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

Running head: Mixing, temperature and cyanobacteria impacts

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Summary

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 km^2) 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.

Introduction

Climate change is impacting phytoplankton communities in lakes across the world through direct and indirect effects of temperature change (Huisman, Codd, Paerl, Ibelings, Verspagen, et al., 2018; Winder & Sommer, 2012). Though 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 cyanobacteria 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 *et al*., 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 ^{o}C decade^{-1} 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 ºC to 25-35 ºC 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; Ptacnik, Diehl & Berger, 2003; Huisman *et al.*, 2004). 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 *et al*. 2002; Huisman, van Oostveen & Weissing, 1999). Phytoplankton have different affinities for light and levels of motility, therefore 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, Diehl & Berger 2003; Visser *et al*. 1996; Reynolds *et al*. 1983). Increased surface water temperature with climatic warming may result in shallower mixed depths for many lakes which may then increase cyanobacteria abundance (Paerl & Huisman, 2009). Many species of cyanobacteria 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 (Peeters *et al*., 2007; Berger *et al*. 2010; 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; Bernhardt, Elliott & Jones, 2008; Berger *et al.*, 2010). 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 *et al*., 2001), we systematically and independently changed the water temperature and mixed depth of a model experimental lake system. We chose a small lake (<1 km^2) 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 cyanobacteria abundance; (5) phytoplankton taxa within the same phylogenetic group may respond differently to changes in physical drivers due to differences in morphology. Though 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.

Methods

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 km^2), 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) (Fig.1). The trophic status of Blelham Tarn lies on the meso-eutrophic boundary (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016) and it is monomictic, typically stratifying from spring to late autumn.

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 UK, Europe and beyond (Elliott, Irish, & Reynolds, 2010) including successful simulations of Blelham Tarn (Elliott, Irish & Reynolds, 2001; Jones & Elliott, 2007; Bernhardt, Elliott & Jones, 2008).

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,

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

where r' is the proportional growth rate over 24 hours, 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 m^{-3}). The growth rate changes with water temperature, light levels and nutrient limitation of phosphorus, nitrate or silica defined by

$$r' = \min\{r'_{(\theta I)}, r'_P, r'_N, r'_{Si}\}, \tag{2}$$

where $r'_{(\theta I)}$ is the growth rate due to temperature and daily photoperiod, and r'_P, r'_N, r'_{Si} are the growth rates determined by phosphorus, nitrate and silica concentrations, respectively. In addition to morphology, each phytoplankton is given appropriate movement characteristics as well as any additional abilities such as nitrogen fixation (Table 1). Further details about the model set up including mortality and respiration rates can be found in Reynolds, Irish & Elliott (2001) and Elliott, Irish & Reynolds (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 2012-2014 (Table 1). These phytoplankton also covered a range of phylogenetic (diatoms, flagellates, chlorophytes and cyanobacteria) and CSR-functional groupings. The use of the CSR classification, developed by Reynolds (1988), helps us understand phytoplankton responses in terms of their traits and morphology, which cut across taxonomical groups (Reynolds, 2006).

Driving data

A three year period (2012-2014) of daily averaged solar radiation data recorded by a Kipp Zonan CMP6 Pyranometer (sensitivity 5 to 20μV/W/m^2) attached to an *in situ* automated monitoring buoy (Fig.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 minutes at 1 m depth intervals in the water column from 1-10 m with additional temperature sensors at 0.5 m 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 m to 14.5 m) to provide a daily water temperature structure to drive the PROTECH model over the simulated three year period.

To calculate daily nutrient loading to the lake, daily average discharge (m^3 s^{-1}) 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; $p<0.05$),

$$y = 0.0076x^{1.253}, \tag{3}$$

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 & 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 & 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).

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 kg m^{-3} 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 (Fig.2).

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 m 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 Blelham 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 ºC intervals from -2 to +6 ºC in the top 5 m of the water column throughout the year. Temperature 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 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 5m 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 twelve phytoplankton species was calculated using the Shannon index according to the following equation,

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

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 ith phytoplankton taxon. For each of the resulting variables, overall annual means were calculated. Seasonal averages were 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 01/03/2012, 11/04/2013, 31/03/2014 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 07/10/2012, 03/11/2013 and 07/11/2014. Outside of these periods, the mixed depth of the model was set at the full depth of the lake irrespective of water column temperatures.

Results

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 (Fig. 2). In terms of the community, annual observed and modelled means for C (modelled = 2.7 ± 2.8 mg m^{-3}, observed = 2.0 ± 3.2 mg m^{-3}), R (modelled = 9.1 ± 7.1 mg m^{-3}, observed = 8.9 ± 8.0 mg m^{-3}) and CS (modelled = 3.2 ± 4.2 mg m^{-3}, observed = 3.1 ± 6.0 mg m^{-3}) strategists were very similar (Fig. 2). The model performed less well for S strategists (modelled=1.2 ± 0.6 mg m^{-3}, observed= 4.2 ± 7.9 mg m^{-3}); this group was therefore not considered in the analysis.

Impacts of temperature change before and after stratification

a. *Phytoplankton biomass*

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

b. *Phytoplankton community*

Increasing temperature prior to stratification also resulted in community shifts with the percentage of *R* strategists increasing by 32 % (from -2 ºC to + 6 ºC) at the expense of *CS* and *C* strategists (Fig. 4a). In comparison, increases in temperature had very little impact on the functional composition of the post-stratification fully mixed community in autumn (Fig. 4b). There was also a decrease in diversity with warming (from H' = 3.0 at -2 ºC to H' = 2.3 at +6 ºC) in spring, but only a small change in diversity of the post-stratification community in autumn (Fig. 5).

Impacts of temperature and mixed depth change during the stratified period

a. *Phytoplankton biomass*

Reducing the mixed depth (to 0.5 m) and increasing the temperature (to + 6 ºC) relative to the baseline increased the annual average chlorophyll *a* biomass (+ 7.2 mg m^{-3}) by over three times compared to changes in temperature (+ 3.0 mg m^{-3}) or mixed depth (+ 2.2 mg m^{-3})

alone (Fig. 6a). However, deepening the mixed depth from the baseline led to greater increases in phytoplankton biomass (e.g. + 3.1 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 ºC 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 (Fig. 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 mg m^{-3} increase from +0 ºC to +6 ºC at the spring baseline mixed depth) (Fig. 6b). There was a strong bimodal pattern in summer, with the greatest increases occurring with combinations of high temperatures and both shallower (< 4 m) (increase of 19.1 mg m^{-3} from baseline conditions to +6 ºC at 0.5 m mixed depth) and deeper mixed depths (> 8.5 m). The largest summer chlorophyll *a* concentration (43.9 mg m^{-3}) occurred at a mixed depth of 11 m at + 5 ºC (Fig.6c). For autumn, the peak in chlorophyll *a* occurred at depths between 10-12 m (Fig.6d).

b. 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 ºC) and mixed depths shallower than 6.5 m (Fig. 7abc). *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) (Fig. 7bc). 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 ºC and *CS*-types contributed 20-40 % of the community when mixing was shallower than 9 m and temperature higher than the baseline (Fig.7def). In summer, contrasting functional types occupied different mixed depth ranges. *CS*-types dominated at shallow mixed depths (< 8 m at temperatures greater than the baseline) and *R*-types with deep mixing (> 8 m), *C*-types contributed a negligible amount to the community (Fig.7ghi). 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 ºC and mixed depths shallower than 6 m (Fig.7jkl).

The responses of the *CS*- and *R*-types during summer and stratified autumn were primarily due to the contrasting responses of the two cyanobacteria taxa: *Dolichospermum* dominated with shallow mixing and *Planktothrix* with deep mixing (Fig.8abcd). In summer *Dolichospermum* dominated when mixing was shallower than 10 m and *Planktothrix* at depths deeper than 10 m (Fig.8ab). Stratified autumn was dominated by *Planktothrix* at most mixed depths and temperatures, although *Dolichospermum* contributed more to the cyanobacteria biomass at shallower mixed depths (Fig.8cd). The annual average and seasonal diversity decreased with deeper mixing (Fig. 9abcd). Low diversity values occurred at mixed depths shallower than 10.5 m and high temperatures (above +2ºC) in summer compared to stratified spring and autumn (Fig.8bcd).

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* values compared to whole water column integrations for both mixed depth methods, but the seasonal patterns were consistent (Tables 3 and 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 *et al.*, 2009; Thackeray, Jones, & Maberly, 2008; Thackeray *et al.*, 2010) and previous modelling experiments (Peeters, Straile, 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 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 two. 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 cyanobacteria 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 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* strategist cyanobacteria, particularly if sizeable temperature increases also occurred (Fig 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 three. 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 cyanobacteria dominance, consistent with previous findings from other modelling studies (Elliott *et al*., 2005; Markensten, Moore, & Persson, 2010) and observed data (Weyhenmeyer, 2001; Dupuis & Hann, 2009; Jacquet *et al*., 2005). In contrast, summer demonstrated the largest synergistic response (+19.0 mg m^{-3} 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 cyanobacteria *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 ± 0.3 ºC 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 four.

The largest cyanobacteria biomass in the model experiments, occurred at deeper mixed depths due to the low light adapted *Planktothrix*. Therefore, contrary to hypothesis four, when the mixed layer moved from deep to intermediate depths there was a reduction in the biomass of phytoplankton and *R* strategist cyanobacteria (*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 cyanobacteria biomass, providing evidence against hypothesis four. 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 *et al*., 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 supports hypothesis five, 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 cyanobacteria 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 (Reynolds *et al*., 1983; Nürnberg, LaZerte & Olding 2003; Selmeczy *et al*., 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 twelve phytoplankton taxa, including two cyanobacteria 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 (Reynolds, Irish & Elliott, 2001, and Elliott, Irish & Reynolds, 2010). 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. On the other hand, 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 cyanobacteria 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 cyanobacteria species.

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Conflict of Interest Statement

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

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Tables

Table 1 Morphometric characteristics of the 12 phytoplankton taxa.

Phytoplankton	**Surface area (μm^2)**	**Volume (μm^3)**	**SA:V**	**Maximum dimension (µm)**	**Phylogentic grouping**	**Competitors (C), stress tolerant (S), ruderals (R)**	**Grazed**	**Nitrogen fixer**
Plagioselmis	108	72	1.5	11	Flagellate	C	Yes	No
Stephanodiscus	404	280	1.4	11	Diatom	C	Yes	No
Dinobryon	629	848	0.7	40	Flagellate	C	Yes	No
Cryptomonas	1030	2710	0.4	21	Flagellate	CS	Yes	No
Synedra	4100	7900	0.5	110	Diatom	R	No	No
Aulacoseira	4350	2970	1.5	240	Diatom	R	No	No
Dolichospermum	6200	29000	0.2	75	Cyanobacteria	CS	No	Yes
Coenochloris	6430	17200	0.4	64	Chlorophyte	S	No	No
Asterionella	6690	5160	1.3	130	Diatom	R	No	No
Planktothrix	7350	13970	0.5	300	Cyanobacteria	R	No	No
Sphaerocystis	7850	65500	0.1	50	Chlorophyte	S	Yes	No
Ceratium	9600	43700	0.2	201	Flagellate	CS	No	No

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

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

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 a (mg m^{-3})		Summer chlorophyll a (mg m^{-3})		Autumn chlorophyll *a* (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 5m	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

Table 4 Seasonal mean phytoplankton biomass (chlorophyll *a* mg m^{-3}) during the stratified period for water column integrated and 5 m integrated results using the percentage mixed depth method.

	Spring chlorophyll a (mg m^{-3})		Summer chlorophyll a (mg m^{-3})		Autumn chlorophyll *a* (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 5m	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

Figure Captions

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)

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

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.

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

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, dashed vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham Tarn, respectively.

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, (j,k,l) stratified autumn, dashed vertical and

horizontal lines mark the baseline mixed depth and temperature for Blelham Tarn, respectively.

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, dashed vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham Tarn, respectively.

Figure 9. Shannon diversity index for each mixed depth and temperature change for (a) annual average (b) stratified spring (c) stratified summer, (d) stratified autumn dashed vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham Tarn, respectively.

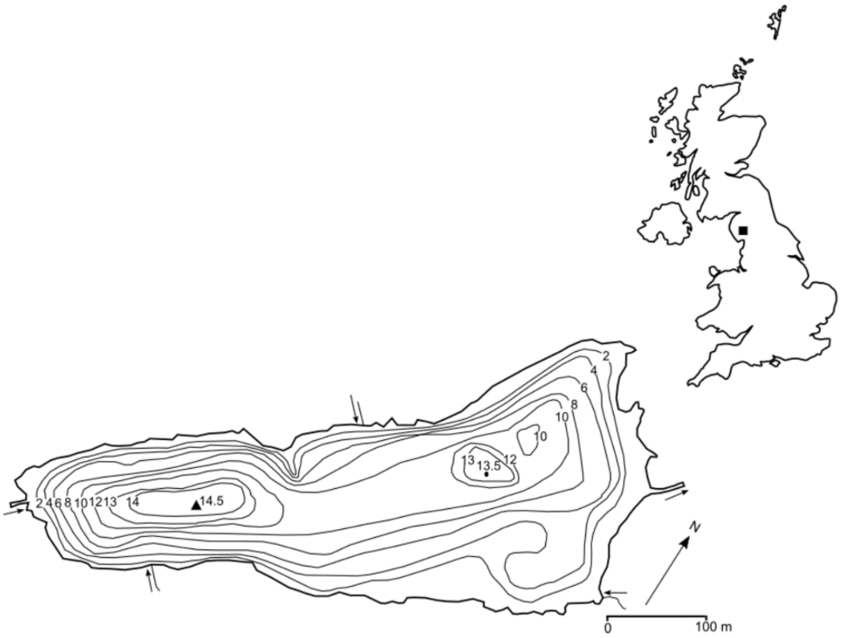

Figure 1

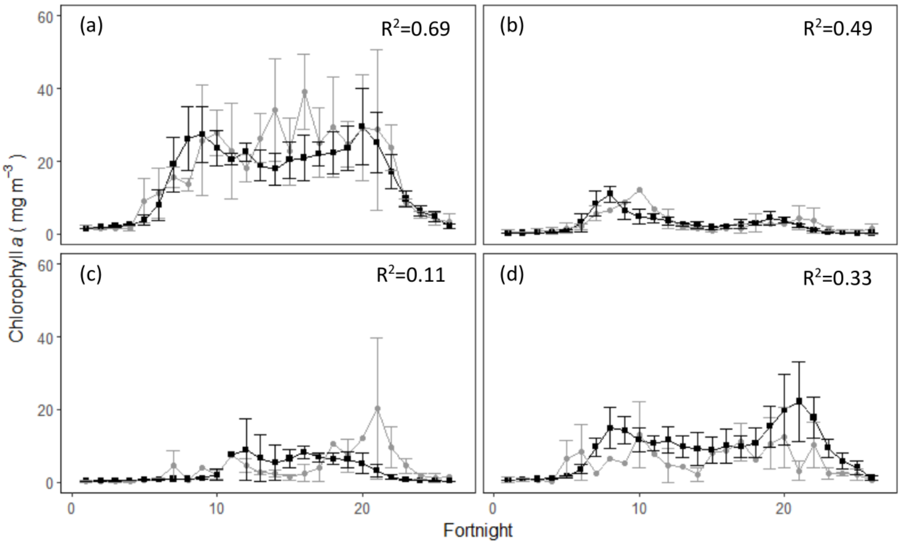
(a)
R²=0.69
(b)
R²=0.49
(c)
R²=0.11
(d)
R²=0.33
Chlorophyll a (mg m⁻³)
0
20
40
60
0
10
20
Fortnight

Figure 2

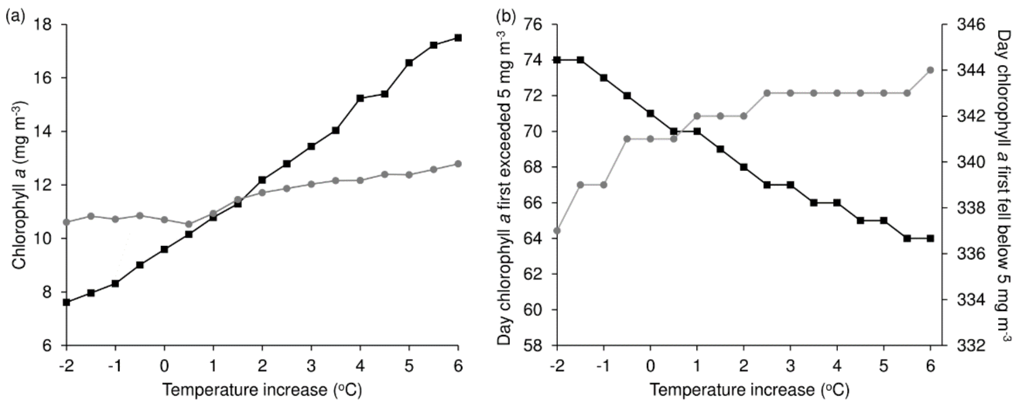
(a)
Chlorophyll *a* (mg m⁻³)
18
16
14
12
10
8
6
-2
-1
0
1
2
3
4
5
6
Temperature increase (°C)
(b)
Day chlorophyll *a* first exceeded 5 mg m⁻³
76
74
72
70
68
66
64
62
60
58
Day chlorophyll *a* first fell below 5 mg m⁻³
346
344
342
340
338
336
334
332
-2
-1
0
1
2
3
4
5
6
Temperature increase (°C)

Figure 3

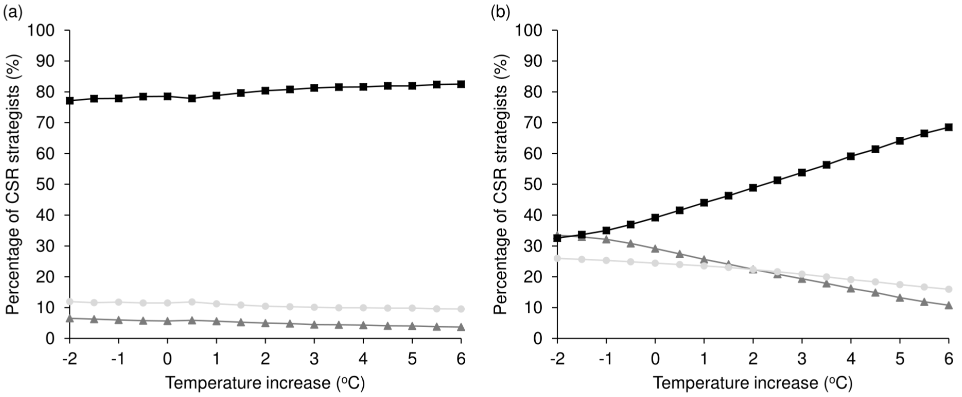
(a)
(b)
Percentage of CSR strategists (%)
0
10
20
30
40
50
60
70
80
90
100
-2
-1
0
1
2
3
4
5
6
Temperature increase (°C)

Figure 4

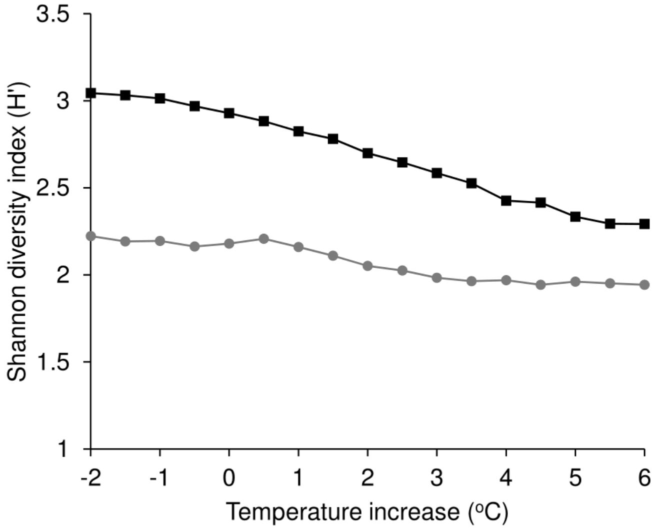
3.5
3
2.5
2
1.5
1
Shannon diversity index (H')
-2
-1
0
1
2
3
4
5
6
Temperature increase (°C)

Figure 5

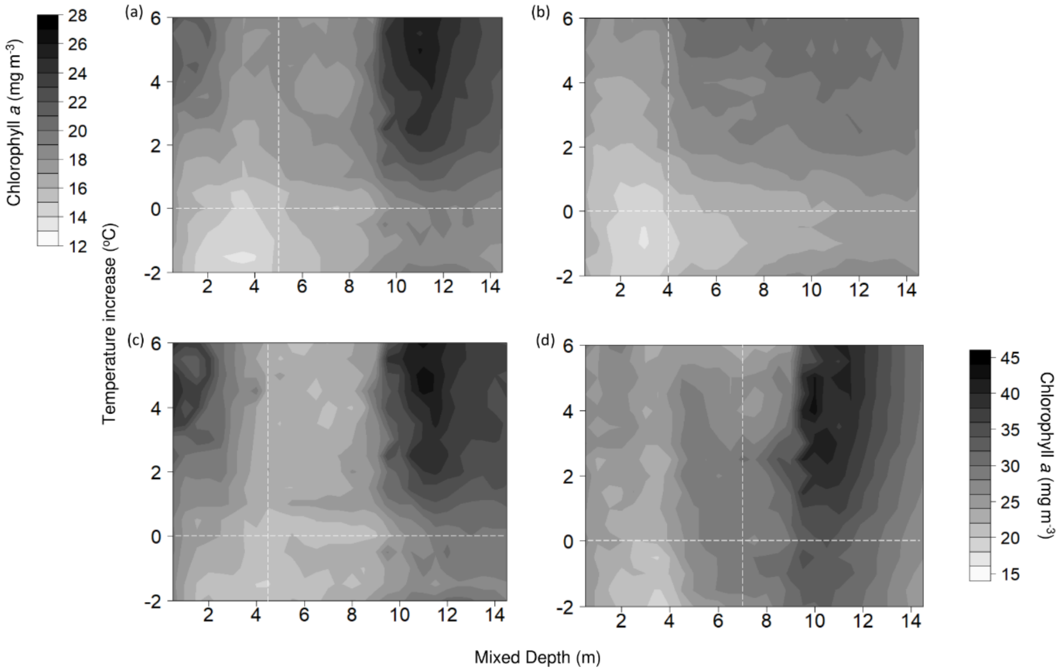
Chlorophyll a (mg m-3)
28
26
24
22
20
18
16
14
12
(a)
(b)
(c)
(d)
6
4
2
0
-2
2
4
6
8
10
12
14
Temperature increase (°C)
Mixed Depth (m)
45
40
35
30
25
20
15
Chlorophyll a (mg m-3)

Figure 6

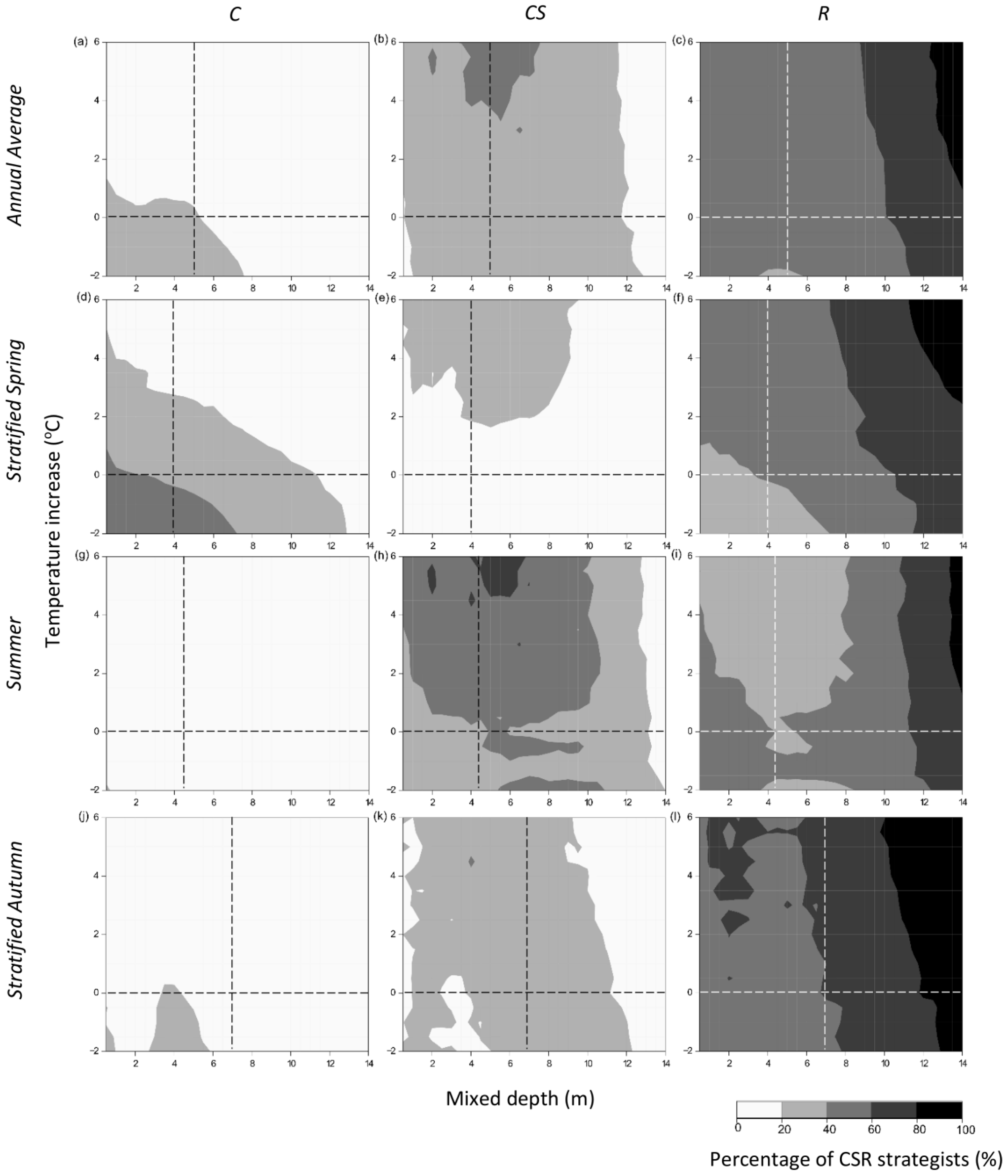
C
CS
R
Annual Average
Stratified Spring
Summer
Stratified Autumn
Temperature increase (°C)
Mixed depth (m)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
−2
0
2
4
6
8
10
12
14
0
20
40
60
80
100
Percentage of CSR strategists (%)

Figure 7

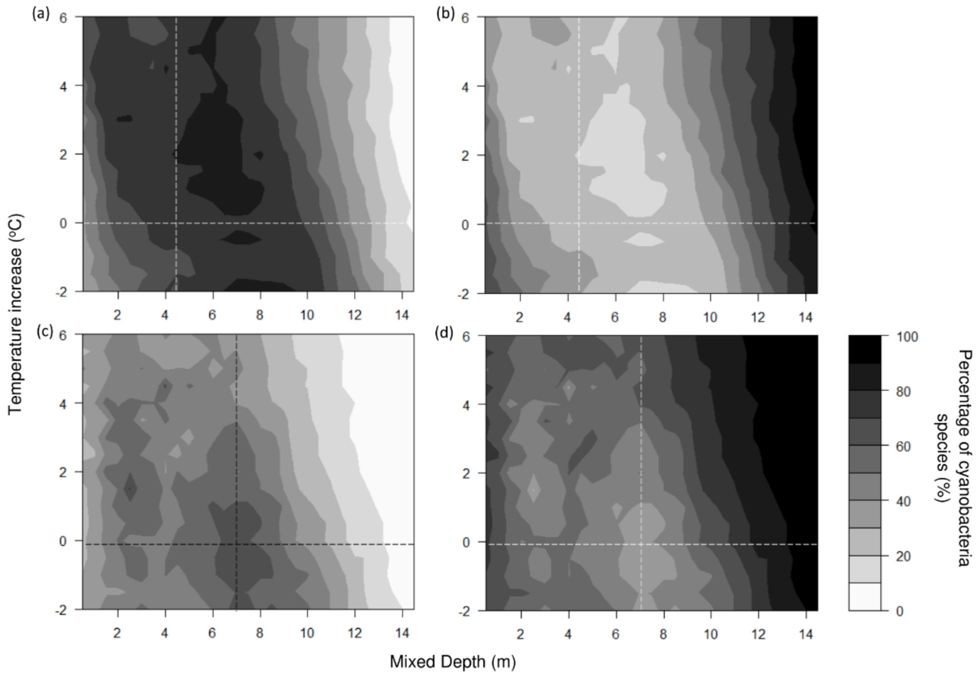
(a)
(b)
(c)
(d)
Temperature increase (°C)
-2
0
2
4
6
2
4
6
8
10
12
14
Mixed Depth (m)
Percentage of cyanobacteria species (%)
100
80
60
40
20
0

Figure 8

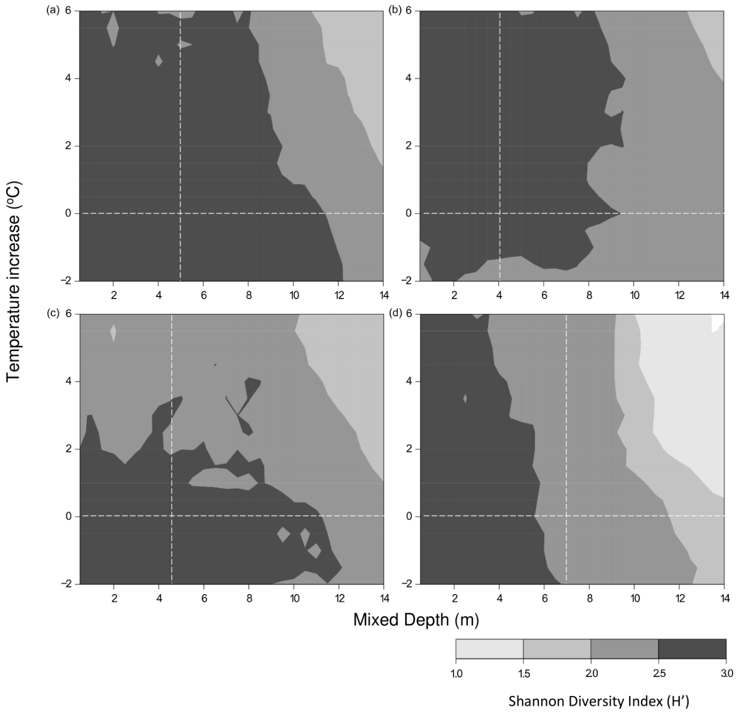
(a)
(b)
(c)
(d)
Temperature increase (°C)
−2
0
2
4
6
2
4
6
8
10
12
14
Mixed Depth (m)
1.0
1.5
2.0
2.5
3.0
Shannon Diversity Index (H')

Figure 9