytoplankton bloom modeling in Lake 227

the ice-free season for lake and stream datasets. We determined trends in lake and stream data over time with a Mann–Kendall test with the Yue and Wang (2004) variance correction approach to account for the presence of autocorrelation in the data and trends in meteorological data with a Seasonal Mann–Kendall test (Supplemental Information). We detected potential change points in each dataset with Pettitt’s test. All statistical analyses and data visualization were carried out in R version 3.6.2 (R Core Team 2013). Code and data available from https://github.com/biogeochemistry/MyLake_Lake-227 (release v1.0; Salk 2021).

Aim 2: Lake modeling

MyLake is a 1D process-oriented model designed to simulate seasonal ice and snow cover, heat exchange and thermal stratification, N and P cycling, phytoplankton growth, oxygen and carbon dynamics, and water-sediment coupling (Saloranta and Andersen 2007; Couture et al. 2015; de Wit et al. 2018; Kiuuru et al. 2019; Markelov et al. 2019). The model has previously been applied to boreal lakes to simulate the response of P cycling to external P loading and climate change (Couture et al. 2014a, 2018). We chose MyLake for its ability to characterize key conditions in Lake 227, namely ice cover, thermal structure, and biogeochemical processes in both the water column and sediment.

At each daily time step of the MyLake model, the thermal structure of the lake is set up from surface and sediment heat fluxes, vertical diffusion, wind stress, and stream inflow. Chemical and biological reactions take place under a system of differential equations, and the vertical distribution of chemical species are influenced by diffusion and advection terms. The parameters associated with reactions may be adjusted by the user. Light attenuation is governed by the absorption, scattering, and shading of light by water, dissolved organic carbon, and phytoplankton cells. Phytoplankton growth and biomass accrual is determined by N and P uptake kinetics, light, and temperature and includes loss terms for respiration, sedimentation, and remineralization. Additional details for the MyLake model can be found in the user guide (Saloranta and Andersen 2007).

The MyLake phytoplankton module operates under P-limited growth kinetics, and carbon and N are subsequently incorporated into phytoplankton biomass according to user-specified stoichiometry. Because P is the main driver of phytoplankton biomass in Lake 227 (Paterson et al. 2011; Higgins et al. 2017), the MyLake module was a sensible choice for a simple model representing the processes relevant for phytoplankton dynamics. Furthermore, based on evidence that N:P loading ratios drive the phytoplankton community composition in Lake 227 (Schindler et al. 2008), we added N uptake kinetics to the reaction network for two phytoplankton groups. In this version, non-diazotrophs were supplied with a new equation that incorporated both P- and N-limited growth:

\[
\mu = \mu'(T) \left( \frac{P}{P^*+P} \times \frac{N}{N^*+N} \right)
\]

where \(\mu\) is the specific growth rate when light is nonlimiting, \(\mu'(T)\) is the temperature-dependent maximum attainable growth rate, \(P\) is the phosphate concentration, \(P^*\) is the half saturation constant for P uptake, \(N\) is the concentration of dissolved inorganic N (DIN), and \(N^*\) is the half saturation constant for N uptake (Zinn et al. 2004). Diazotrophs retained P-limited growth kinetics only, because N limitation was expected to be alleviated by N fixation:

\[
\mu = \mu'(T) \frac{P}{P^*+P}
\]

Particulate P (PP) was chosen as a proxy for phytoplankton biomass to assess model performance. PP is a state variable in MyLake, unlike biomass and chlorophyll that would require conversion factors and vary considerably in situ (Hecky et al. 1993). PP is monitored in Lake 227, enabling direct comparisons between observed and modeled concentrations. The vast majority of PP in Lake 227 is present in phytoplankton tissues rather than bacterial or allochthonous pools (Hecky et al. 1993; Elser et al. 1995).

MyLake includes a global parameter accounting for phytoplankton loss rates (a first-order rate constant as a proportion of total biomass), which could encompass natural cell death and grazing by zooplankton. While a separate parameter for grazing does not currently exist for MyLake, this was deemed an acceptable tradeoff. Prior work suggests filamentous phytoplankton were a low-quality food source for the rotifer-dominated zooplankton community in Lake 227 (Paterson et al. 2011). We prioritized the reproduction of physical and biogeochemical aspects of the system over food web interactions.

We simulated limnological and biogeochemical conditions in Lake 227 from 1969 to 2016. Initial temperature and chemistry profiles of the water column were specified from measurements made immediately prior to the first fertilization event in June 1969. Initial sediment chemistry and redox profiles were determined from sediment core data isolated for the pre-fertilization period (Hesslein 1980; Schindler et al. 1987; Ansems 2012). Subsequent daily time steps of the model required input data for meteorological conditions and the temperature and chemical concentrations of stream inflows to the lake. Parameters for each reaction equation were specified, and the reactions as well as external meteorological and inflow forcings drove daily water column conditions in the lake. Parameter values for reaction equations were based on an application of the model to the humic and eutrophic Lake Vansjø, Norway (Saloranta and Andersen 2007; Couture et al. 2014b, 2018). When available, direct measurements from Lake 227 (e.g., C:N:P ratios of phytoplankton) were supplied as parameter values.

Parameters affecting diazotroph PP, nondiazotroph PP, and TDP were optimized using the Genetic Algorithm function of the MATLAB Global Optimization Toolbox, which seeks to

\[
\mu = \mu'(T) \left( \frac{P}{P^*+P} \times \frac{N}{N^*+N} \right)
\]
minimize the sum of squared error between observed and modeled diazotroph PP, nondiazotroph PP, and TDP by varying parameters within the maximum probable range. Based on sensitivity analysis in previous MyLake applications (Saloranta and Andersen 2007; Couture et al. 2014b), PP and TDP concentrations are most sensitive to the following parameters: the PAR saturation level for phytoplankton growth, half saturation growth P level, growth rate, loss rate, and sinking rate. Two optimization periods were tested, 1975–1979 and 1990–1994, and validation was performed for 1970–2016. The parameters from the 1990–1994 optimization (Table S1) resulted in a significantly better fit across the validation period and were used in subsequent modeling (full parameter list in data repository). 1969 was designated as a model spin-up year and was excluded from final analyses. Model output from 1996 was also left out of postprocessing analyses due to a trophic cascade experiment that resulted in unusually high zooplankton grazing in that year (Elser et al. 2000). Model code, input and output files are available from https://github.com/biogeochemistry/Lake-227 (Salk et al. 2021).

The goodness of fit between modeled and observed conditions in Lake 227 was assessed for (1) daily values, (2) cumulative seasonal values, and (3) aggregated metrics for each period. We evaluated daily values for dates of ice break-up and freeze, temperature, epilimnetic PP, and epilimnetic TDP with root-mean squared error (RMSE), which quantifies the average deviation of modeled values from observed values in the units of interest. Epilimnion, for both observed and modeled data, was defined as the integrated depth from the surface until a temperature gradient of 1°C/1 m was detected. Cumulative PP was calculated as the sum of epilimnetic PP concentrations between 16 May and 31 October each year (the period when the lake is reliably ice-free), sourced from daily model output and estimated by linear interpolation for monitoring data.

We computed aggregated performance metrics, normalized bias ($B^*$) and normalized unbiased root mean squared difference ($\text{RMSD}^*$), for temperature, PP, TDP, and dissolved oxygen at 4 m (generally representing metalimnion) to represent the fit of physical, nutrient, and redox conditions:

$$B^* = \frac{M - D}{\sigma_D}$$

$$\text{RMSD}^* = \frac{\text{sgn}(\sigma_M - \sigma_D)}{\sigma_D} \left(\frac{M'_n - D'_n}{\sigma_D}\right)^{0.5}$$

where $M$ indicates model output, $D$ indicates observations, $\sigma_D$ and $\sigma_M$ are the standard deviations of the observations and model output, respectively, sgn is the sign of the standard deviation difference, and $M'_n$ and $D'_n$ are the residuals of individual modeled and observed values compared to the average modeled and observed values, respectively. The overbar in Eqs. 2 and 3 denotes averaging. $B^*$ describes a systematic over- or underestimation of the modeled values. $\text{RMSD}^*$ represents the difference in standard deviation between modeled and observed values, with negative values indicating lower variance in the observed values than the modeled

Fig. 1. Observed historical trends in the epilimnion of Lake 227 for the ice-free season. Points represent twice-monthly data collections. Shadings represent different N:P fertilization periods. Dotted line represents breakpoint as determined by Pettitt’s test. Color of point indicates direction of trend before or after breakpoint as indicated by Mann–Kendall test (yellow = significant positive trend, purple = significant negative trend, gray = nonsignificant trend). (a) Molar ratios of fertilizer N:P. (b) Proportion of phytoplankton cells identified as diazotrophic. (c) and (d) In situ molar ratios of total and dissolved N:P, respectively. (e) and (f) In situ concentrations of particulate phosphorus and chlorophyll a.
values and vice versa. We plotted $B^*$ and RMSD$^*$ in a target diagram (Taylor 2001), allowing for comparisons of model performance independent of the magnitude of each variable.

**Aim 3: Scenario testing**

Finally, to separate the potential effects of climate change and fertilization on phytoplankton blooms in the P-only period (1990–2016), three model scenarios were run. The first scenario included observed air temperature and external fertilization (climate change + fertilization), the conditions modeled in the optimization/validation run. The second scenario included observed air temperature and natural stream inflow but excluded external fertilization (climate change only). The third scenario included external fertilization and a detrended air temperature input relative to the beginning of the experiment (fertilization only), computed using a loess-based time series decomposition on a 365-d seasonal cycle (i.e., assumes a moving trend rather than a monotonic trend). This detrending approach preserved seasonal and random variability in temperature but removed the increase in temperature since 1969 (difference in observed minus detrended daily temperature: 3.2°C ± 1.3°C, range 0.7–6.5; Figs. S1, S2).

**Results**

**Aim 1: Historical trends**

In response to decreased fertilizer N:P ratios (Fig. 1a), diazotrophic cyanobacteria (*Aphanizomenon* spp.) became dominant during the summer phytoplankton bloom (Fig. 1b). Based on the Mann–Kendall tests (Table S2), epilimnetic TN:TP molar concentrations increased through the high and low N:P periods, and then remained steady after 1996 (Fig. 1c). Epilimnetic TDN:TDP molar concentrations increased through the high N:P period, then decreased through the low N:P and P-only periods (Fig. 1d). PP concentrations decreased starting at the change point in 1978 and throughout the low N:P and P-only fertilization periods (Fig. 1e). Chlorophyll concentrations displayed a significant decreasing trend both before and after

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**Table 1.** RMSE values, representing the average deviation of modeled values from observed values in the units of interest, for three fertilization periods in Lake 227. PP, particulate phosphorus; TDP, total dissolved phosphorus; Temp, water temperature.

|          | High N:P | Low N:P | P-only | Units |
|----------|----------|---------|--------|-------|
| Ice break| 1.4      | 3.2     | 6.2    | d     |
| Ice freeze| 1.1     | 4.9     | 5.0    | d     |
| Temp 1 m  | 1.8      | 1.4     | 2.1    | °C    |
| Temp 4 m  | 1.2      | 1.7     | 1.6    | °C    |
| Temp 9 m  | 0.3      | 0.3     | 0.6    | °C    |
| PP        | 20.5     | 21.7    | 9.8    | μg L$^{-1}$ |
| PP (nondiazotroph) | 20.5   | 21.7    | 9.8    | μg L$^{-1}$ |
| PP (diazotroph)    | NA     | 21.0    | 14.1   | μg L$^{-1}$ |
| TDP       | 4.9      | 3.6     | 3.4    | μg L$^{-1}$ |
the change point in 1987, seemingly unrelated to fertilization regime and likely driven by instances of markedly high concentrations (Fig. 1f).

Climatic drivers displayed substantial inter- and intra-annual variation (Fig. S3, detailed results in Tables S2, S3). A seasonal Mann–Kendall test indicated a significant increase in overall air temperature over the 48-yr period, while the total temperature range has narrowed. Wind speed and daily radiation decreased significantly over time. Precipitation increased significantly, with largest intensity rain events occurring after 1980. Annual catchment inflows of P and N were generally a small fraction of fertilizer inputs (P: 3.2% ± 1.5%, N: 1.2% ± 1.1%), with TP inflow concentrations decreasing significantly over time and DIN concentrations displaying no monotonic trend.

**Aim 2: Lake modeling**

Across the 48-yr period, ice break-up and freeze dates were predicted within 6 d or fewer, indicating the model simulated the lake response to local climatic drivers appropriately (Fig. 2a). Modeled ice cover ranged from 0.5 to 0.9 m each year, with water at 1 m and below remaining liquid. Modeled water temperatures followed the seasonal trends of warming and cooling observed in Lake 227 (Fig. 2b). Temperatures at 1-, 4-, and 9-m depth were predicted within 1.4–2.0°C, 1.3–1.8°C, and 0.3–0.6°C (total range), respectively. Model performance for lake thermal structure was similar across fertilization periods (Table 1). Model performance for temperature was within one unit of $B^*$ and RMSD$^*$ for all fertilization periods (Fig. 3). $O_2$ at 4 m depth, an indicator of redox conditions, was modeled with similar success for the three periods, within 0.5 units of $B^*$ and within 2 units of RMSD$^*$. MyLake predicted a fairly consistent seasonal bloom across the three fertilization periods, whereas observed blooms were more variable from year to year (Fig. 4). RMSE values for PP were 20.5 and 21.7 µg L$^{-1}$ in the high and low N:P periods, respectively, but accuracy in the P-only period was doubled with an RMSE of 9.8 µg L$^{-1}$ (Table 1). Cumulative annual PP and PP residuals show that PP was sometimes underestimated and sometimes overestimated for the high and low N:P periods, whereas PP was typically overestimated in the P-only period (Fig. 4). $B^*$ values were within 1.3 units across periods. RMSD$^*$ revealed a greater underestimation of variance for the high N:P ($−13.09$) and low N:P ($−15.33$) periods, with a lesser underestimation of variance for the P-only period ($−1.29$; Fig. 3). Overall, the fit indicators show the overall magnitude and timing of blooms was captured, but MyLake struggled to simulate the day-to-day variability and interannual variation in PP observed in the high and low N:P periods.

When PP was divided into diazotroph and nondiazotroph biomass, model performance was similar to total PP across fertilization periods (Table 1). Diazotroph PP was predicted within 21.0 µg L$^{-1}$ in the low N:P period and 14.1 µg L$^{-1}$ in the P-only period (fit metrics could not be calculated for the high N:P period because diazotrophs were not encountered). Nondiazotroph PP was predicted within 20.5, 17.7, and 9.8 µg L$^{-1}$ in the high N:P, low N:P, and P-only periods, respectively. Bias was low for all groupings ($B^* < 0.6$), and RMSD$^*$ was higher for the high and low N:P periods than for the P-only period. MyLake predicted the highest proportion of diazotroph PP,total PP during the P-only period and lowest in the high N:P period, similar to observations. However, the modeled seasonal peak of diazotroph relative abundance was earlier and lower than observed (Fig. 5).

TDP concentrations displayed a similar fit across periods, with RMSE values ranging from 3.4 to 4.9 (Table 1). $B^*$ was $−0.88$ units for the low N:P period and $−0.19$ and $−0.13$ units

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**Fig. 3.** Target plot evaluating model fit for three periods. Values of normalized unbiased root mean squared difference (RMSD$^*$) and normalized bias ($B^*$) near zero represent a model fit with similar variance and minimal over- or underestimation of values compared to observations, respectively. The circle represents absolute values of RMSD$^*$ and $B^*$ of 10 and 1, respectively.
for the high N:P and P-only periods, respectively. Variance was overestimated for all periods, with the worst model fit for the high N:P period (RMSD$^* = 18.61$) and best for the P-only period (RMSD$^* = 9.09$).

**Aim 3: Scenario testing**

Detrended air temperature in the fertilization only scenario resulted in shifts in mean monthly surface water temperature ranging from $-0.04^\circ$C to $0.07^\circ$C with the greatest difference occurring in April (range $-0.13$ to $0.33$) and May (range $-0.02$ to $0.21$; Fig. S6). Paired comparisons of modeled daily PP concentrations between all combinations of scenarios showed a significant difference (paired Wilcoxon tests, $p < 0.0001$; Fig. 6a). Daily PP concentrations for the ice-free season in the climate change + fertilization scenario exceeded those in the fertilization only scenario $88\%$ of the time, with the greatest differences occurring from June to September (Fig. 6b). Peak annual PP concentrations differed significantly among scenarios (Kruskall–Wallis test; $X^2 = 61.15$, $p < 0.0001$) and were greatest in the climate change + fertilization (observed) scenario ($49.8 \pm 5.4 \mu g L^{-1}$, range 41.7–65.8), intermediate in the fertilization only scenario ($42.4 \pm 5.9 \mu g L^{-1}$, range 33.5–55.1), and lowest in the climate change only scenario ($1.4 \pm 0.6 \mu g L^{-1}$, range 0.5–3.9). Peak PP concentration occurred in the early part of the ice-free season in the climate change only scenario and generally occurred in the late part of the ice-free season in the fertilization only scenario (Fig. 6a).

**Discussion**

Lake 227 has responded to shifts in N and P loading through changes in nutrient stoichiometry, phytoplankton community composition, and biomass. Although ratios of TDN : TDP in Lake 227 decreased concomitantly with a reduction in external N fertilization, biological N fixation by cyanobacterial diazotrophs maintained TN:TP ratios across the fertilization regimes. The shift from an increasing trend in TN:
TP to a steady ratio of TN:TP occurred in 1996, potentially due to a lag time coinciding with the 7-yr hydraulic residence time of the lake or a trophic cascade experiment that left the lake fishless and potentially altered recycling pathways of N and P (Elser et al. 2000). Although annual mean phytoplankton biomass has remained steady (Paterson et al. 2011; Higgins et al. 2018), the time series analysis revealed shifts in intra- and interannual bloom composition. PP and chlorophyll concentrations decreased moving from the low N:P to P-only fertilization regime, and PP and chlorophyll concentrations above 100 μg L⁻¹ were not observed in the P-only period. These findings suggest that blooms have become lower in peak magnitude but spread out over a longer season in the P-only period, in contrast to the more intense yet short-lived blooms in the high and low N:P periods.

The addition of N-limited growth kinetics to the MyLake model structure enabled us to simulate the competition between diazotrophs and nondiazotrophs in Lake 227 as nutrient stoichiometry changed. By incorporating both P- and N-limitation to the model, we were able to reproduce phytoplankton community structure as is possible with other algal modules such as PROTECH (Reynolds et al. 2001) while keeping with the benefit of MyLake’s simple open-access code. As anticipated from historical data (Schindler et al. 2008), the modeled proportion of diazotroph biomass increased as N:P ratios decreased. However, the relative proportion of diazotrophs relative to total phytoplankton biomass was dampened in the model output compared to the observed data; monitoring data indicated 0% of the phytoplankton community was diazotrophic during the high N:P period and approached seasonal peaks of 100% during the P-only period, but the model output was bounded by 25% and 50% on the low and high limits of diazotroph relative abundance (Fig. 5). While the model reproduced the general pattern of diazotroph relative abundance in line with expectations from N:P stoichiometry, evidently some aspects of the competitive pressure alternatively favoring nondiazotrophs and diazotrophs were not able to be fully reproduced by the model structure. For instance, model kinetics may generate nondiazotroph biomass when water column N becomes periodically available during the P-only period, when in actuality nondiazotroph growth may not be able to quickly respond to transient pools of bioavailable N.

An additional future improvement to MyLake may be the addition of zooplankton grazing dynamics. While the zooplankton grazing has been empirically demonstrated as unimportant in Lake 227 (Paterson et al. 2011) and grazing can be accounted for as part of the global parameter for phytoplankton loss (m_twty, Table S1), zooplankton may play a larger role in other lake food webs and thus necessitate separate parameterization in the MyLake model.

MyLake simulated the lake physical structure with accuracy along with the behavior of phytoplankton groups with different growth strategies; these were crucial prerequisites for modeling the phytoplankton community in Lake 227. The overall timing and magnitude of phytoplankton blooms, as measured by PP, were captured by the model. However, our model application illuminates the complexity associated with phytoplankton blooms and the ongoing challenge of applying process-oriented ecosystem models to simulate systems under shifting external pressure, even those that are exceptionally well-characterized in terms of time series. Lake 227 is small, bowl-shaped lake with a well-known fertilization regime and long-term monitoring record, providing a “best case” to examine model performance. Many systems experience dramatic shifts in stoichiometry and nutrient loading (Jeppesen et al. 2005; Hessen et al. 2009), inducing changes in lake ecosystem functioning that are difficult to capture by the fixed structures of process-oriented models. This challenge is exemplified here by variable model performance with respect to fertilization regime. The best performance indicators for PP and TDP were

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**Fig. 5.** Relative proportion of diazotrophs, divided by fertilization period, for (a) modeled conditions and (b) observed conditions. Shaded areas around lines represent the 95% confidence interval around mean values.
observed in the P-only period, whereas the variance in PP and TDP were substantially underestimated and overestimated, respectively, during the high and low N:P periods (Fig. 3). Adjusting or re-parameterizing Eqs. 2 and 3 for future applications of this model may be helpful in addressing phytoplankton community responses to changing N:P ratios. The high and low N:P periods experienced both the highest and the lowest peak and cumulative PP concentrations, but this variability was not captured by the model (Fig. 4). Nevertheless, the performance metrics are within the range, for example, of those achieved by a recent application of the General Lake Model which reported RMSE ranges for epilimnetic TP of $6 - 118 \mu g L^{-1}$/C0 (Farrell et al. 2020). Given that nutrient additions were well-constrained and annual P additions were consistent over the study period, the large swings in observed PP concentrations among years are unexpected. Evidently, there are sources of variability introduced during the high and low N:P regimes that are unaccounted for by the model structure. Because of the performance of the hydrodynamics model component, this source of variability is more likely in the biological component, namely a suite of processes that function alternatively to retain or remove P in the epilimnion (e.g., rapid release and uptake, vertical movement to and from the metalimnion) throughout the course of a season.

We observed a significant interaction of climate change and P fertilization on phytoplankton blooms in Lake 227. Although P fertilization is clearly the major driver of blooms in Lake 227, removing the confounding influence of climate change (Nielsen et al. 2014) enables a better understanding of the two drivers concurrently. The scenario with no external fertilization (climate change only) yielded markedly low PP concentrations, in line with experimental observations in Lake 227 and scenario modeling in other systems (Ward et al. 2020). The scenario that reproduced observed conditions in the lake (climate change + fertilization) produced larger and earlier blooms than the scenario with detrended temperature relative to 1969 (fertilization only). Although increases in water temperature were an order of magnitude smaller than increases in air temperature, the timing and persistence of this shift impacted the modeled rates such that differences in PP concentrations were substantial. Specifically, the greatest increases in water temperature in the climate change + fertilization scenario occurred in the early part of the ice-free season, allowing blooms to establish earlier and reach concentrations from June to September that were $11.7 \pm 6.9 \mu g L^{-1}$/C0 greater than in the fertilization only scenario. MyLake scenario modeling thus suggests that warmer surface water temperatures in the spring, in combination with steady P loading, have resulted in higher bloom biomass and an earlier peak bloom than would have occurred in the absence of climate change. These results are likely to be applicable to other lake systems, as has been recently demonstrated by Ward et al. (2020).

**Fig. 6.** Climate and fertilization scenario analysis for the P-only regime (1990–2016). (a) Daily PP concentrations for the climate change + fertilization (i.e., actual historical conditions; red), climate change only (i.e., no external P loading; yellow), and fertilization only (i.e., historical P loading and detrended temperature; purple) model scenarios. (b) The difference in mean monthly PP measurements between the climate change + fertilization and fertilization only scenarios across modeled years (1990–2016). Positive values indicate higher PP in the climate change + fertilization scenario than in the fertilization only scenario.
Many systems worldwide experience HABs where they were historically uncommon. Causes include increased nutrient loading, changes in N:P stoichiometry, and increased temperature, all of which have occurred in Lake 227. However, specific drivers often occur concurrently, making it difficult to manage HABs given the complexity of drivers and responses (Filstrup and Downing 2017). Lake 227 represents a system where nutrient inputs have been tightly controlled, conditions have been monitored over a long period of time, and modeling has disentangled concurrent drivers of blooms. In particular, we found a significant interaction of temperature and nutrient loading that caused higher than anticipated bloom biomass, suggesting that climate change needs to be incorporated into lake management efforts that typically focus on nutrients alone (Scavia et al. 2016; US EPA 2019). In practice, adjustments to lake management efforts may entail expanding monitoring efforts earlier in the season and with more frequency during peak bloom conditions, incorporating climate impacts into uncertainty estimates around nutrient-phytoplankton relationships, and including temperature-related metrics in stressor-response models. Even in well-studied systems, the complex biology of blooms can be difficult to predict, with stochastic behavior evading process-oriented models (Buelo et al. 2018). The value of this type of modeling may thus be to characterize seasonal conditions in response to changing drivers rather than instantaneous conditions. Nonetheless, the ability for such models to capture the seasonality of blooms and competition among phytoplankton groups highlights their value for HAB management, including modeling scenarios that incorporate nutrient reduction and future climate projections (Ralston and Moore 2020).

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Conflict of Interest
None declared.