



Modelling lake cyanobacterial blooms: Disentangling the climate-driven impacts of changing mixed depth and water temperature

Emma Gray^{1,2} | J. Alex Elliott¹ | Eleanor B. Mackay¹ | Andrew M. Folkard² | Patrick O. Keenan¹ | Ian D. Jones¹

¹Centre for Ecology and Hydrology, Lancaster, Lancaster Environment Centre, Lancaster, U.K

²Lancaster Environment Centre, Lancaster University, Lancaster, U.K

Correspondence

Emma Gray, Centre for Ecology and Hydrology Lancaster, Lancaster Environment Centre, Lancaster, U.K.
Email: emma.gray9229@gmail.com

Present address

Ian D. Jones, Biological and Environmental Sciences, University of Stirling, Stirling, U.K

Funding information

UK Natural Environment Research Council (NERC); Envision Doctoral Training Partnership, Grant/Award Number: NE/L002604/1

Abstract

1. Climate change is already having profound impacts upon the state and dynamics of lake ecosystems globally. A specific concern is that climate change will continue to promote the growth of phytoplankton, particularly blooms of toxic cyanobacteria, via lake physical processes including warming surface waters and shallowing of the mixed layer. These two mechanisms will have different impacts on lake phytoplankton communities, but their inter-connectedness has made it difficult to disentangle their independent effects.
2. We fill this knowledge gap by performing 1666 numerical modelling experiments with the phytoplankton community model, PROTECH, in which we separated the independent effects on lake phytoplankton of temperature change and changes in the depth of the surface mixed layer. Given the large global abundance of small lakes (<1 km²) and the importance of their ecosystems in global processes and budgets, we used a small meso-eutrophic lake as an example study site for the modelling experiments.
3. Increasing the lake temperature and positioning the mixed layer at a shallower depth had different ecological impacts, with warming typically resulting in more biomass and a dominance of cyanobacteria.
4. The response to mixed depth shallowing depended on the original depth where mixing occurred. As anticipated, where the original mixed depth was moderate (4–6 m) and there was a simultaneous increase in water temperature, cyanobacterial biomass increased. However, when the same absolute difference in shallowing and temperature increase were applied to a deeper mixed depth (9–13 m), lower cyanobacterial biomass resulted, owing to poorer conditions for low-light tolerant cyanobacteria.
5. Our study shows that the response of cyanobacterial blooms to climate-induced warming and shallowing of mixed layers in lakes around the world will not be universal, but rather will be system-specific, depending upon the average mixed layer depth of the lake in question and the light affinity of the dominant cyanobacteria species.

KEYWORDS

climate change, phytoplankton, *Planktothrix*, PROTECH, stratification

1 | INTRODUCTION

Climate change is impacting phytoplankton communities in lakes across the world through direct and indirect effects of temperature change (Huisman et al., 2018; Winder & Sommer, 2012). Although intrinsically linked, water temperature, the duration of lake stratification and the depth of the surface mixed layer have independent and separate consequences for phytoplankton growth (Winder & Sommer, 2012). Phytoplankton are a key part of lake food-webs, therefore shifts in community composition in response to changing physical drivers can have consequences for higher trophic levels and water quality (Huisman et al., 2018; Winder & Sommer, 2012). The increase in the magnitude and frequency of cyanobacterial blooms associated with climatic warming are a global water quality concern because they can increase water turbidity, cause oxygen depletion during bloom die back, and certain species produce toxins (Michalak, 2016; Paerl & Huisman, 2008). It is therefore important to understand how phytoplankton growth will respond to changing physical drivers.

Lake water temperatures are increasing with climatic warming, as lakes and climate are closely coupled (Winder & Schindler, 2004). The pattern of warming is complex and varies globally (O'Reilly et al., 2015), seasonally (Winslow, Read, Hansen, Rose, & Robertson, 2017), with lake size (Woolway et al., 2016), and vertically within lakes (Winslow, Read, Hansen, & Hanson, 2015). On average, surface summer water temperatures are warming at a global mean of 0.34°C per decade, which is likely to significantly change the physical structure of lakes (O'Reilly et al., 2015). Higher spring and autumn temperatures are increasing the duration of lake stratification (Livingstone, 2003; Peeters, Straile, Lorke, & Livingstone, 2007), whilst periods of sustained high temperatures and low wind speeds also strengthen stratification, inhibiting mixing, resulting in shallower surface mixed layers (Livingstone, 2003; Winder & Sommer, 2012). These changing physical drivers have separate consequences for phytoplankton growth.

The first driver, water temperature, directly affects phytoplankton growth because it influences the rate of important cellular processes such as photosynthesis. Most phytoplankton will exhibit an exponential increase in growth rate with temperature from 0 to 25–35°C provided they are not limited by any other resource (Reynolds, 2006). The range of maximum temperatures for exponential growth reflects that growth rates are species-specific, varying with cell size, indicating that different species will respond to warming at different rates (Reynolds, 2006). Research suggests that increasing water temperatures will favour the dominance of smaller phytoplankton due to their faster growth rates and greater nutrient uptake efficiency at higher temperatures compared with larger cells (Rasconi, Gall, Winter, & Kainz, 2015). Cyanobacteria are also likely to increase at higher water temperatures owing to some species having higher

optimal temperatures for growth compared to some species in other taxa (Carey, Ibelings, Hoffmann, Hamilton, & Brookes, 2012; Paerl & Paul, 2012).

The depth of the mixed layer is a fundamental driver of phytoplankton growth because it affects the light and nutrient environment they are exposed to and thus their vertical distribution and the rate of sinking losses (Diehl, 2002; Huisman et al., 2004; Ptacnik, Diehl, & Berger, 2003). Deeper mixed layers can create a lower light environment, reduce sinking losses and increase nutrient availability, whereas shallow mixed layers may increase light availability and sinking losses and reduce nutrient availability (Diehl, Berger, Ptacnik, & Wild, 2002; Huisman, van Oostveen, & Weissing, 1999). Phytoplankton have different affinities for light and levels of motility, so changes in the mixed depth can result in large shifts in taxonomic composition (Huisman et al., 2004; Lehman, Mugidde, & Lehman, 1998). Generally, sinking phytoplankton, such as diatoms and chlorophytes that are adapted to low light conditions, tend to dominate in deeper layers whereas buoyant or motile phytoplankton (buoyant cyanobacteria and flagellates) often dominate in shallow mixed layers (Jäger, Diehl, & Schmidt, 2008; Ptacnik et al., 2003; Reynolds, Wiseman, Godfrey, & Butterwick, 1983; Visser, Ibelings, Van Der Veer, Koedood, & Mur, 1996). Increased surface water temperature with climatic warming may result in shallower mixed depths for many lakes which may then increase cyanobacterial abundance (Paerl & Huisman, 2009). Many species of cyanobacterium have traits suited to shallow mixed layers (Carey et al., 2012) including gas vesicles that allow them to control and maintain their position and exploit optimal light conditions (Walsby, Hayes, Boje, & Stal, 1997). Buoyancy can also be facilitated further at higher water temperatures due to reduced water viscosity (Reynolds, Oliver, & Walsby, 1987). Other cyanobacteria, such as *Planktothrix*, are well adapted to low light conditions and thrive in lakes where the mixed depth is deeper (Dokulil & Teubner, 2012; Ernst, Hoeger, O'Brien, & Dietrich, 2009).

Although not the focus of this study, the duration of stratification is also influenced by climate warming and can affect the length of the phytoplankton growing season, with warmer spring air temperatures being associated with earlier onset of stratification and spring phytoplankton blooms (Berger, Diehl, Stibor, Trommer, & Ruhlenstroth, 2010; Peeters, Straile, Lorke, & Ollinger, 2007; Winder & Sommer, 2012). Persistent high temperatures during autumn can also delay overturn (Hondzo & Stefan, 1993; Peeters, Kerimoglu, & Straile, 2013) although the impact of this on the phytoplankton growing season is uncertain.

The impacts of temperature change, stratification, and mixing have previously been studied in combination using observed data, models, and experiments (e.g. Berger et al., 2006, 2010; Bernhardt, Elliott, & Jones, 2008). These studies, however, did not disentangle

the impacts of these separate physical drivers on phytoplankton communities throughout the stratified period. Using a phytoplankton community model, PROTECH (Reynolds, Irish, & Elliott, 2001), we systematically and independently changed the water temperature and mixed depth of a model experimental lake system. We chose a small lake (<1 km²) for the experiment due to the worldwide abundance and significance of small lakes in global budgets and processes (Downing et al., 2006; Verpoorter, Kutser, Seekell, & Tranvik, 2014). The experiment therefore aimed to separate the impacts of the depth of mixing and temperature change on phytoplankton communities whilst keeping the length of stratification constant. We hypothesised that: (1) increases in temperature during fully mixed periods will extend the length of the growing season; (2) changes in water temperature alone will have different impacts on the phytoplankton community than changes in the depth of mixing alone; (3) together, changes in mixed depth and temperature will have greater impacts on phytoplankton than changes in either factor alone; (4) shallower mixing depths and increases in temperature will lead to an increase in cyanobacterial abundance; (5) phytoplankton taxa within the same phylogenetic group may respond differently to changes in physical drivers due to differences in morphology. Although the model runs were based on morphometry of a single lake, they were designed so that the results would be relevant to monomictic, nutrient-rich lakes across the globe.

2 | METHODS

2.1 | Site description

Blelham Tarn is the modelled lake for the experiment, using three consecutive years of in situ driving data (2012–2014). Blelham Tarn is a small (surface area 0.1 km²), shallow (mean depth 6.8 m, maximum

depth 14.5 m) (Ramsbottom, 1976) lake located in the English Lake District (54°24'N, 2°58'W; Figure 1). The trophic status of Blelham Tarn lies on the meso-eutrophic boundary (mean total phosphorus 24.5 mg/m³) (Maberly et al., 2016) and it is monomictic, typically stratifying from spring to late autumn.

2.2 | PROTECH model

PROTECH is a process-based phytoplankton community model that simulates the daily growth of selected phytoplankton taxa within a lake. PROTECH is a well-established model that has been successfully used in numerous studies of lakes and reservoirs within the U.K., Europe, and beyond (Elliott, Irish, & Reynolds, 2010) including successful simulations of Blelham Tarn (Bernhardt et al., 2008; Elliott, Irish, & Reynolds, 2001; Jones & Elliott, 2007).

Phytoplankton growth rates within the model are based on morphological characteristics including the surface area to volume ratio and maximum linear dimension as defined by Reynolds (1989) (Table 1). The overall growth rate ($\Delta X/\Delta t$) is also determined by losses due to sinking and grazing using the equation,

$$\Delta X/\Delta t = (r' - S - G - D)X, \quad (1)$$

where r' is the proportional growth rate over 24 hr, S represents the losses due to settling, G the losses due to grazing, D the losses due to dilution, and X is the chlorophyll a concentration (mg/m³). The growth rate changes with water temperature, light levels, and nutrient limitation of phosphorus, nitrate, or silica defined by,

$$r' = \min\{r'_{\theta}, r'_{P}, r'_{N}, r'_{Si}\} \quad (2)$$

where r'_{θ} is the growth rate due to temperature and daily photo-period, and r'_{P}, r'_{N}, r'_{Si} are the growth rates determined by phosphorus, nitrate, and silica concentrations, respectively. In addition to

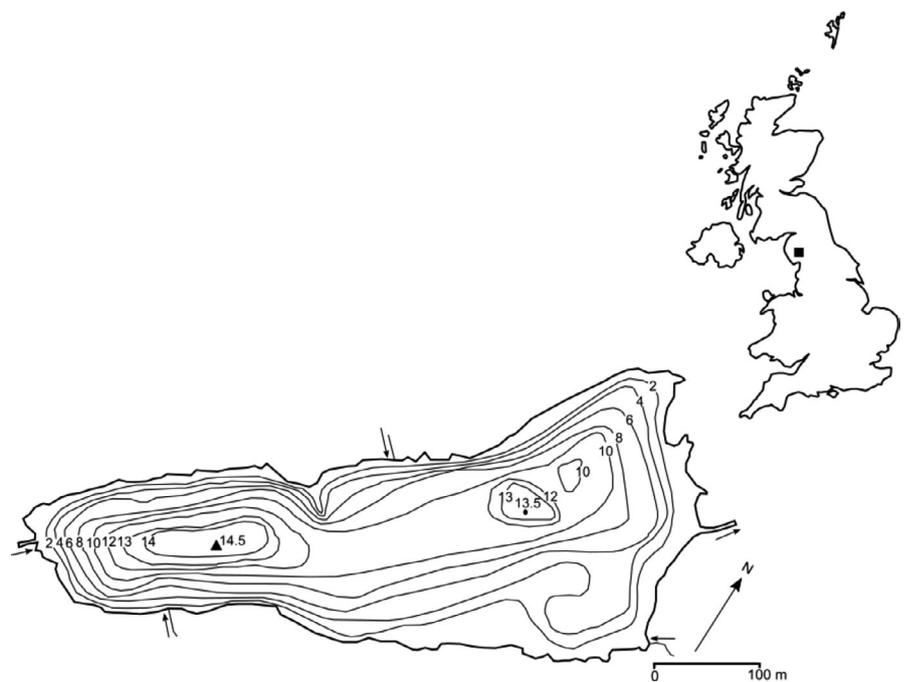


FIGURE 1 Blelham Tarn is located in the lake district in North West England (square), with the monitoring buoy (triangle) located at the deepest point in the lake (14.5 m) bathymetry from Ramsbottom (1976)

TABLE 1 Morphometric characteristics of the 12 phytoplankton taxa

Phytoplankton	Surface area (μm^2)	Volume (μm^3)	SA:V	Maximum dimension (μm)	Phylogenetic grouping	Competitors (C), stress tolerant (S), ruderals (R)	Grazed	Nitrogen fixer
<i>Plagioselmis</i>	108	72	1.5	11	Flagellate	C	Yes	No
<i>Stephanodiscus</i>	404	280	1.4	11	Diatom	C	Yes	No
<i>Dinobryon</i>	629	848	0.7	40	Flagellate	C	Yes	No
<i>Cryptomonas</i>	1,030	2,710	0.4	21	Flagellate	CS	Yes	No
<i>Synedra</i>	4,100	7,900	0.5	110	Diatom	R	No	No
<i>Aulacoseira</i>	4,350	2,970	1.5	240	Diatom	R	No	No
<i>Dolichospermum</i>	6,200	29,000	0.2	75	Cyanobacterium	CS	No	Yes
<i>Coenochloris</i>	6,430	17,200	0.4	64	Chlorophyte	S	No	No
<i>Asterionella</i>	6,690	5,160	1.3	130	Diatom	R	No	No
<i>Planktothrix</i>	7,350	13,970	0.5	300	Cyanobacterium	R	No	No
<i>Sphaerocystis</i>	7,850	65,500	0.1	50	Chlorophyte	S	Yes	No
<i>Ceratium</i>	9,600	43,700	0.2	201	Flagellate	CS	No	No

morphology, each phytoplankton is given appropriate movement characteristics as well as any additional abilities such as nitrogen fixation (Tables 1 and 2). Further details about the model set up including mortality and respiration rates can be found in Reynolds et al. (2001) and Elliott et al. (2010).

The phytoplankton chosen to be included in the model set up represented common taxa observed in Blelham Tarn during a fortnightly monitoring programme carried out from 2012 to 2014 (Table 1). These phytoplankton also covered a range of phylogenetic (diatoms, flagellates, chlorophytes, and cyanobacteria) and CSR-functional groupings. The use of the competitors (C), stress tolerant (S), ruderals (R) classification (CSR), developed by Reynolds (1988), helps us understand phytoplankton responses in terms of their traits and morphology, which cut across taxonomical groups (Reynolds, 2006).

2.3 | Driving data

A 3-year period (2012–2014) of daily averaged solar radiation data recorded by a Kipp Zonen CMP6 Pyranometer (sensitivity 5–20 $\mu\text{V}/\text{W}/\text{m}^2$) attached to an in situ automated monitoring buoy (Figure 1) was used to calculate the photosynthetically active radiation available to the phytoplankton within the model. The buoy also measured lake water temperatures every 4 min at 1-m depth intervals in the water column from 1 to 10 m with additional temperature sensors at 0.5 and 12 m. Whilst PROTECH can estimate temperature from external physical drivers in this study, the buoy data were linearly interpolated into the equivalent 0.1-m PROTECH layers (0.1–14.5 m) to provide a daily water temperature structure to drive the PROTECH model over the simulated 3-year period.

To calculate daily nutrient loading to the lake, daily average discharge (m^3/s) from the nearby River Leven was obtained from the Environment Agency. As the outflow from Blelham Tarn is not continuously gauged, a relationship between this daily data and Blelham Tarn outflow was established for 1974, when daily measurements were available for both sites. A power law relationship provided the best regression fit between the two discharges ($R^2 = 0.92$; $p < 0.05$),

$$y = 0.0076x^{1.253}, \quad (3)$$

where y is the outflow discharge of Blelham Tarn and x is the discharge from the River Leven. Daily discharges for each inflow were then calculated based on the proportion of discharge that each inflow contributed to the outflow discharge for 2017 based on monthly spot samples. Monthly concentrations of nitrate and silica in three of the inflows into Blelham Tarn were also sampled during 2017. The calculated daily discharges were averaged for each month and multiplied by the monthly spot concentration for nitrate and silica, assuming that the nutrient load was the same for each day in the sample month, following Walling and Webb (1981). The monthly pattern for nutrient load calculated for 2017 was repeated for each year in the sample

period (2012–2014) therefore daily variations in discharge resulted in different daily nutrient concentrations. The same monthly nutrient loading pattern was used here as the analyses focusses on changes in mixed depth and temperature rather than nutrients. Daily nutrient concentrations for phosphorus were based on estimates modelled from land use type using an export coefficient approach previously calculated by Gasca, Maberly, and Mackay (2015).

Monthly sampling of nutrients has been reported to underestimate nutrient loading by up to 50–60% (Cassidy & Jordan, 2011); therefore, an extra 50% was added onto the calculated values for nitrate, silica, and phosphorus to account for this. The nutrient loading for phosphorus was also increased by a further 50% to account for the internal phosphorus release from the sediments during anoxic conditions in the hypolimnion during stratification (Foley, Jones, Maberly, & Rippey, 2012).

2.4 | Model validation

In PROTECH, phytoplankton are actively mixed throughout the mixed layer, therefore changes in the depth of mixing determine the light and nutrient availability for phytoplankton. The average mixed depths used as a baseline during the stratified period were: 5 m for the entire stratified period, 4 m in spring, 4.5 m in summer and 7 m in autumn. They were derived from water temperature profiles measured in 2012–2014 using Lake Analyzer (Read et al., 2011) and defined as the depths at which the vertical gradient of water density first exceeded

$0.1 \text{ kg m}^{-3} \text{ m}^{-1}$. These baseline mixed depths and the control water temperature profiles measured at the monitoring buoy were used in the model validation run. The benchmark of acceptability for the model was that it produced, on average, a reasonable seasonal pattern of phytoplankton chlorophyll *a* and functional groupings compared to observed data from recent years. Therefore, for comparison, fortnightly means were calculated for both the simulated and observed chlorophyll *a* and functional groupings from the whole period. These were then compared both visually and by calculating the coefficient of determination for the data (Figure 2).

2.5 | Model experiment

The validated model was run in a series of experiments in which the mixed depth was systematically changed by 0.5-m intervals from 0.5 to 14.5 m. These depths were fixed for each model run during the identified period of stratification determined in the baseline run. It is not expected that the mixed depth of Belham Tarn will fluctuate through this full range; rather, the experiment is seen as a template for similar monomictic lakes with naturally different starting depths of mixing. Furthermore, for each mixed depth, the baseline water temperatures (which remain fixed according to the observed buoy data) were systematically changed in 0.5°C intervals from -2 to $+6^\circ\text{C}$ in the top 5 m of the water column throughout the year. Temperature

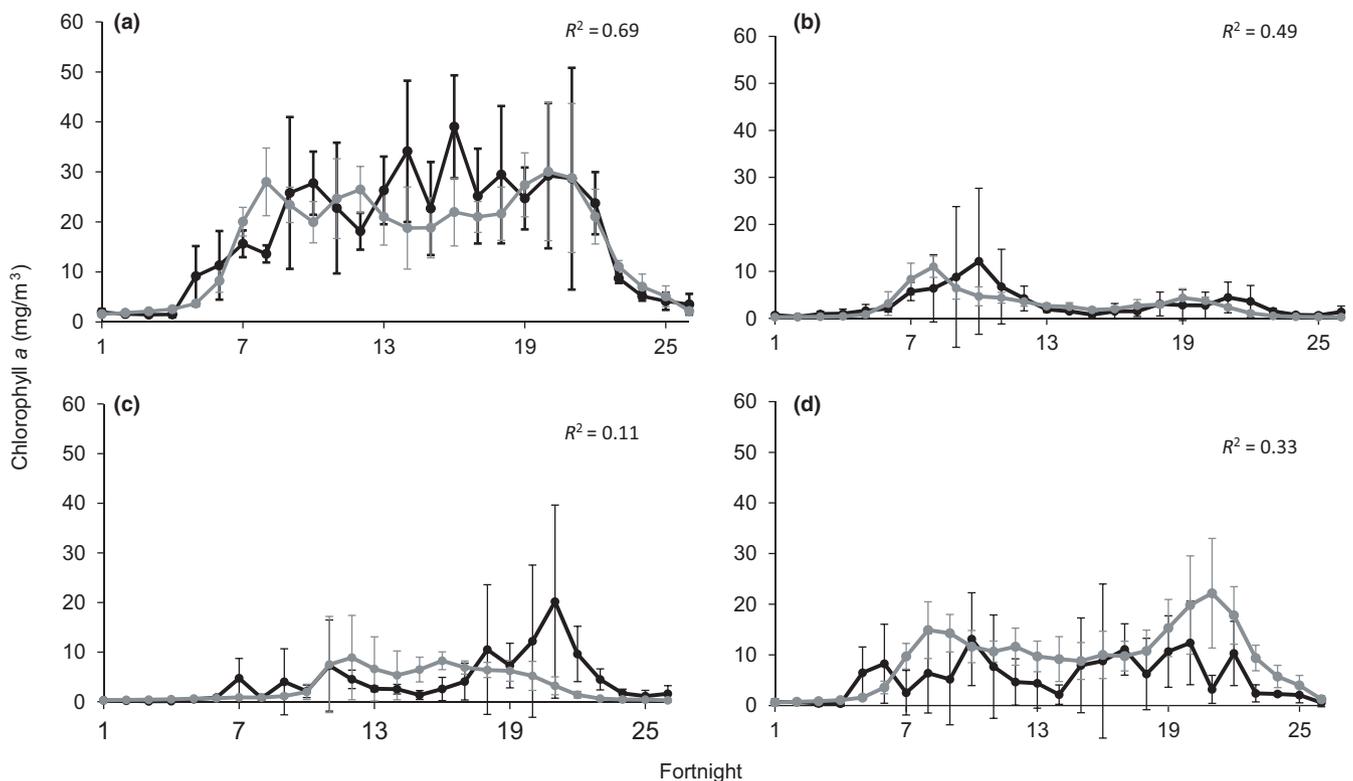


FIGURE 2 Observed (black line) and simulated (grey line) mean fortnightly (a) total chlorophyll *a* biomass, (b) C strategists biomass, (c) CS strategists biomass, and (d) R strategists biomass for Belham Tarn for the 3-year period simulated with the range of fortnightly values for that period (error bars)

was changed at the surface rather than through the whole water column because analysis of long-term temperature trends from Blelham Tarn suggests that warming is accelerated in surface waters only, with little change in deep water temperature (Foley et al., 2012). This means that in scenarios when mixing occurred deeper than 5 m, phytoplankton will not be exposed to warming at those depths, where temperatures will remain at baseline

TABLE 2 Summary of phytoplankton movement characteristics at different light thresholds within PROTECH

Phytoplankton	Light condition ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	Movement (m/day)
Nonbuoyant nonmotile diatoms		
<i>Asterionella</i> and <i>Synedra</i>	≤ 500	Sink 0.2
	> 500	Sink 1.0
<i>Stephanodiscus</i>	All	Sink 0.2
<i>Aulacoseira</i>	≤ 500	Sink 0.8
	> 500	Sink 1.0
Buoyancy-regulating cyanobacteria		
<i>Dolichospermum</i>	> 100	Sink 0.3
	≤ 100 but > 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
<i>Planktothrix</i>	> 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Swimming flagellates		
<i>Cryptomonas</i> and <i>Dinobryon</i>	> 100	Rise 0.1
	≤ 100	Rise 0.2
<i>Ceratium</i>	> 100	Sink 0.1
	≤ 100	Rise 0.1
<i>Plagioselmis</i>	> 150	Sink 0.5
	≤ 100 but > 30	No move
	≤ 30	Rise 0.5
Nonbuoyant nonmotile chlorophytes		
<i>Coenochloris</i> and <i>Sphaerocystis</i>	All	Sink 0.1

values. Overall, this gave a total of 493 model simulations. The phytoplankton concentrations were integrated over the top 5 m of the water column so the model could be validated against the observed data.

In addition to the main experiment a series of extra runs were performed to check some of the methodological assumptions made. To determine if changing the water temperature in the top 5 m of the water column only influenced the results, the experiment was repeated by applying the water temperature change to the whole water column, producing an additional 493 model simulations. Furthermore, fixing the mixed depth in defined intervals throughout the stratified period meant that short term fluctuations in light and nutrient availability were lost. To determine if the absence of this variability impacted the results, additional model runs were completed in which the baseline mixed depth was shifted in 10% intervals from 10% to 200%, again keeping the baseline duration of stratification the same. This was repeated for both a top 5-m water temperature change and a whole water column temperature change, resulting in 680 more model simulations. To determine whether sampling depth had an impact on the results, all results from each experiment were also calculated for the whole water column. Results from these additional runs have been summarised in Tables 3 and 4.

The model outputs from the experiments analysed were daily total chlorophyll *a* (mg/m^3) concentrations, individual phytoplankton taxa chlorophyll *a* (mg/m^3) concentrations, the percentage abundance of each taxonomic group (diatoms, flagellates, chlorophytes, and cyanobacteria) and the percentage abundance of each C, S, R, and CS functional group. The diversity (H') of the 12 phytoplankton species was calculated using the Shannon index according to the following equation,

$$H' = - \sum \left(\frac{b_i}{B} \right) \log_2 \left(\frac{b_i}{B} \right), \quad (4)$$

where B is biomass measured as the total concentration of chlorophyll *a* (mg/m^3) and i is the biomass (chlorophyll *a*, mg/m^3) of the i th phytoplankton taxon. For each of the resulting variables, overall annual means were calculated. Seasonal averages were

TABLE 3 Seasonal mean phytoplankton biomass (chlorophyll *a* mg/m^3) during the stratified period for water column integrated and 5 m integrated results using the fixed mixed depth method

	Spring chlorophyll <i>a</i> (mg/m^3)		Summer chlorophyll <i>a</i> (mg/m^3)		Autumn chlorophyll <i>a</i> (mg/m^3)	
	5 m integrated	Water column integrated	5 m integrated	Water column integrated	5 m integrated	Water column integrated
Temperature change in the top 5 m	27.0	23.8	29.1	24.0	28.1	25.9
Temperature change in the whole water column	26.2	24.3	28.4	24.3	29.4	26.2

calculated with spring being defined as March, April, and May; summer as June, July, and August; autumn as September, October, and November; and winter as December, January, and February. Spring and autumn were split into their respective stratified and fully mixed periods of time and analysed separately. The stratified seasons, that is the period when the *in situ* temperature data showed there had been a surface mixed layer were: spring beginning on 01 March 2012, 11 April 2013, and 31 March 2014 and ending on the last day of May; summer as June, July, and August; and autumn as the beginning of September until lake overturn on 07 October 2012, 03 November 2013, and 07 November 2014. Outside of these periods, the mixed depth of the model was set at the full depth of the lake irrespective of water column temperatures.

3 | RESULTS

3.1 | Validation

The intention of the experiments was not to create an exact reproduction of Blelham Tarn's phytoplankton community but to simulate an experimental community with a realistic biomass, seasonal growth pattern and morphological and taxonomic diversity. The model performed well in terms of biomass, capturing both the amount and seasonal pattern of mean observed total chlorophyll (Figure 2). In terms of the community, annual observed, and modelled means for C (modelled = $2.7 \pm 2.8 \text{ mg/m}^3$, observed = $2.0 \pm 3.2 \text{ mg/m}^3$), R (modelled = $9.1 \pm 7.1 \text{ mg/m}^3$, observed = $8.9 \pm 8.0 \text{ mg/m}^3$) and CS (modelled = $3.2 \pm 4.2 \text{ mg/m}^3$, observed = $3.1 \pm 6.0 \text{ mg/m}^3$) strategists were

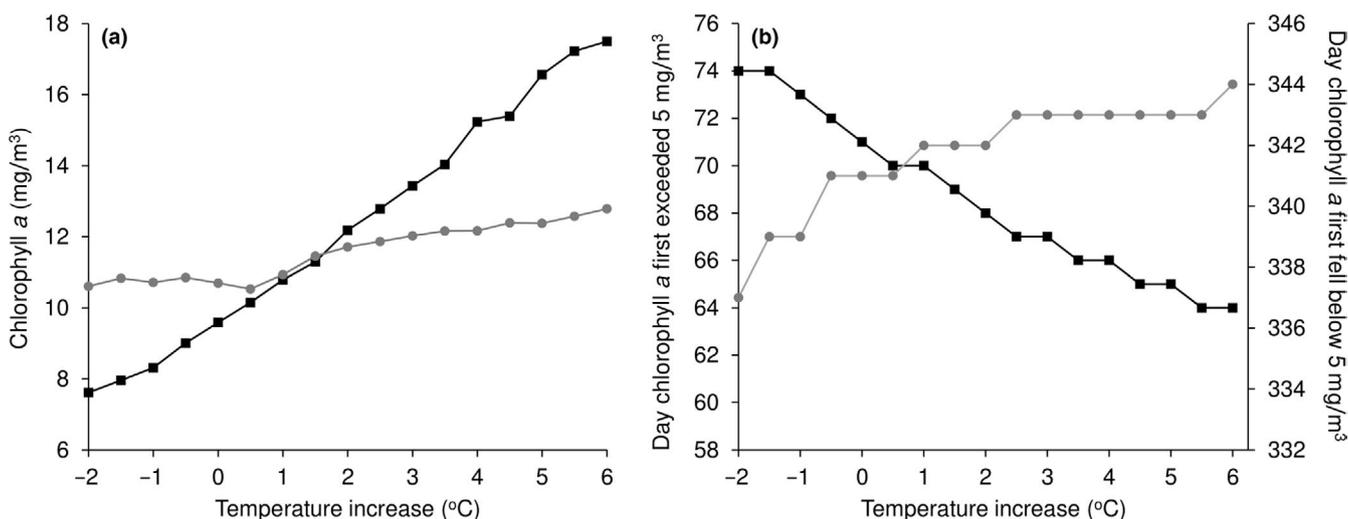


FIGURE 3 (a) Chlorophyll a concentrations with temperature in fully mixed spring prior to stratification (black square) and fully mixed autumn following stratification (grey circle) and (b) average day of the year when chlorophyll a first exceeded (black square) and dropped below (grey circle) 5 mg/m^3 with temperature change

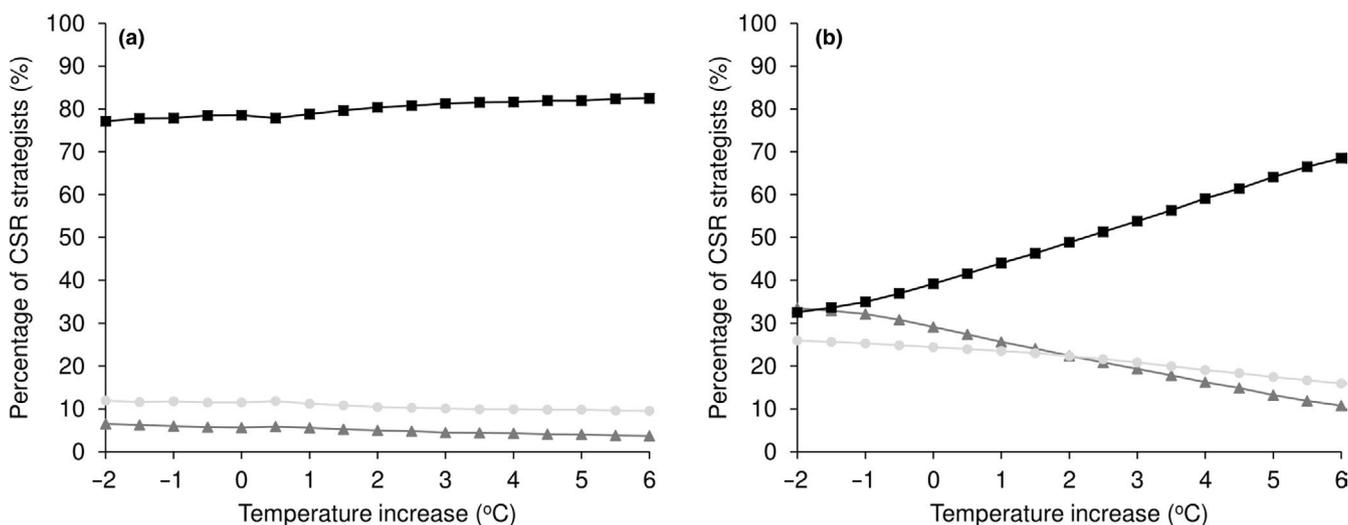


FIGURE 4 Percentage of C (dark grey triangle), CS (light grey circle), and R (black square) strategists in (a) fully mixed spring and (b) fully mixed autumn

very similar (Figure 2). The model performed less well for 5 strategists (modelled = 1.2 ± 0.6 mg/m³, observed = 4.2 ± 7.9 mg/m³); this group was therefore not considered in the analysis.

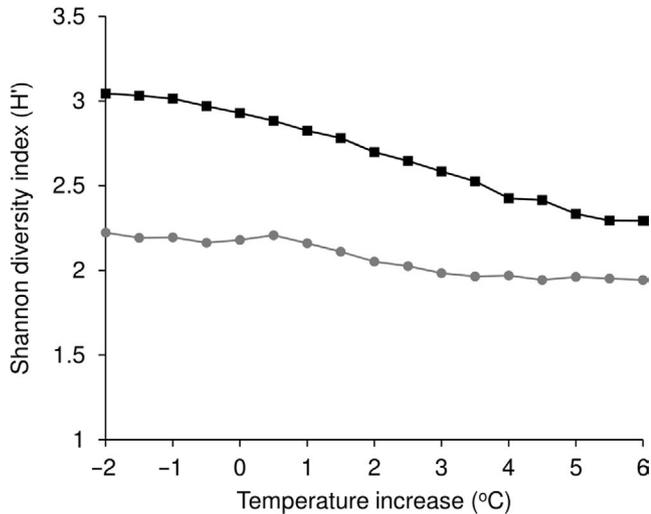


FIGURE 5 Shannon diversity index with temperature change for fully mixed spring (black squares) and fully mixed autumn (grey circles)

3.2 | Impacts of temperature change before and after stratification

3.2.1 | Phytoplankton biomass

Prior to stratification in spring, chlorophyll *a* concentrations increased at an average rate of 1.2 mg m⁻³ °C⁻¹, leading to elevated concentrations at higher temperatures (17.5 mg/m³ at +6°C compared to 9.6 mg/m³ at +0°C; Figure 3a). Post-stratification, in autumn, chlorophyll *a* concentrations remained slightly higher at the highest temperature increases (12.8 mg/m³ at +6°C, cf. 10.6 mg/m³ at -2°C; Figure 3a). Higher temperatures also advanced the onset of the spring bloom; at +6°C chlorophyll *a* concentrations reached 5 mg/m³ 11 days earlier than at -2°C (Figure 3b). The end of the growing season, defined as the first day when chlorophyll *a* < 5 mg/m³, was extended by 7 days at +6°C compared to -2°C (Figure 3b).

3.2.2 | Phytoplankton community

Increasing temperature prior to stratification also resulted in community shifts with the percentage of *R* strategists increasing by 32% (from -2°C to +6°C) at the expense of *CS* and *C* strategists (Figure 4a). In comparison, increases in temperature had very little

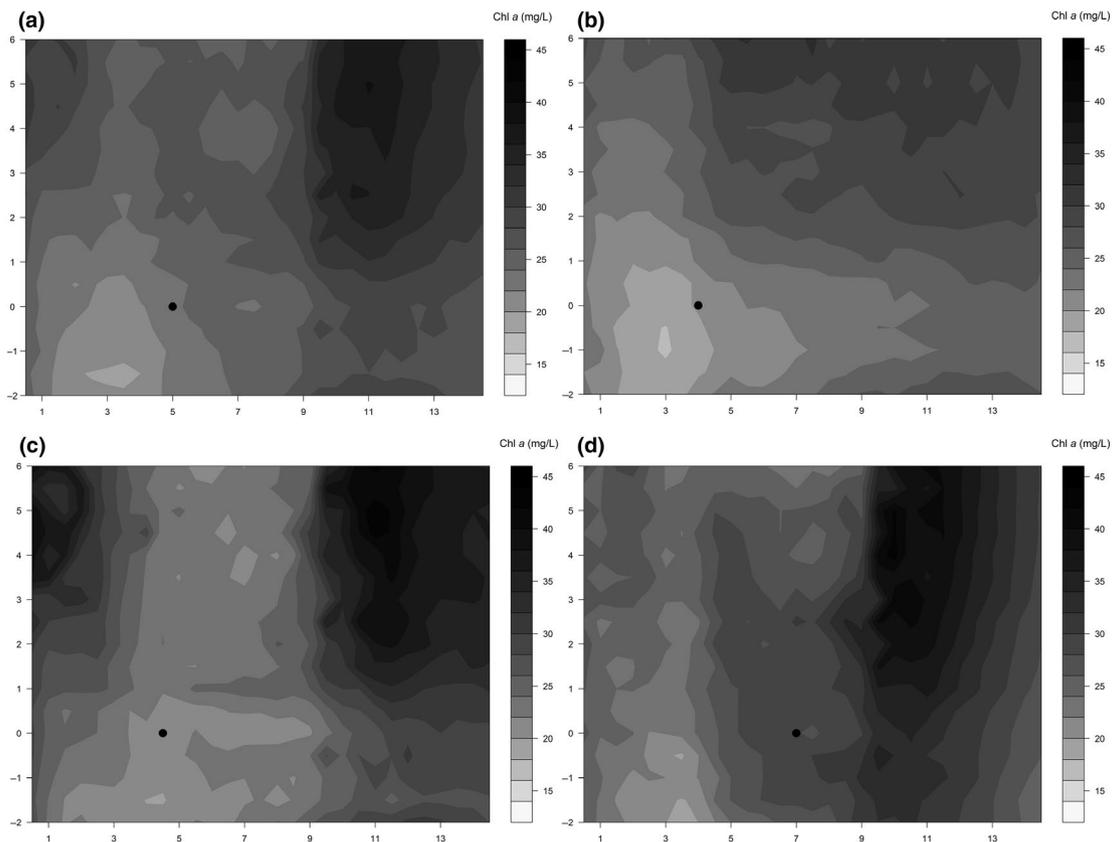


FIGURE 6 Mean chlorophyll *a* concentrations at each mixed depth and temperature change for (a) annual mean (note different scale for chlorophyll *a*), (b) stratified spring, (c) stratified summer, and (d) stratified autumn, black circle marks the baseline mixed depth and temperature for Blelham Tarn

impact on the functional composition of the post-stratification fully mixed community in autumn (Figure 4b). There was also a decrease in diversity with warming (from $H' = 3.0$ at -2°C to $H' = 2.3$ at $+6^{\circ}\text{C}$) in spring, but only a small change in diversity of the post-stratification community in autumn (Figure 5).

3.3 | Impacts of temperature and mixed depth change during the stratified period

3.3.1 | Phytoplankton biomass

Reducing the mixed depth (to 0.5 m) and increasing the temperature (to $+6^{\circ}\text{C}$) relative to the baseline increased the annual average chlorophyll *a* biomass ($+7.2\text{ mg/m}^3$) by over three times compared to changes in temperature ($+3.0\text{ mg/m}^3$) or mixed depth ($+2.2\text{ mg/m}^3$) alone (Figure 6a). However, deepening the mixed depth from the baseline led to greater increases in phytoplankton biomass (e.g. $+3.1\text{ mg/m}^3$ from the baseline to 11 m) compared to mixed depth shallowing. This was further enhanced by increases in temperature. Increasing the temperature by 6°C at a mixed depth of 11 m, for example, led to an increase in phytoplankton biomass of 10.4 mg/m^3 compared to baseline conditions (Figure 6a).

The impact of changing temperatures and depths of mixing varied with season. In spring, increases in phytoplankton biomass were driven by increases in temperature with smaller variations in biomass with changing mixed depth (e.g. $+8.5\text{ mg/m}^3$ increase from 0°C to $+6^{\circ}\text{C}$ at the spring baseline mixed depth; Figure 6b). There was a strong bimodal pattern in summer, with the greatest increases occurring with combinations of high temperatures and both shallower ($<4\text{ m}$; increase of 19.1 mg/m^3 from baseline conditions to $+6^{\circ}\text{C}$ at 0.5 m mixed depth) and deeper mixed depths ($>8.5\text{ m}$). The largest summer chlorophyll *a* concentration (43.9 mg/m^3) occurred at a mixed depth of 11 m at $+5^{\circ}\text{C}$ (Figure 6c). For autumn, the peak in chlorophyll *a* occurred at depths between 10–12 m (Figure 6d).

3.3.2 | Phytoplankton community

The annual average phytoplankton biomass was dominated by CS and *R* strategists, with *C* strategists occurring only in notable concentrations at lower temperatures (below $+0.5^{\circ}\text{C}$) and mixed depths shallower than 6.5 m (Figure 7a–c). *R* strategists increased at the expense of CS strategists when the mixing deepened (e.g. a decrease in CS strategists of 11% from the baseline mixed depth to 14.5 m; Figure 7b,c). Shifts in functional groups followed a broad seasonal pattern, which was modified by changes in mixing and temperature.

Spring was dominated by *R*-types at most mixed depths and temperatures, *C*-types increased at the expense of *R*-types for mixed depths shallower than 6.5 m and temperatures below $+0.5^{\circ}\text{C}$ and CS-types contributed 20%–40% of the community when mixing was shallower than 9 m and temperature higher than the baseline (Figure 7d–f). In summer, contrasting functional types occupied different mixed depth ranges. CS-types dominated at shallow mixed

depths ($<8\text{ m}$ at temperatures greater than the baseline) and *R*-types with deep mixing ($>8\text{ m}$), *C*-types contributed a negligible amount to the community (Figure 7g–i). The stratified autumn community reverted back to *R*-type dominance at the expense of CS-types, with *C*-types occurring at temperatures below $+0.5^{\circ}\text{C}$ and mixed depths shallower than 6 m (Figure 7j–l).

The responses of the CS- and *R*-types during summer and stratified autumn were primarily due to the contrasting responses of the two cyanobacterium taxa: *Dolichospermum* dominated with shallow mixing and *Planktothrix* with deep mixing (Figure 8a–d). In summer *Dolichospermum* dominated when mixing was shallower than 10 m and *Planktothrix* at depths $>10\text{ m}$ (Figure 8a,b). Stratified autumn was dominated by *Planktothrix* at most mixed depths and temperatures, although *Dolichospermum* contributed more to the cyanobacterial biomass at shallower mixed depths (Figure 8c,d). The annual average and seasonal diversity decreased with deeper mixing (Figure 9a–d). Low diversity values occurred at mixed depths $<10.5\text{ m}$ and high temperatures (above $+2^{\circ}\text{C}$) in summer compared to stratified spring and autumn (Figure 9b–d).

3.4 | Comparing experimental methods

Full analyses of the results were performed for each method of temperature change (top 5 m of the water column and whole water column), mixed depth method (fixed mixed depths and percentage shifts) and sampling depth (top 5 m and whole water column). The different methods of mixed depth change (fixed and percentage shifts) produced very similar seasonal mean chlorophyll *a* concentrations (Tables 3 and 4). Applying the change in water temperature to the top 5 m of the water column or the whole water column made very little difference to seasonal mean chlorophyll *a* concentrations for both mixed depth methods (Tables 3 and 4). Integrating the results over the top 5 m of the water column consistently produced slightly higher chlorophyll *a* concentrations compared to whole water column integrations for both mixed depth methods, but the seasonal patterns were consistent (Tables 3 and 4).

4 | DISCUSSION

Regarding the first hypothesis, we found that the timing of the spring bloom advanced with increases in water temperature. This extension of the growing season has also been observed in field studies (Meis, Thackeray, & Jones, 2009; Thackeray, Jones, & Maberly, 2008; Thackeray et al., 2010) and previous modeling experiments (Peeters, Straille, Lorke, & Livingstone, 2007). In these studies, however, spring warming was accompanied by earlier onset of stratification, obfuscating whether changes in water temperature or changes in stratification were the key driver. As our study kept the length of stratification the same for all model runs, it demonstrated that advance in the spring bloom can be solely due to temperature accelerating growth rates rather than

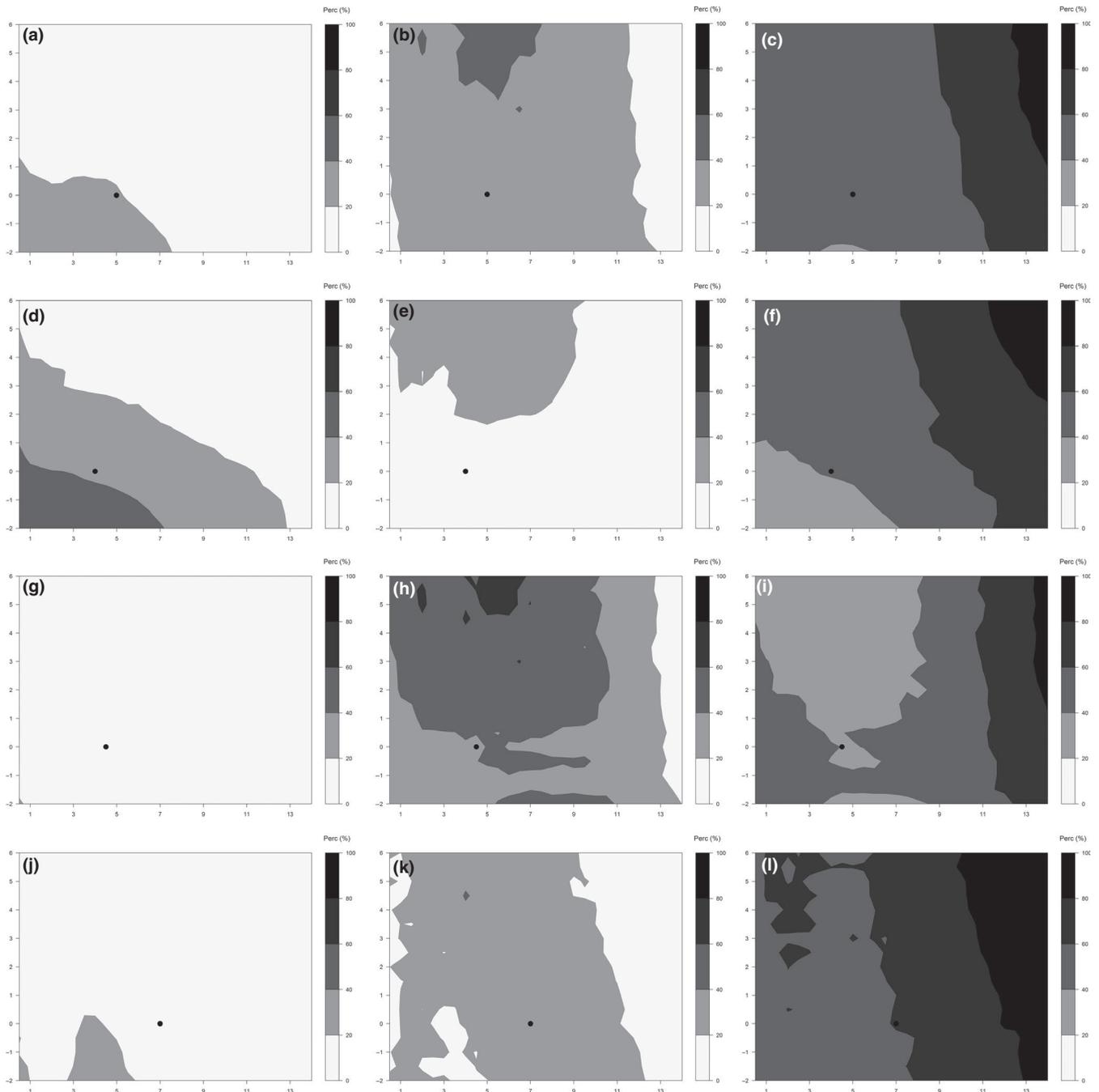


FIGURE 7 Percentage of (a, d, g, j) C, (b, e, h, k) CS, (c, f, i, l), and R strategists in (a, b, c) annual average, (d, e, f) stratified spring, (g, h, i) summer, and (j, k, l) stratified autumn. Black circle marks the baseline mixed depth and temperature for Blelham Tarn

the higher light availability that ordinarily accompanies changes in stratification and shallower mixed depths. At this time of year, nutrients are plentiful after being replenished during the winter, therefore, the growth rate of the *R*-strategist diatoms, which are adapted to low light conditions in the fully mixed layer, accelerated with increasing temperature. The growing season in autumn was also extended by temperature increases alone, although for a shorter length of time than in the spring. By independently changing mixed depth and temperature, model outcomes have also highlighted that temperature changes had different impacts

on this modelled phytoplankton community compared to mixed depth changes, supporting hypothesis 2. Increases in temperature increased phytoplankton biomass and increased the proportion of the community made up of cyanobacteria consisting of two functional groups (CS and R) for most mixed depths. This result was expected due to accelerated growth rates at higher temperatures and the favourable morphologies of the cyanobacterial taxa (Carey et al., 2012). However, the experimental results showed that shallower mixed depths could have contrasting impacts on the phytoplankton community depending on the typical current

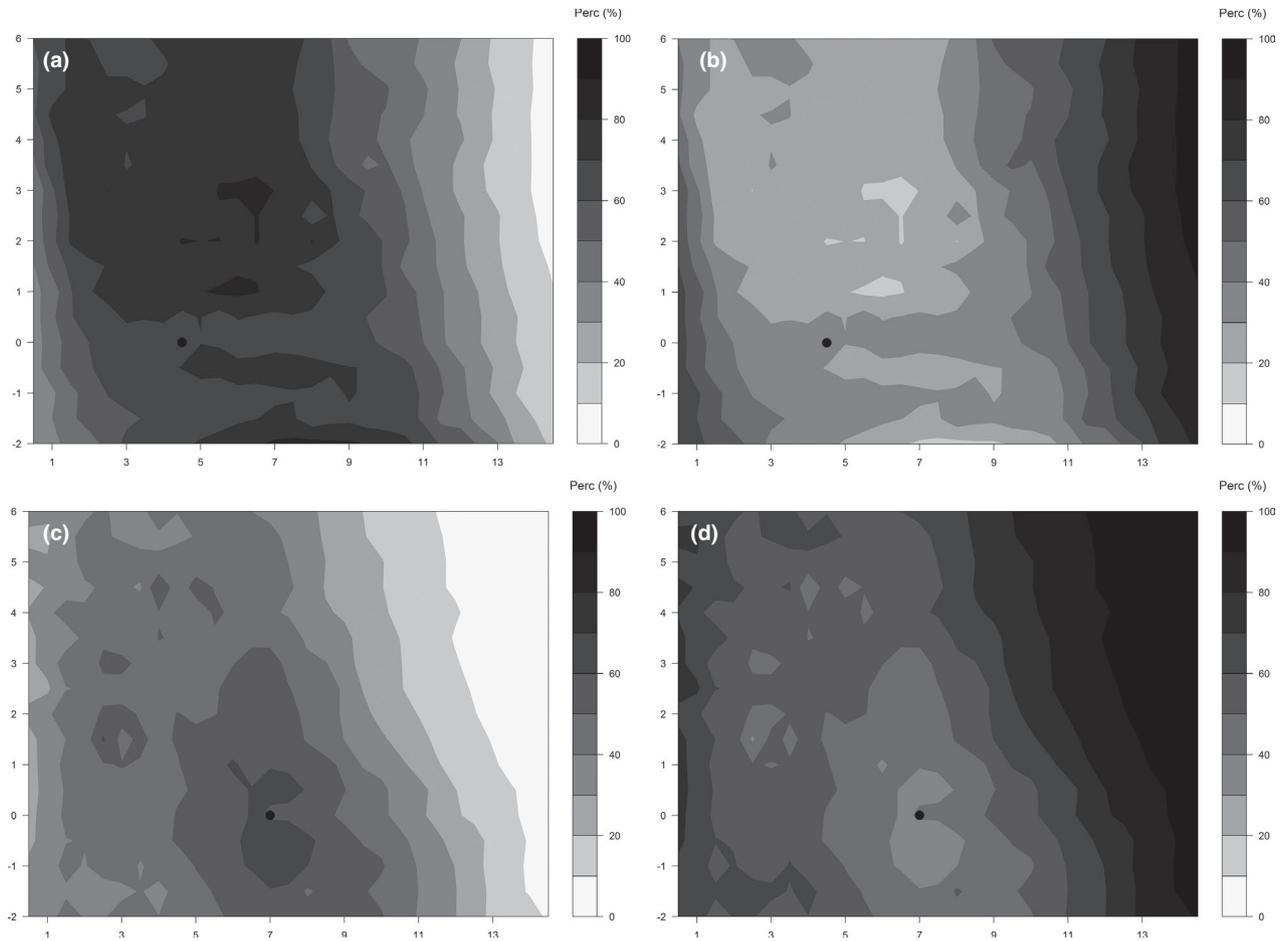


FIGURE 8 Percentage of total cyanobacteria at each mixed depth and temperature change for (a) *Dolichospermum* in stratified summer, (b) *Planktothrix* in stratified summer, (c) *Dolichospermum* in stratified autumn, and (d) *Planktothrix* in stratified autumn. Black circle marks the baseline mixed depth and temperature for Blelham Tarn

position of the mixing layer. If the original depth of mixing was located at intermediate depths (4–9 m), shallowing could increase biomass and the proportion of the community made up of the CS cyanobacteria. However, if the original depth of mixing was naturally deeper (9.5–14.5 m), shallowing to intermediate depths could decrease biomass and reduce the percentage of *R* strategists cyanobacteria, particularly if sizeable temperature increases also occurred (Figure 6).

Mixed depth and water temperature change do not necessarily occur in isolation and this modelling study has found that combined increases in water temperature and shallower depths of mixing (from baseline conditions) had a synergistic effect on phytoplankton biomass, supporting hypothesis 3. The magnitude of the synergistic response varied with season. Modelled increases in biomass and community change in spring were primarily driven by temperature increases as opposed to combined mixed depth and temperature changes. The highest temperature increases in spring led to cyanobacterial dominance, consistent with previous findings from other modelling studies (Elliott, Thackeray, Huntingford, & Jones, 2005; Markensten, Moore, & Persson, 2010) and observed data (Dupuis & Hann, 2009; Jacquet et al., 2005; Weyhenmeyer, 2001). In contrast,

summer demonstrated the largest synergistic response (+19.0 mg/m³ chlorophyll *a* with rising temperature and mixed depth shallowing from the baseline) with large changes in community composition and phytoplankton biomass occurring when both the depth of mixing and water temperature changed.

Previous work has suggested that warming and shallower mixed depths combined will create conditions favourable for cyanobacteria (Paerl & Huisman, 2009; Paerl & Paul, 2012). In this experiment, they did produce an increase in phytoplankton biomass overall and an increase in the biomass of the buoyant cyanobacterium *Dolichospermum*. Faster growth rates at high temperatures and the ability to regulate buoyancy at shallow mixed depths meant that *Dolichospermum* was able to outcompete other CS-strategists within the model. This suggests that lakes with shallow surface mixed layers similar to Blelham Tarn (4 m annual average), which are experiencing accelerated warming in surface waters (increase of $1.1 \pm 0.3^{\circ}\text{C}$ in Blelham Tarn 1968–2008) (Foley et al., 2012), may experience a deterioration in water quality with warming and shallower surface mixing. This finding is in agreement with expectations and predicted trends (Paerl & Huisman, 2009; Paerl & Paul, 2012), supporting hypothesis 4.

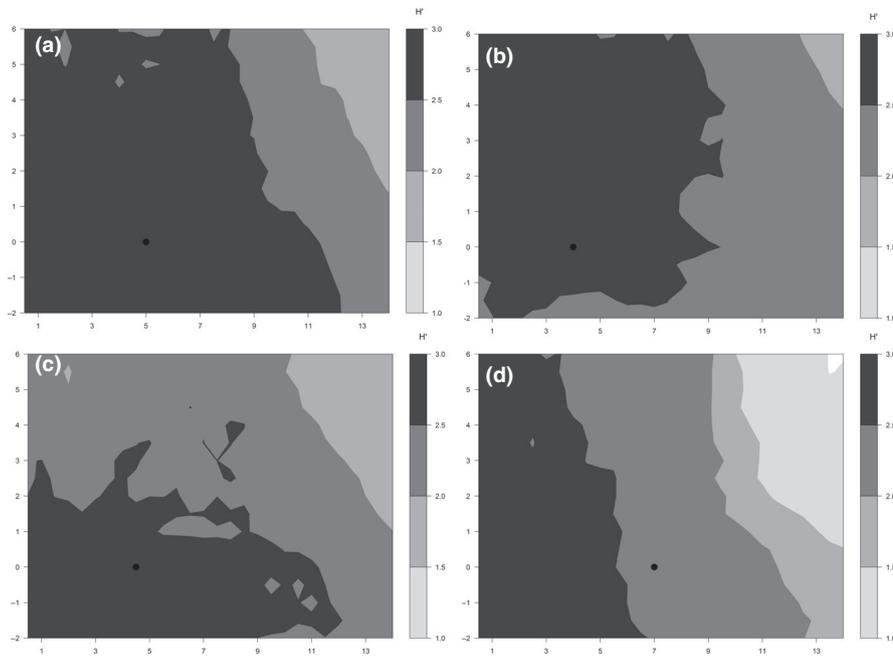


FIGURE 9 Shannon diversity index for each mixed depth and temperature change for (a) annual average, (b) stratified spring, (c) stratified summer, and (d) stratified autumn. Black circle marks the baseline mixed depth and temperature for Blelham Tarn

TABLE 4 Seasonal mean phytoplankton biomass (chlorophyll *a* mg/m³) during the stratified period for water column integrated and 5 m integrated results using the percentage mixed depth method

	Spring chlorophyll <i>a</i> (mg/m ³)		Summer chlorophyll <i>a</i> (mg/m ³)		Autumn chlorophyll <i>a</i> (mg/m ³)	
	5 m integrated	Water column integrated	5 m integrated	Water column integrated	5 m integrated	Water column integrated
Temperature change in the top 5 m	25.5	23.1	28.5	22.6	28.3	24.5
Temperature change in the whole water column	26.1	23.6	28.9	22.8	28.5	24.8

The largest cyanobacterial biomass in the model experiments, occurred at deeper mixed depths due to the low light adapted *Planktothrix*. Therefore, contrary to hypothesis 4, when the mixed layer moved from deep to intermediate depths there was a reduction in the biomass of phytoplankton and *R* strategist cyanobacterium (*Planktothrix*). This suggests that for lakes with naturally deeper mixed depths than Blelham Tarn, shallowing and warming of the mixed layer may reduce phytoplankton biomass and biomass of low light adapted cyanobacteria. These experimental findings indicate that shallower mixed depths and increases in temperature may not always lead to increases in cyanobacterial biomass, providing evidence against hypothesis 4. This is also relevant when considering artificial mixing to mitigate against surface cyanobacterial blooms. Indeed, previous artificial mixing experiments have found it to be ineffective at reducing *Planktothrix* populations (Reynolds et al., 1983; Visser, Ibelings, Bormans, & Huisman, 2016).

Dolichospermum and *Planktothrix* are both genera of cyanobacteria but they have different morphologies and affinities for light (Table 2) and therefore responded differently to changes in mixing depth in this modelling experiment. The contrasting responses of

two phytoplankton taxa belonging to the same phylogenetic group support hypothesis 5, that phytoplankton responses in these modelled results would differ depending on their morphology and traits (Reynolds et al., 1983). *Dolichospermum* dominated in shallow mixed layers as its ability to regulate buoyancy allowed it to maintain its position in a favourable light climate whereas non-motile or negatively buoyant species would be lost from the mixed layer through sedimentation (Huisman et al., 2004). These findings are consistent with previous observations of *Dolichospermum* being associated with problematic surface blooms in lakes with shallow surface mixing (Salmaso, Capelli, Shams, & Cerasino, 2015). In contrast, deeper mixed layers were dominated by *Planktothrix*, a cyanobacterium adapted to low light conditions (Dokulil & Teubner, 2012). *Planktothrix* has been associated with persistent blooms in deep mixed layers in observed data (Ernst et al., 2009) and experimental systems, often forming a sub-surface peak or a deep chlorophyll *a* maxima (Nürnberg, LaZerte, & Olding, 2003; Reynolds et al., 1983; Selmečzy, Krienitz, Casper, & Padišák, 2018). Studies in Lake Zurich and Lake Geneva have suggested that *Planktothrix* will benefit from warming in extremely deep lakes due to a reduction in full water

column mixing, which contrasts with the reduction in *Planktothrix* for shallow lakes found in this study (Gallina, Beniston, & Jacquet, 2017; Posch, Köster, & Salcher, 2012).

This modelling experiment made a number of assumptions and simplifications in order to disentangle the separate impacts of complex physical drivers. Here we have modelled only 12 phytoplankton taxa, including two cyanobacterial taxa. While these were chosen to represent a wide range of morphological traits, real lakes typically contain a richer phytoplankton community than this. Similarly, we simplified the modelling by keeping a fixed nutrient pattern between years. The model itself also contains a number of assumptions and simplifications in order to represent complex biological processes (Elliott et al., 2010, and Reynolds et al., 2001). Nevertheless, the model is mechanistic and has been widely tested on many systems around the world and the results allow an understanding of the separate impacts of mixed layer and temperature change on a phytoplankton community, which cannot be achieved using observed data alone (Elliott et al., 2010).

This study has highlighted the important role of temperature as a driver for increasing spring biomass and extending the length of the growing season. By modelling the depth of surface mixing and temperature independently we have shown that they have different impacts on phytoplankton growth: increases in temperature accelerate growth rates but changes in the mixed layer depth have contrasting impacts depending on the baseline depth, but also on the traits of the extant cyanobacteria. Mixed depth and temperature change are intrinsically linked, both being functions of warming processes, and these experimental findings show that combined changes have a synergistic impact on phytoplankton biomass. Furthermore, shallower surface mixing and temperature increases may lead to an increase in buoyant cyanobacterial taxa such as *Dolichospermum* if the original depth is relatively shallow. By contrast, mixed layer shallowing from deep to intermediate depths could lead to a reduction in cyanobacterial biomass by removing the competitive advantage of low-light adapted taxa, such as *Planktothrix*. Thus, the response of cyanobacterial blooms to climate warming in small lakes around the world should not be a universal increase but, rather, will depend on the current depth of mixing and light tolerance of the dominant cyanobacterium species.

ACKNOWLEDGMENTS

This work was funded in part by a PhD studentship awarded to E.G. from the UK Natural Environment Research Council (NERC) through the Envision Doctoral Training Partnership (grant ref. NE/L002604/1). We would like to thank CEH colleagues for the collection of chlorophyll *a* data used in the model validation. We also thank the Environment Agency for providing the flow data used to calculate nutrient loading and colleagues in the Freshwater Biological Association who collected comparative Blelham Tarn flow data in 1974. We would also like to thank the two anonymous reviewers for their constructive feedback on draft versions of this work.

CONFLICT OF INTEREST

The authors of this research article have no conflicts of interest to disclose.

ORCID

Emma Gray  <https://orcid.org/0000-0003-3074-1945>

REFERENCES

- Berger, S. A., Diehl, S., Stibor, H., Trommer, G., & Ruhlenstroth, M. (2010). Water temperature and stratification depth independently shift cardinal events during plankton spring succession. *Global Change Biology*, 16(7), 1954–1965. <https://doi.org/10.1111/j.1365-2486.2009.02134.x>
- Berger, S. A., Diehl, S., Stibor, H., Trommer, G., Ruhlenstroth, M., Wild, A., ... Striebel, M. (2006). Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia*, 150(4), 643–654. <https://doi.org/10.1007/s00442-006-0550-9>
- Bernhardt, J., Elliott, J. A., & Jones, I. D. (2008). Modelling the effects on phytoplankton communities of changing mixed depth and background extinction coefficient on three contrasting lakes in the English Lake District. *Freshwater Biology*, 53(12), 2573–2586. <https://doi.org/10.1111/j.1365-2427.2008.02083.x>
- Carey, C. C., Ibelings, B. W., Hoffmann, E. P., Hamilton, D. P., & Brookes, J. D. (2012). Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research*, 46(5), 1394–1407. <https://doi.org/10.1016/j.watres.2011.12.016>
- Cassidy, R., & Jordan, P. (2011). Limitations of instantaneous water quality sampling in surface-water catchments: Comparison with near-continuous phosphorus time-series data. *Journal of Hydrology*, 405(1), 182–193. <https://doi.org/10.1016/j.jhydrol.2011.05.020>
- Diehl, S. (2002). Phytoplankton, light, and nutrients in a gradient of mixing depths: Theory. *Ecology*, 83(2), 386–398. [https://doi.org/10.1890/0012-9658\(2002\)083\[0386:PLANIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0386:PLANIA]2.0.CO;2)
- Diehl, S., Berger, S., Ptacnik, R., & Wild, A. (2002). Phytoplankton, light, and nutrients in a gradient of mixing depths: Field experiments. *Ecology*, 83(2), 399–411. [https://doi.org/10.1890/0012-9658\(2002\)083\[0399:PLANIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0399:PLANIA]2.0.CO;2)
- Dokulil, M. T., & Teubner, K. (2012). Deep living *Planktothrix rubescens* modulated by environmental constraints and climate forcing. *Hydrobiologia*, 698(1), 29–46. <https://doi.org/10.1007/s10750-012-1020-5>
- Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., ... Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, 51(5), 2388–2397. <https://doi.org/10.4319/lo.2006.51.5.2388>
- Dupuis, A. P., & Hann, B. J. (2009). Warm spring and summer water temperatures in small eutrophic lakes of the Canadian prairies: Potential implications for phytoplankton and zooplankton. *Journal of Plankton Research*, 31(5), 489–502. <https://doi.org/10.1093/plankt/fbp001>
- Elliott, J. A., Irish, A. E., & Reynolds, C. S. (2001). The effects of vertical mixing on a phytoplankton community: A modelling approach to the intermediate disturbance hypothesis. *Freshwater Biology*, 46, 1291–1297. <https://doi.org/10.1046/j.1365-2427.2001.00754.x>
- Elliott, J. A., Irish, A. E., & Reynolds, C. S. (2010). Modelling phytoplankton dynamics in fresh waters: Affirmation of the PROTECH approach to simulation. *Freshwater Reviews*, 3(1), 75–96. <https://doi.org/10.1608/frj-3.1.4>
- Elliott, J. A., Thackeray, S. J., Huntingford, C., & Jones, R. G. (2005). Combining a regional climate model with a phytoplankton community model to

- predict future changes in phytoplankton in lakes. *Freshwater Biology*, 50(8), 1404–1411. <https://doi.org/10.1111/j.1365-2427.2005.01409.x>
- Ernst, B., Hoeger, S. J., O'Brien, E., & Dietrich, D. R. (2009). Abundance and toxicity of *Planktothrix rubescens* in the pre-alpine Lake Ammersee, Germany. *Harmful Algae*, 8(2), 329–342. <https://doi.org/10.1016/j.hal.2008.07.006>
- Foley, B., Jones, I. D., Maberly, S. C., & Rippey, B. (2012). Long-term changes in oxygen depletion in a small temperate lake: Effects of climate change and eutrophication. *Freshwater Biology*, 57(2), 278–289. <https://doi.org/10.1111/j.1365-2427.2011.02662.x>
- Gallina, N., Beniston, M., & Jacquet, S. (2017). Estimating future cyanobacterial occurrence and importance in lakes: A case study with *Planktothrix rubescens* in Lake Geneva. *Aquatic Sciences*, 79(2), 249–263. <https://doi.org/10.1007/s00027-016-0494-z>
- Gasca, D., Maberly, S., & Mackay, E. (2015). Investigation into the perceived enrichment of five Lakeland SSSIs: Blelham Tarn. Retrieved from <http://nora.nerc.ac.uk/id/eprint/510720/>
- Hondzo, M., & Stefan, H. G. (1993). Regional water temperature characteristics of lakes subjected to climate change. *Climatic Change*, 24(3), 187–211. <https://doi.org/10.1007/bf01091829>
- Huisman, J., Codd, G. A., Paerl, H. W., Ibelings, B. W., Verspagen, J. M. H., & Visser, P. M. (2018). Cyanobacterial blooms. *Nature Reviews Microbiology*, 16(8), 471–483. <https://doi.org/10.1038/s41579-018-0040-1>
- Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M. H., & Sommeijer, B. (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, 85(11), 2960–2970. <https://doi.org/10.1890/03-0763>
- Huisman, J., van Oostveen, P., & Weissing, F. J. (1999). Species dynamics in phytoplankton blooms: Incomplete mixing and competition for light. *The American Naturalist*, 154(1), 46–68. <https://doi.org/10.1086/303220>
- Jacquet, S., Briand, J.-F., Le Boulanger, C., Avois-Jacquet, C., Oberhaus, L., Tassin, B., ... Humbert, J.-F. (2005). The proliferation of the toxic cyanobacterium *Planktothrix rubescens* following restoration of the largest natural French lake (Lac du Bourget). *Harmful Algae*, 4(4), 651–672. <https://doi.org/10.1016/j.hal.2003.12.006>
- Jäger, C. G., Diehl, S., & Schmidt, G. M. (2008). Influence of water-column depth and mixing on phytoplankton biomass, community composition, and nutrients. *Limnology and Oceanography*, 53(6), 2361–2373. <https://doi.org/10.4319/lo.2008.53.6.2361>
- Jones, I. D., & Elliott, J. A. (2007). Modelling the effects of changing retention time on abundance and composition of phytoplankton species in a small lake. *Freshwater Biology*, 52(6), 988–997. <https://doi.org/10.1111/j.1365-2427.2007.01746.x>
- Lehman, J. T., Mugidde, R., & Lehman, D. A. (1998). *Lake Victoria plankton ecology: Mixing depth and climate-driven control of lake condition* (pp. 99–116). https://doi.org/10.1007/978-94-017-1437-2_8
- Livingstone, D. (2003). Impact of secular climate change on the thermal structure of a large temperate central European lake. *Climatic Change*, 57, 205–225. <https://doi.org/10.1023/a:1022119503144>
- Maberly, S. C., De Ville, M. M., Thackeray, S. J., Ciar, D., Clarke, M., Fletcher, J. M., ... Webb, P. (2016). A survey of the status of the lakes of the English Lake District: the Lakes Tour 2015. Retrieved from <http://nora.nerc.ac.uk/id/eprint/513514/>
- Markensten, H., Moore, K., & Persson, I. (2010). Simulated lake phytoplankton composition shifts toward cyanobacteria dominance in a future warmer climate. *Ecological Applications*, 20(3), 752–767. <https://doi.org/10.1890/08-2109.1>
- Meis, S., Thackeray, S., & Jones, I. (2009). Effects of recent climate change on phytoplankton phenology in a temperate lake. *Freshwater Biology*, 54, 1888–1898. <https://doi.org/10.1111/j.1365-2427.2009.02240.x>
- Michalak, A. M. (2016). Study role of climate change in extreme threats to water quality. *Nature*, 535, 349–350. <https://doi.org/10.1038/535349a>
- Nürnberg, G. K., LaZerte, B. D., & Olding, D. D. (2003). An artificially induced *Planktothrix rubescens* surface bloom in a small Kettle Lake in Southern Ontario compared to blooms world-wide. *Lake and Reservoir Management*, 19(4), 307–322. <https://doi.org/10.1080/07438140309353941>
- O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., ... Zhang, G. (2015). Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters*, 42(24), 10773–10781. <https://doi.org/10.1002/2015gl066235>
- Paerl, H. W., & Huisman, J. (2008). Blooms like it hot. *Science*, 320(5872), 57–58. <https://doi.org/10.1126/science.1155398>
- Paerl, H. W., & Huisman, J. (2009). Climate change: A catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports*, 1(1), 27–37. <https://doi.org/10.1111/j.1758-2229.2008.00004.x>
- Paerl, H. W., & Paul, V. J. (2012). Climate change: Links to global expansion of harmful cyanobacteria. *Water Research*, 46(5), 1349–1363. <https://doi.org/10.1016/j.watres.2011.08.002>
- Peeters, F., Kerimoglu, O., & Straile, D. (2013). Implications of seasonal mixing for phytoplankton production and bloom development. *Theoretical Ecology*, 6(2), 115–129. <https://doi.org/10.1007/s12080-012-0164-2>
- Peeters, F., Straile, D., Lorke, A., & Livingstone, D. M. (2007). Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Global Change Biology*, 13(9), 1898–1909. <https://doi.org/10.1111/j.1365-2486.2007.01412.x>
- Peeters, F., Straile, D., Lorke, A., & Ollinger, D. (2007). Turbulent mixing and phytoplankton spring bloom development in a deep lake. *Limnology and Oceanography*, 52(1), 286–298. <https://doi.org/10.4319/lo.2007.52.1.0286>
- Posch, T., Köster, O., & Salcher, M. (2012). Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. *Nature Climate Change*, 2, 809–813. <https://doi.org/10.1038/nclimate1581>
- Ptácnik, R., Diehl, S., & Berger, S. (2003). Performance of sinking and non-sinking phytoplankton taxa in a gradient of mixing depths. *Limnology and Oceanography*, 48(5), 1903–1912. <https://doi.org/10.4319/lo.2003.48.5.1903>
- Ramsbottom, A. (1976). *Depth charts of the Cumbrian lakes*. Kendal: Freshwater Biological Association.
- Rasconi, S., Gall, A., Winter, K., & Kainz, M. J. (2015). Increasing water temperature triggers dominance of small freshwater plankton. *PLoS ONE*, 10(10), <https://doi.org/10.1371/journal.pone.0140449>
- Read, J. S., Hamilton, D. P., Jones, I. D., Muraoka, K., Winslow, L. A., Kroiss, R., ... Gaiser, E. (2011). Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software*, 26(11), 1325–1336. <https://doi.org/10.1016/j.envsoft.2011.05.006>
- Reynolds, C. S. (1988). The concept of ecological succession applied to seasonal periodicity of freshwater phytoplankton. *SIL Proceedings*, 1922–2010, 23(2), 683–691. <https://doi.org/10.1080/03680770.1987.11899692>
- Reynolds, C. S. (1989). *Physical determinants of phytoplankton succession* (pp. 9–56). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-74890-5_2
- Reynolds, C. (2006). *The ecology of phytoplankton*. Cambridge, UK: Cambridge University Press.
- Reynolds, C. S., Irish, A. E., & Elliott, J. A. (2001). The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecological Modelling*, 140(3), 271–291. [https://doi.org/10.1016/s0304-3800\(01\)00330-1](https://doi.org/10.1016/s0304-3800(01)00330-1)
- Reynolds, C. S., Oliver, R. L., & Walsby, A. E. (1987). Cyanobacterial dominance: The role of buoyancy regulation in dynamic lake environments. *New Zealand Journal of Marine and Freshwater Research*, 21(3), 379–390. <https://doi.org/10.1080/00288330.1987.9516234>

- Reynolds, C. S., Wiseman, S. W., Godfrey, B. M., & Butterwick, C. (1983). Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. *Journal of Plankton Research*, 5(2), 203–234. <https://doi.org/10.1093/plankt/5.2.203>
- Salmaso, N., Capelli, C., Shams, S., & Cerasino, L. (2015). Expansion of bloom-forming *Dolichospermum lemmermannii* (Nostocales, Cyanobacteria) to the deep lakes south of the Alps: Colonization patterns, driving forces and implications for water use. *Harmful Algae*, 50, 76–87. <https://doi.org/10.1016/j.hal.2015.09.008>
- Selmeczy, G. B., Krienitz, L., Casper, P., & Padisák, J. (2018). Phytoplankton response to experimental thermocline deepening: A mesocosm experiment. *Hydrobiologia*, 805(1), 259–271. <https://doi.org/10.1007/s10750-017-3308-y>
- Thackeray, S. J., Jones, I. D., & Maberly, S. C. (2008). Long-term change in the phenology of spring phytoplankton: Species-specific responses to nutrient enrichment and climatic change. *Journal of Ecology*, 96(3), 523–535. <https://doi.org/10.1111/j.1365-2745.2008.01355.x>
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
- Verpoorter, C., Kutser, T., Seekell, D. A., & Tranvik, L. J. (2014). A global inventory of lakes based on high-resolution satellite imagery. *Geophysical Research Letters*, 41(18), 6396–6402. <https://doi.org/10.1002/2014gl060641>
- Visser, P. M., Ibelings, B. W., Bormans, M., & Huisman, J. (2016). Artificial mixing to control cyanobacterial blooms: A review. *Aquatic Ecology*, 50(3), 423–441. <https://doi.org/10.1007/s10452-015-9537-0>
- Visser, P., Ibelings, B., Van Der Veer, B., Koedood, J., & Mur, R. (1996). Artificial mixing prevents nuisance blooms of the cyanobacterium *Microcystis* in Lake Nieuwe Meer, the Netherlands. *Freshwater Biology*, 36(2), 435–450. <https://doi.org/10.1046/j.1365-2427.1996.00093.x>
- Walling, D. E., & Webb, B. W. (1981). The reliability of suspended sediment load data [River Creedy, England]. International Association of Hydrological Sciences. Retrieved from <http://agris.fao.org/agris-search/search.do?recordID=US8203182>
- Walsby, A. E., Hayes, P. K., Boje, R., & Stal, L. J. (1997). The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytologist*, 136(3), 407–417. <https://doi.org/10.1046/j.1469-8137.1997.00754.x>
- Weyhenmeyer, G. A. (2001). Warmer winters: Are planktonic algal populations in Sweden's largest lakes affected? *AMBIO: A Journal of the Human Environment*, 30(8), 565–571. <https://doi.org/10.1579/0044-7447-30.8.565>
- Winder, M., & Schindler, D. E. (2004). Climatic effects on the phenology of lake processes. *Global Change Biology*, 10(11), 1844–1856. <https://doi.org/10.1111/j.1365-2486.2004.00849.x>
- Winder, M., & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, 698(1), 5–16. <https://doi.org/10.1007/s10750-012-1149-2>
- Winslow, L. A., Read, J. S., Hansen, G. J. A., & Hanson, P. C. (2015). Small lakes show muted climate change signal in deepwater temperatures. *Geophysical Research Letters*, 42(2), 355–361. <https://doi.org/10.1002/2014gl062325>
- Winslow, L. A., Read, J. S., Hansen, G. J. A., Rose, K. C., & Robertson, D. M. (2017). Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. *Limnology and Oceanography*, 62(5), 2168–2178. <https://doi.org/10.1002/lno.10557>
- Woolway, R. I., Jones, I. D., Maberly, S. C., French, J. R., Livingstone, D. M., Monteith, D. T., ... Weyhenmeyer, G. A. (2016). Diel surface temperature range scales with lake size. *PLoS ONE*, 11(3), e0152466. <https://doi.org/10.1371/journal.pone.0152466>

How to cite this article: Gray E, Elliott JA, Mackay EB, Folkard AM, Keenan PO, Jones ID. Modelling lake cyanobacterial blooms: Disentangling the climate-driven impacts of changing mixed depth and water temperature. *Freshw Biol.* 2019;64:2141–2155. <https://doi.org/10.1111/fwb.13402>