

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

3 Running head: Mixing, temperature and cyanobacteria impacts

4 Emma Gray^{1,2}, J. Alex Elliott¹, Eleanor B. Mackay¹, Andrew M. Folkard², Patrick O.

5 Keenan¹, Ian D. Jones^{1,3*}

6 1. Centre for Ecology and Hydrology, Lancaster, Lancaster Environment Centre, Library
7 Avenue, Bailrigg, Lancaster, LA1 4AP, UK

8 2. Lancaster Environment Centre, Library Avenue, Lancaster University, Lancaster LA1
9 4YQ

10 3. Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA,
11 UK *(present address)

12 Correspondence: Emma Gray, tel. +44 1524 595952, e-mail: emma.gray9229@gmail.com

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14 **Summary**

- 15 1. Climate change is already having profound impacts upon the state and dynamics of
16 lake ecosystems globally. A specific concern is that climate change will continue to
17 promote the growth of phytoplankton, particularly blooms of toxic cyanobacteria, via
18 lake physical processes including warming surface waters and shallowing of the
19 mixed layer. These two mechanisms will have different impacts on lake
20 phytoplankton communities, but their inter-connectedness has made it difficult to
21 disentangle their independent effects.
- 22 2. We fill this knowledge gap by performing 1666 numerical modelling experiments
23 with the phytoplankton community model, PROTECH, in which we separated the
24 independent effects on lake phytoplankton of temperature change and changes in the
25 depth of the surface mixed layer. Given the large global abundance of small lakes (< 1
26 km^2) and the importance of their ecosystems in global processes and budgets, we used
27 a small meso-eutrophic lake as an example study site for the modelling experiments.
- 28 3. Increasing the lake temperature and positioning the mixed layer at a shallower depth
29 had different ecological impacts, with warming typically resulting in more biomass
30 and a dominance of cyanobacteria.
- 31 4. The response to mixed depth shallowing depended on the original depth where mixing
32 occurred. As anticipated, where the original mixed depth was moderate (4–6 m) and
33 there was a simultaneous increase in water temperature, cyanobacterial biomass
34 increased. However, when the same absolute difference in shallowing and
35 temperature increase were applied to a deeper mixed depth (9–13 m), lower
36 cyanobacterial biomass resulted, owing to poorer conditions for low-light tolerant
37 cyanobacteria.

38 5. Our study shows that the response of cyanobacterial blooms to climate-induced
39 warming and shallowing of mixed layers in lakes around the world will not be
40 universal, but rather will be system-specific, depending upon the average mixed layer
41 depth of the lake in question and the light affinity of the dominant cyanobacteria
42 species.

43 **Introduction**

44 Climate change is impacting phytoplankton communities in lakes across the world through
45 direct and indirect effects of temperature change (Huisman, Codd, Paerl, Ibelings, Verspagen,
46 et al., 2018; Winder & Sommer, 2012). Though intrinsically linked, water temperature, the
47 duration of lake stratification and the depth of the surface mixed layer have independent and
48 separate consequences for phytoplankton growth (Winder & Sommer, 2012). Phytoplankton
49 are a key part of lake food-webs, therefore shifts in community composition in response to
50 changing physical drivers can have consequences for higher trophic levels and water quality
51 (Huisman *et al.*, 2018; Winder & Sommer, 2012). The increase in the magnitude and
52 frequency of cyanobacteria blooms associated with climatic warming are a global water
53 quality concern because they can increase water turbidity, cause oxygen depletion during
54 bloom die back, and certain species produce toxins (Michalak, 2016; Paerl & Huisman,
55 2008). It is therefore important to understand how phytoplankton growth will respond to
56 changing physical drivers.

57 Lake water temperatures are increasing with climatic warming, as lakes and climate are
58 closely coupled (Winder & Schindler, 2004). The pattern of warming is complex and varies
59 globally (O'Reilly *et al.*, 2015), seasonally (Winslow *et al.*, 2017), with lake size (Woolway
60 *et al.*, 2016) and vertically within lakes (Winslow, Read, Hansen, & Hanson, 2015). On
61 average, surface summer water temperatures are warming at a global mean of 0.34 °C decade⁻¹
62 ¹ which is likely to significantly change the physical structure of lakes (O'Reilly *et al.*, 2015).

63 Higher spring and autumn temperatures are increasing the duration of lake stratification
64 (Livingstone, 2003; Peeters, Straile, Lorke, & Livingstone, 2007), whilst periods of sustained
65 high temperatures and low wind speeds also strengthen stratification, inhibiting mixing,
66 resulting in shallower surface mixed layers (Livingstone 2003; Winder & Sommer, 2012).
67 These changing physical drivers have separate consequences for phytoplankton growth.

68 The first driver, water temperature, directly affects phytoplankton growth because it
69 influences the rate of important cellular processes such as photosynthesis. Most
70 phytoplankton will exhibit an exponential increase in growth rate with temperature from 0 °C
71 to 25-35 °C provided they are not limited by any other resource (Reynolds, 2006). The range
72 of maximum temperatures for exponential growth reflects that growth rates are species
73 specific, varying with cell size, indicating that different species will respond to warming at
74 different rates (Reynolds, 2006). Research suggests that increasing water temperatures will
75 favour the dominance of smaller phytoplankton due to their faster growth rates and greater
76 nutrient uptake efficiency at higher temperatures compared with larger cells (Rasconi, Gall,
77 Winter & Kainz, 2015). Cyanobacteria are also likely to increase at higher water
78 temperatures owing to some species having higher optimal temperatures for growth
79 compared to some species in other taxa (Carey, Ibelings, Hoffmann, Hamilton & Brookes,
80 2012; Paerl & Paul, 2012).

81 The depth of the mixed layer is a fundamental driver of phytoplankton growth because it
82 affects the light and nutrient environment they are exposed to and thus their vertical
83 distribution and the rate of sinking losses (Diehl, 2002; Ptacnik, Diehl & Berger, 2003;
84 Huisman *et al.*, 2004). Deeper mixed layers can create a lower light environment, reduce
85 sinking losses and increase nutrient availability, whereas shallow mixed layers may increase
86 light availability and sinking losses and reduce nutrient availability (Diehl *et al.* 2002;
87 Huisman, van Oostveen & Weissing, 1999). Phytoplankton have different affinities for light

88 and levels of motility, therefore changes in the mixed depth can result in large shifts in
89 taxonomic composition (Huisman *et al.*, 2004; Lehman, Mugidde, & Lehman, 1998).
90 Generally, sinking phytoplankton, such as diatoms and chlorophytes that are adapted to low
91 light conditions, tend to dominate in deeper layers whereas buoyant or motile phytoplankton
92 (buoyant cyanobacteria and flagellates) often dominate in shallow mixed layers (Jäger, Diehl
93 & Schmidt 2008; Ptacnik, Diehl & Berger 2003; Visser *et al.* 1996; Reynolds *et al.* 1983).
94 Increased surface water temperature with climatic warming may result in shallower mixed
95 depths for many lakes which may then increase cyanobacteria abundance (Paerl & Huisman,
96 2009). Many species of cyanobacteria have traits suited to shallow mixed layers (Carey *et al.*,
97 2012) including gas vesicles that allow them to control and maintain their position and
98 exploit optimal light conditions (Walsby, Hayes, Boje, & Stal, 1997). Buoyancy can also be
99 facilitated further at higher water temperatures due to reduced water viscosity (Reynolds,
100 Oliver & Walsby, 1987). Other cyanobacteria, such as *Planktothrix*, are well adapted to low
101 light conditions and thrive in lakes where the mixed depth is deeper (Dokulil & Teubner,
102 2012; Ernst, Hoeger, O'Brien, & Dietrich, 2009).

103 Although not the focus of this study, the duration of stratification is also influenced by
104 climate warming and can affect the length of the phytoplankton growing season, with warmer
105 spring air temperatures being associated with earlier onset of stratification and spring
106 phytoplankton blooms (Peeters *et al.*, 2007; Berger *et al.* 2010; Winder & Sommer 2012).
107 Persistent high temperatures during autumn can also delay overturn (Hondzo & Stefan 1993;
108 Peeters, Kerimoglu & Straile, 2013) although the impact of this on the phytoplankton
109 growing season is uncertain.

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

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

131

132 **Methods**

133 *Site description*

134 Blelham Tarn is the modelled lake for the experiment, using three consecutive years of *in situ*
135 driving data (2012-2014). Blelham Tarn is a small (surface area 0.1 km²), shallow (mean
136 depth 6.8 m, maximum depth 14.5 m) (Ramsbottom, 1976) lake located in the English Lake
137 District (54°24'N, 2°58'W) (Fig.1). The trophic status of Blelham Tarn lies on the meso-

138 eutrophic boundary (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016) and it is
139 monomictic, typically stratifying from spring to late autumn.

140 *PROTECH model*

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

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

$$151 \quad \Delta X/\Delta t = (r' - S - G - D)X, \quad (1)$$

152 where r' is the proportional growth rate over 24 hours, S represents the losses due to settling,
153 G the losses due to grazing, D the losses due to dilution, and X is the chlorophyll a
154 concentration (mg m^{-3}). The growth rate changes with water temperature, light levels and
155 nutrient limitation of phosphorus, nitrate or silica defined by

$$156 \quad r' = \min\{r'_{(\theta I)}, r'_{P}, r'_{N}, r'_{Si}\}, \quad (2)$$

157 where $r'_{(\theta I)}$ is the growth rate due to temperature and daily photoperiod, and r'_{P}, r'_{N}, r'_{Si} are
158 the growth rates determined by phosphorus, nitrate and silica concentrations, respectively. In
159 addition to morphology, each phytoplankton is given appropriate movement characteristics as
160 well as any additional abilities such as nitrogen fixation (Table 1). Further details about the

161 model set up including mortality and respiration rates can be found in Reynolds, Irish &
162 Elliott (2001) and Elliott, Irish & Reynolds (2010).

163 The phytoplankton chosen to be included in the model set up represented common taxa
164 observed in Blelham Tarn during a fortnightly monitoring programme carried out from 2012-
165 2014 (Table 1). These phytoplankton also covered a range of phylogenetic (diatoms,
166 flagellates, chlorophytes and cyanobacteria) and CSR-functional groupings. The use of the
167 CSR classification, developed by Reynolds (1988), helps us understand phytoplankton
168 responses in terms of their traits and morphology, which cut across taxonomical groups
169 (Reynolds, 2006).

170 *Driving data*

171 A three year period (2012-2014) of daily averaged solar radiation data recorded by a Kipp
172 Zonan CMP6 Pyranometer (sensitivity 5 to 20 μ V/W/m²) attached to an *in situ* automated
173 monitoring buoy (Fig.1) was used to calculate the photosynthetically active radiation
174 available to the phytoplankton within the model. The buoy also measured lake water
175 temperatures every 4 minutes at 1 m depth intervals in the water column from 1-10 m with
176 additional temperature sensors at 0.5 m and 12 m. Whilst PROTECH can estimate
177 temperature from external physical drivers in this study, the buoy data were linearly
178 interpolated into the equivalent 0.1 m PROTECH layers (0.1 m to 14.5 m) to provide a daily
179 water temperature structure to drive the PROTECH model over the simulated three year
180 period.

181 To calculate daily nutrient loading to the lake, daily average discharge (m³ s⁻¹) from the
182 nearby River Leven was obtained from the Environment Agency. As the outflow from
183 Blelham Tarn is not continuously gauged, a relationship between this daily data and Blelham
184 Tarn outflow was established for 1974, when daily measurements were available for both

185 sites. A power law relationship provided the best regression fit between the two discharges
186 ($R^2=0.92$; $p<0.05$),

$$187 \quad y = 0.0076x^{1.253}, \quad (3)$$

188 where y is the outflow discharge of Blelham Tarn and x is the discharge from the River
189 Leven. Daily discharges for each inflow were then calculated based on the proportion of
190 discharge that each inflow contributed to the outflow discharge for 2017 based on monthly
191 spot samples. Monthly concentrations of nitrate and silica in three of the inflows into
192 Blelham Tarn were also sampled during 2017. The calculated daily discharges were averaged
193 for each month and multiplied by the monthly spot concentration for nitrate and silica,
194 assuming that the nutrient load was the same for each day in the sample month, following
195 Walling & Webb (1981). The monthly pattern for nutrient load calculated for 2017 was
196 repeated for each year in the sample period (2012-2014) therefore daily variations in
197 discharge resulted in different daily nutrient concentrations. The same monthly nutrient
198 loading pattern was used here as the analyses focusses on changes in mixed depth and
199 temperature rather than nutrients. Daily nutrient concentrations for phosphorus were based
200 on estimates modelled from land use type using an export coefficient approach previously
201 calculated by Gasca, Maberly & Mackay (2015).

202 Monthly sampling of nutrients has been reported to underestimate nutrient loading by up to
203 50-60% (Cassidy & Jordan, 2011), therefore an extra 50% was added onto the calculated
204 values for nitrate, silica and phosphorus to account for this. The nutrient loading for
205 phosphorus was also increased by a further 50% to account for the internal phosphorus
206 release from the sediments during anoxic conditions in the hypolimnion during stratification
207 (Foley, Jones, Maberly & Rippey, 2012).

208 *Model validation*

209 In PROTECH, phytoplankton are actively mixed throughout the mixed layer, therefore
210 changes in the depth of mixing determine the light and nutrient availability for
211 phytoplankton. The average mixed depths used as a baseline during the stratified period were:
212 5 m for the entire stratified period, 4 m in spring, 4.5 m in summer and 7 m in autumn. They
213 were derived, from water temperature profiles measured in 2012-2014, using Lake Analyzer
214 (Read *et al.*, 2011) and defined as the depths at which the vertical gradient of water density
215 first exceeded $0.1 \text{ kg m}^{-3} \text{ m}^{-1}$. These baseline mixed depths and the control water temperature
216 profiles measured at the monitoring buoy were used in the model validation run. The
217 benchmark of acceptability for the model was that it produced, on average, a reasonable
218 seasonal pattern of phytoplankton chlorophyll *a* and functional groupings compared to
219 observed data from recent years. Therefore, for comparison, fortnightly means were
220 calculated for both the simulated and observed chlorophyll *a* and functional groupings from
221 the whole period. These were then compared both visually and by calculating the coefficient
222 of determination for the data (Fig.2).

223 *Model Experiment*

224 The validated model was run in a series of experiments in which the mixed depth was
225 systematically changed by 0.5 m intervals from 0.5 m to 14.5 m. These depths were fixed for
226 each model run during the identified period of stratification determined in the baseline run. It
227 is not expected that the mixed depth of Blelham Tarn will fluctuate through this full range,
228 rather the experiment is seen as a template for similar monomictic lakes with naturally
229 different starting depths of mixing. Furthermore, for each mixed depth, the baseline water
230 temperatures (which remain fixed according to the observed buoy data) were systematically
231 changed in 0.5 °C intervals from -2 to +6 °C in the top 5 m of the water column throughout
232 the year. Temperature was changed at the surface rather than through the whole water column
233 because analysis of long term temperature trends from Blelham Tarn suggests that warming

234 is accelerated in surface waters only, with little change in deep water temperature (Foley *et*
235 *al.*, 2012). This means that in scenarios when mixing occurred deeper than 5 m,
236 phytoplankton will not be exposed to warming at those depths, where temperatures will
237 remain at baseline values. Overall, this gave a total of 493 model simulations. The
238 phytoplankton concentrations were integrated over the top 5 m of the water column so the
239 model could be validated against the observed data.

240 In addition to the main experiment a series of extra runs were performed to check some of the
241 methodological assumptions made. To determine if changing the water temperature in the top
242 5 m of the water column only influenced the results, the experiment was repeated by applying
243 the water temperature change to the whole water column, producing an additional 493 model
244 simulations. Furthermore, fixing the mixed depth in defined intervals throughout the stratified
245 period meant that short term fluctuations in light and nutrient availability were lost. To
246 determine if the absence of this variability impacted the results, additional model runs were
247 completed in which the baseline mixed depth was shifted in 10 % intervals from 10 % to 200
248 %, again keeping the baseline duration of stratification the same. This was repeated for both
249 a top 5m water temperature change and a whole water column temperature change, resulting
250 in 680 more model simulations. To determine whether sampling depth had an impact on the
251 results, all results from each experiment were also calculated for the whole water column.
252 Results from these additional runs have been summarised in Tables 3 and 4.

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

259
$$H' = -\sum \left(\frac{b_i}{B}\right) \log_2\left(\frac{b_i}{B}\right), \quad (4)$$

260 where B is biomass measured as the total concentration of chlorophyll a (mg m^{-3}) and i is the
261 biomass (chlorophyll a (mg m^{-3})) of the i th phytoplankton taxon. For each of the resulting
262 variables, overall annual means were calculated. Seasonal averages were calculated with
263 spring being defined as March, April and May, summer as June, July and August, autumn as
264 September, October and November and Winter as December, January and February. Spring
265 and Autumn were split into their respective stratified and fully mixed periods of time and
266 analysed separately. The *stratified* seasons, that is the period when the *in situ* temperature
267 data showed there had been a surface mixed layer were: spring beginning on 01/03/2012,
268 11/04/2013, 31/03/2014 and ending on the last day of May; summer as June, July and
269 August; and autumn as the beginning of September until lake overturn on 07/10/2012,
270 03/11/2013 and 07/11/2014. Outside of these periods, the mixed depth of the model was set
271 at the full depth of the lake irrespective of water column temperatures.

272 **Results**

273 *Validation*

274 The intention of the experiments was not to create an exact reproduction of Blelham Tarn's
275 phytoplankton community but to simulate an experimental community with a realistic
276 biomass, seasonal growth pattern and morphological and taxonomic diversity. The model
277 performed well in terms of biomass, capturing both the amount and seasonal pattern of mean
278 observed total chlorophyll (Fig. 2). In terms of the community, annual observed and modelled
279 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
280 $\pm 7.1 \text{ mg m}^{-3}$, observed = $8.9 \pm 8.0 \text{ mg m}^{-3}$) and CS (modelled = $3.2 \pm 4.2 \text{ mg m}^{-3}$, observed =
281 $3.1 \pm 6.0 \text{ mg m}^{-3}$) strategists were very similar (Fig. 2). The model performed less well for S
282 strategists (modelled = $1.2 \pm 0.6 \text{ mg m}^{-3}$, observed = $4.2 \pm 7.9 \text{ mg m}^{-3}$); this group was
283 therefore not considered in the analysis.

284 *Impacts of temperature change before and after stratification*

285 *a. Phytoplankton biomass*

286 Prior to stratification in spring, chlorophyll *a* concentrations increased at an average rate of
287 $1.2 \text{ mg m}^{-3} \text{ }^{\circ}\text{C}^{-1}$, leading to elevated concentrations at higher temperatures (17.5 mg m^{-3} at +6
288 $^{\circ}\text{C}$ compared to 9.6 mg m^{-3} at +0 $^{\circ}\text{C}$) (Fig. 3a). Post-stratification, in autumn, chlorophyll *a*
289 concentrations remained slightly higher at the highest temperature increases (12.8 mg m^{-3} at
290 +6 $^{\circ}\text{C}$, cf. 10.6 mg m^{-3} at -2 $^{\circ}\text{C}$) (Fig. 3a). Higher temperatures also advanced the onset of the
291 spring bloom; at +6 $^{\circ}\text{C}$ chlorophyll *a* concentrations reached 5 mg m^{-3} eleven days earlier
292 than at -2 $^{\circ}\text{C}$ (Fig. 3b). The end of the growing season, defined as the first day when
293 chlorophyll *a* < 5 mg m^{-3} , was extended by seven days at +6 $^{\circ}\text{C}$ compared to -2 $^{\circ}\text{C}$ (Fig. 3b).

294 *b. Phytoplankton community*

295 Increasing temperature prior to stratification also resulted in community shifts with the
296 percentage of *R* strategists increasing by 32 % (from -2 $^{\circ}\text{C}$ to + 6 $^{\circ}\text{C}$) at the expense of *CS*
297 and *C* strategists (Fig. 4a). In comparison, increases in temperature had very little impact on
298 the functional composition of the post-stratification fully mixed community in autumn (Fig.
299 4b). There was also a decrease in diversity with warming (from $H' = 3.0$ at -2 $^{\circ}\text{C}$ to $H' = 2.3$
300 at +6 $^{\circ}\text{C}$) in spring, but only a small change in diversity of the post-stratification community
301 in autumn (Fig. 5).

302 *Impacts of temperature and mixed depth change during the stratified period*

303 *a. Phytoplankton biomass*

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

307 alone (Fig. 6a). However, deepening the mixed depth from the baseline led to greater
308 increases in phytoplankton biomass (e.g. + 3.1 mg m⁻³ from the baseline to 11 m) compared
309 to mixed depth shallowing. This was further enhanced by increases in temperature. Increasing
310 the temperature by 6 °C at a mixed depth of 11 m, for example, led to an increase in
311 phytoplankton biomass of 10.4 mg m⁻³ compared to baseline conditions (Fig. 6a).

312 The impact of changing temperatures and depths of mixing varied with season. In spring,
313 increases in phytoplankton biomass were driven by increases in temperature with smaller
314 variations in biomass with changing mixed depth (e.g. + 8.5 mg m⁻³ increase from +0 °C to
315 +6 °C at the spring baseline mixed depth) (Fig. 6b). There was a strong bimodal pattern in
316 summer, with the greatest increases occurring with combinations of high temperatures and
317 both shallower (< 4 m) (increase of 19.1 mg m⁻³ from baseline conditions to +6 °C at 0.5 m
318 mixed depth) and deeper mixed depths (> 8.5 m). The largest summer chlorophyll *a*
319 concentration (43.9 mg m⁻³) occurred at a mixed depth of 11 m at + 5 °C (Fig.6c). For
320 autumn, the peak in chlorophyll *a* occurred at depths between 10-12 m (Fig.6d).

321 *b. Phytoplankton community*

322 The annual average phytoplankton biomass was dominated by *CS* and *R* strategists, with *C*
323 strategists occurring only in notable concentrations at lower temperatures (below + 0.5 °C)
324 and mixed depths shallower than 6.5 m (Fig. 7abc). *R* strategists increased at the expense of
325 *CS* strategists when the mixing deepened (e.g. a decrease in *CS* strategists of 11 % from the
326 baseline mixed depth to 14.5 m) (Fig. 7bc). Shifts in functional groups followed a broad
327 seasonal pattern, which was modified by changes in mixing and temperature.

328 Spring was dominated by *R*-types at most mixed depths and temperatures, *C*-types increased
329 at the expense of *R*-types for mixed depths shallower than 6.5 m and temperatures below +0.5
330 °C and *CS*-types contributed 20-40 % of the community when mixing was shallower than 9 m

331 and temperature higher than the baseline (Fig.7def). In summer, contrasting functional types
332 occupied different mixed depth ranges. *CS*-types dominated at shallow mixed depths (< 8 m
333 at temperatures greater than the baseline) and *R*-types with deep mixing (> 8 m), *C*-types
334 contributed a negligible amount to the community (Fig.7ghi). The stratified autumn
335 community reverted back to *R*-type dominance at the expense of *CS*-types, with *C*-types
336 occurring at temperatures below +0.5 °C and mixed depths shallower than 6 m (Fig.7jkl).

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

347 *Comparing experimental methods*

348 Full analyses of the results were performed for each method of temperature change (top 5 m
349 of the water column and whole water column), mixed depth method (fixed mixed depths and
350 percentage shifts) and sampling depth (top 5 m and whole water column). The different
351 methods of mixed depth change (fixed and percentage shifts) produced very similar seasonal
352 mean chlorophyll *a* concentrations (Tables 3 and 4). Applying the change in water
353 temperature to the top 5 m of the water column or the whole water column made very little
354 difference to seasonal mean chlorophyll *a* concentrations for both mixed depth methods

355 (Tables 3 and 4). Integrating the results over the top 5 m of the water column consistently
356 produced slightly higher chlorophyll *a* values compared to whole water column integrations
357 for both mixed depth methods, but the seasonal patterns were consistent (Tables 3 and 4).

358 **Discussion**

359 Regarding the first hypothesis, we found that the timing of the spring bloom advanced with
360 increases in water temperature. This extension of the growing season has also been observed
361 in field studies (Meis *et al.*, 2009; Thackeray, Jones, & Maberly, 2008; Thackeray *et al.*,
362 2010) and previous modelling experiments (Peeters, Straile, Lorke, & Livingstone, 2007). In
363 these studies, however, spring warming was accompanied by earlier onset of stratification,
364 obfuscating whether changes in water temperature or changes in stratification were the key
365 driver. As our study kept the length of stratification the same for all model runs, it
366 demonstrated that advance in the spring bloom can be solely due to temperature accelerating
367 growth rates rather than the higher light availability that ordinarily accompanies changes in
368 stratification and shallower mixed depths. At this time of year nutrients are plentiful after
369 being replenished during the winter, therefore, the growth rate of the *R*-strategist diatoms,
370 which are adapted to low light conditions in the fully mixed layer, accelerated with increasing
371 temperature. The growing season in autumn was also extended by temperature increases
372 alone, although for a shorter length of time than in the spring. By independently changing
373 mixed depth and temperature, model outcomes have also highlighted that temperature
374 changes had different impacts on this modelled phytoplankton community compared to
375 mixed depth changes, supporting hypothesis two. Increases in temperature increased
376 phytoplankton biomass and increased the proportion of the community made up of
377 cyanobacteria consisting of two functional groups (*CS* and *R*) for most mixed depths. This
378 result was expected due to accelerated growth rates at higher temperatures and the favourable
379 morphologies of the cyanobacteria taxa (Carey *et al.*, 2012). However, the experimental

380 results showed that shallower mixed depths could have contrasting impacts on the
381 phytoplankton community depending on the typical current position of the mixing layer. If
382 the original depth of mixing was located at intermediate depths (4-9 m), shallowing could
383 increase biomass and the proportion of the community made up of the *CS* cyanobacteria.
384 However, if the original depth of mixing was naturally deeper (9.5-14.5 m), shallowing to
385 intermediate depths could decrease biomass and reduce the percentage of *R* strategist
386 cyanobacteria, particularly if sizeable temperature increases also occurred (Fig 6).

387 Mixed depth and water temperature change do not necessarily occur in isolation and this
388 modelling study has found that combined increases in water temperature and shallower
389 depths of mixing (from baseline conditions) had a synergistic effect on phytoplankton
390 biomass, supporting hypothesis three. The magnitude of the synergistic response varied with
391 season. Modelled increases in biomass and community change in spring were primarily
392 driven by temperature increases as opposed to combined mixed depth and temperature
393 changes. The highest temperature increases in spring led to cyanobacteria dominance,
394 consistent with previous findings from other modelling studies (Elliott *et al.*, 2005;
395 Markensten, Moore, & Persson, 2010) and observed data (Weyhenmeyer, 2001; Dupuis &
396 Hann, 2009; Jacquet *et al.*, 2005). In contrast, summer demonstrated the largest synergistic
397 response (+19.0 mg m⁻³ chlorophyll *a* with rising temperature and mixed depth shallowing
398 from the baseline) with large changes in community composition and phytoplankton biomass
399 occurring when both the depth of mixing and water temperature changed.

400 Previous work has suggested that warming and shallower mixed depths combined will create
401 conditions favourable for cyanobacteria (Paerl & Huisman, 2009; Paerl & Paul, 2012). In
402 this experiment, they did produce an increase in phytoplankton biomass overall and an
403 increase in the biomass of the buoyant cyanobacteria *Dolichospermum*. Faster growth rates at
404 high temperatures and the ability to regulate buoyancy at shallow mixed depths meant that

405 *Dolichospermum* was able to outcompete other CS-strategists within the model. This suggests
406 that lakes with shallow surface mixed layers similar to Blelham Tarn (4 m annual average),
407 which are experiencing accelerated warming in surface waters (increase of 1.1 ± 0.3 °C in
408 Blelham Tarn 1968-2008) (Foley *et al.*, 2012), may experience a deterioration in water
409 quality with warming and shallower surface mixing. This finding is in agreement with
410 expectations and predicted trends (Paerl & Huisman, 2009; Paerl & Paul, 2012), supporting
411 hypothesis four.

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

424 *Dolichospermum* and *Planktothrix* are both genera of cyanobacteria but they have different
425 morphologies and affinities for light (Table 2) and therefore responded differently to changes
426 in mixing depth in this modelling experiment. The contrasting responses of two
427 phytoplankton taxa belonging to the same phylogenetic group supports hypothesis five, that
428 phytoplankton responses in these modelled results would differ depending on their
429 morphology and traits (Reynolds *et al.*, 1983). *Dolichospermum* dominated in shallow mixed

430 layers as its ability to regulate buoyancy allowed it to maintain its position in a favourable
431 light climate whereas non-motile or negatively buoyant species would be lost from the mixed
432 layer through sedimentation (Huisman *et al.*, 2004). These findings are consistent with
433 previous observations of *Dolichospermum* being associated with problematic surface blooms
434 in lakes with shallow surface mixing (Salmaso, Capelli, Shams, & Cerasino, 2015). In
435 contrast, deeper mixed layers were dominated by *Planktothrix*, a cyanobacteria adapted to
436 low light conditions (Dokulil & Teubner, 2012). *Planktothrix* has been associated with
437 persistent blooms in deep mixed layers in observed data (Ernst *et al.*, 2009) and experimental
438 systems, often forming a sub-surface peak or a deep chlorophyll *a* maxima (Reynolds *et al.*,
439 1983; Nürnberg, LaZerte & Olding 2003; Selmečzy *et al.*, 2018). Studies in Lake Zurich and
440 Lake Geneva have suggested that *Planktothrix* will benefit from warming in extremely deep
441 lakes due to a reduction in full water column mixing, which contrasts with the reduction in
442 *Planktothrix* for shallow lakes found in this study (Gallina, Beniston & Jacquet, 2017; Posch,
443 Köster & Salcher, 2012).

444 This modelling experiment made a number of assumptions and simplifications in order to
445 disentangle the separate impacts of complex physical drivers. Here we have modelled only
446 twelve phytoplankton taxa, including two cyanobacteria taxa. While these were chosen to
447 represent a wide range of morphological traits, real lakes typically contain a richer
448 phytoplankton community than this. Similarly, we simplified the modelling by keeping a
449 fixed nutrient pattern between years. The model itself also contains a number of assumptions
450 and simplifications in order to represent complex biological processes (Reynolds, Irish &
451 Elliott, 2001, and Elliott, Irish & Reynolds, 2010). Nevertheless, the model is mechanistic
452 and has been widely tested on many systems around the world and the results allow an
453 understanding of the separate impacts of mixed layer and temperature change on a

454 phytoplankton community which cannot be achieved using observed data alone (Elliott et al.,
455 2010).

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

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481 **Conflict of Interest Statement**

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

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690

691 **Tables**

692 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
<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>	1030	2710	0.4	21	Flagellate	CS	Yes	No
<i>Synedra</i>	4100	7900	0.5	110	Diatom	R	No	No
<i>Aulacoseira</i>	4350	2970	1.5	240	Diatom	R	No	No
<i>Dolichospermum</i>	6200	29000	0.2	75	Cyanobacteria	CS	No	Yes
<i>Coenochloris</i>	6430	17200	0.4	64	Chlorophyte	S	No	No
<i>Asterionella</i>	6690	5160	1.3	130	Diatom	R	No	No
<i>Planktothrix</i>	7350	13970	0.5	300	Cyanobacteria	R	No	No
<i>Sphaerocystis</i>	7850	65500	0.1	50	Chlorophyte	S	Yes	No
<i>Ceratium</i>	9600	43700	0.2	201	Flagellate	CS	No	No

693

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

Phytoplankton	Light condition ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	Movement (m day ⁻¹)
Nonbuoyant nonmotile diatoms		
<i>Asterionella & 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 & 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 & Sphaerocystis</i>	All	Sink 0.1

696

697

698 Table 3 Seasonal mean phytoplankton biomass (chlorophyll *a* mg m⁻³) during the stratified
 699 period for water column integrated and 5 m integrated results using the fixed mixed depth
 700 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 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

701

702 Table 4 Seasonal mean phytoplankton biomass (chlorophyll *a* mg m⁻³) during the stratified
 703 period for water column integrated and 5 m integrated results using the percentage mixed
 704 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 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

705

706 **Figures**

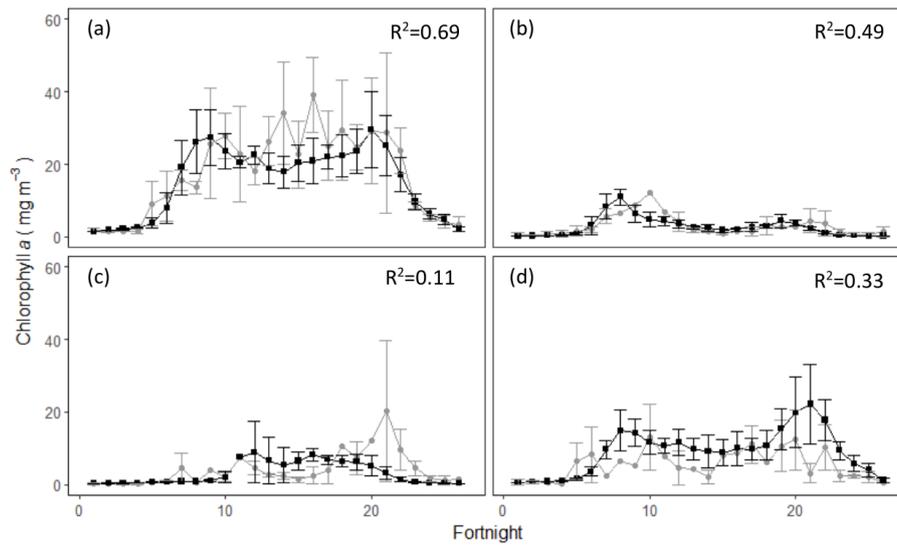
707 Figure 1. Blelham Tarn is located in the lake district in North West England (square), with
708 the monitoring buoy (triangle) located at the deepest point in the lake (14.5 m) bathymetry
709 from Ramsbottom (1976)



710

711

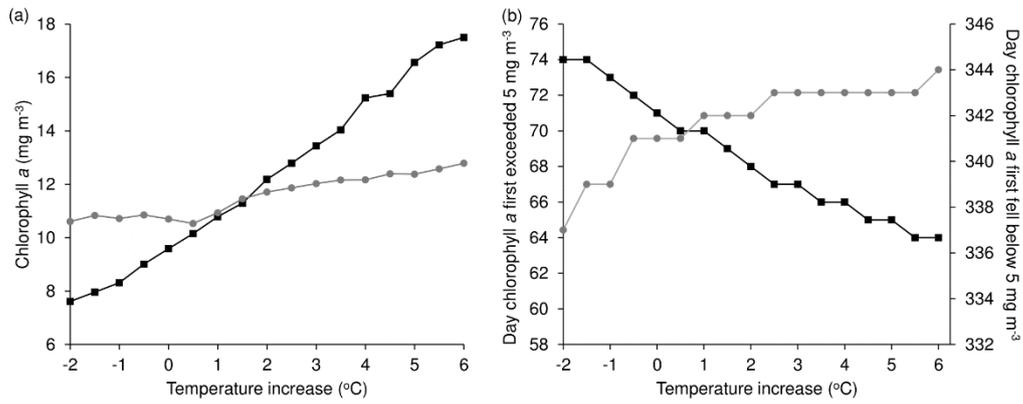
712 Figure 2. Observed (black line) and simulated (grey line) mean fortnightly (a) total
713 chlorophyll *a* biomass, (b) *C* strategists biomass, (c) *CS* strategist biomass and (d) *R* strategist
714 biomass for Blelham Tarn for the three year period simulated with the range of fortnightly
715 values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



716

717

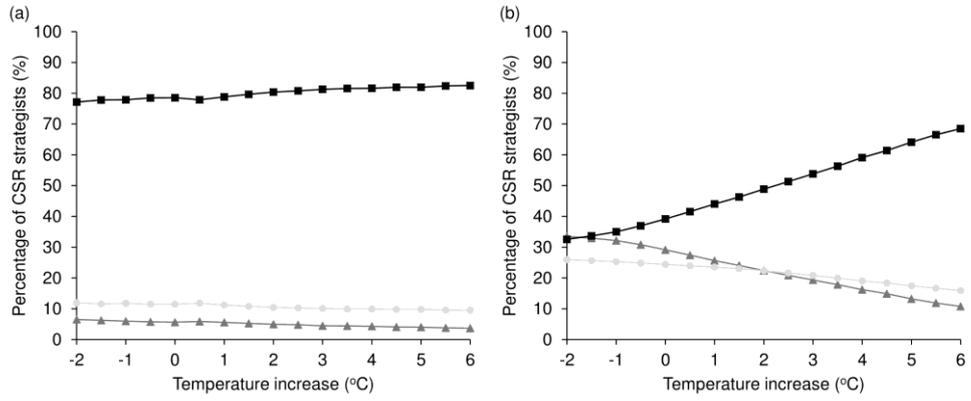
718 Figure 3. (a) Chlorophyll *a* concentrations with temperature in fully mixed spring prior to
 719 stratification (black square) and fully mixed autumn following stratification (grey circle) and
 720 (b) average day of the year when chlorophyll *a* first exceeded (black square) and dropped
 721 below (grey circle) 5 mg m⁻³ with temperature change.



722

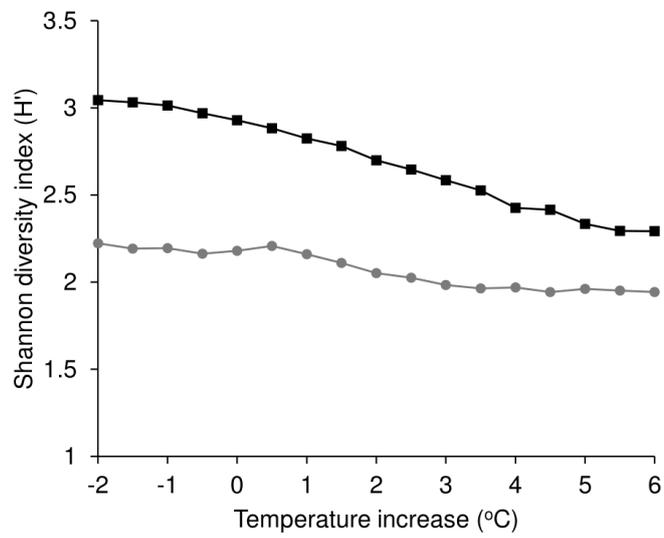
723

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



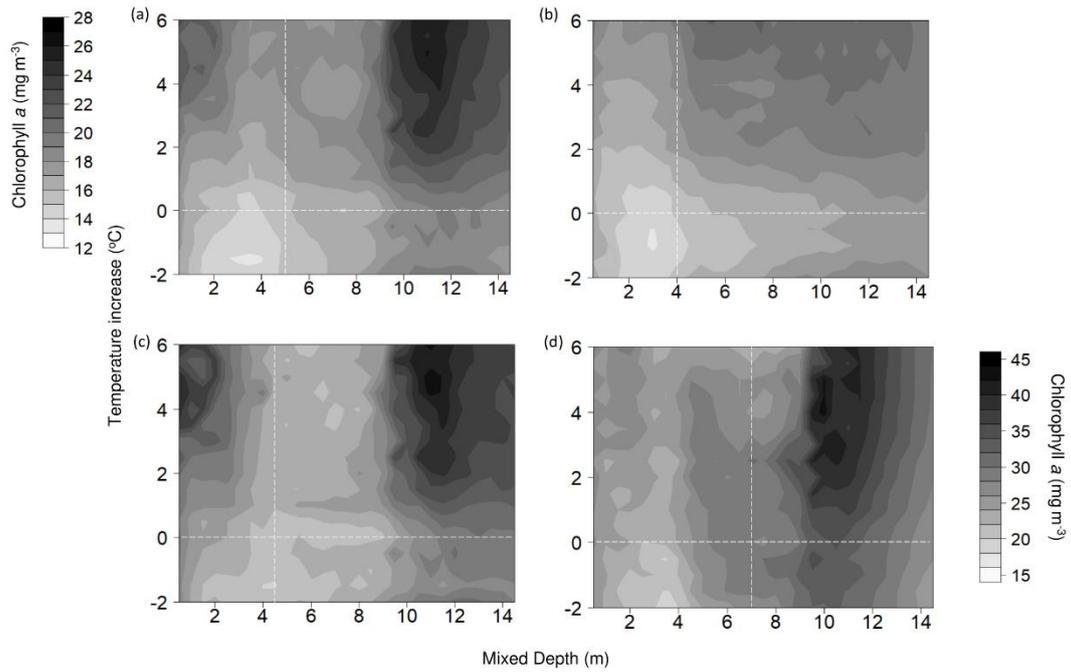
726

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



729

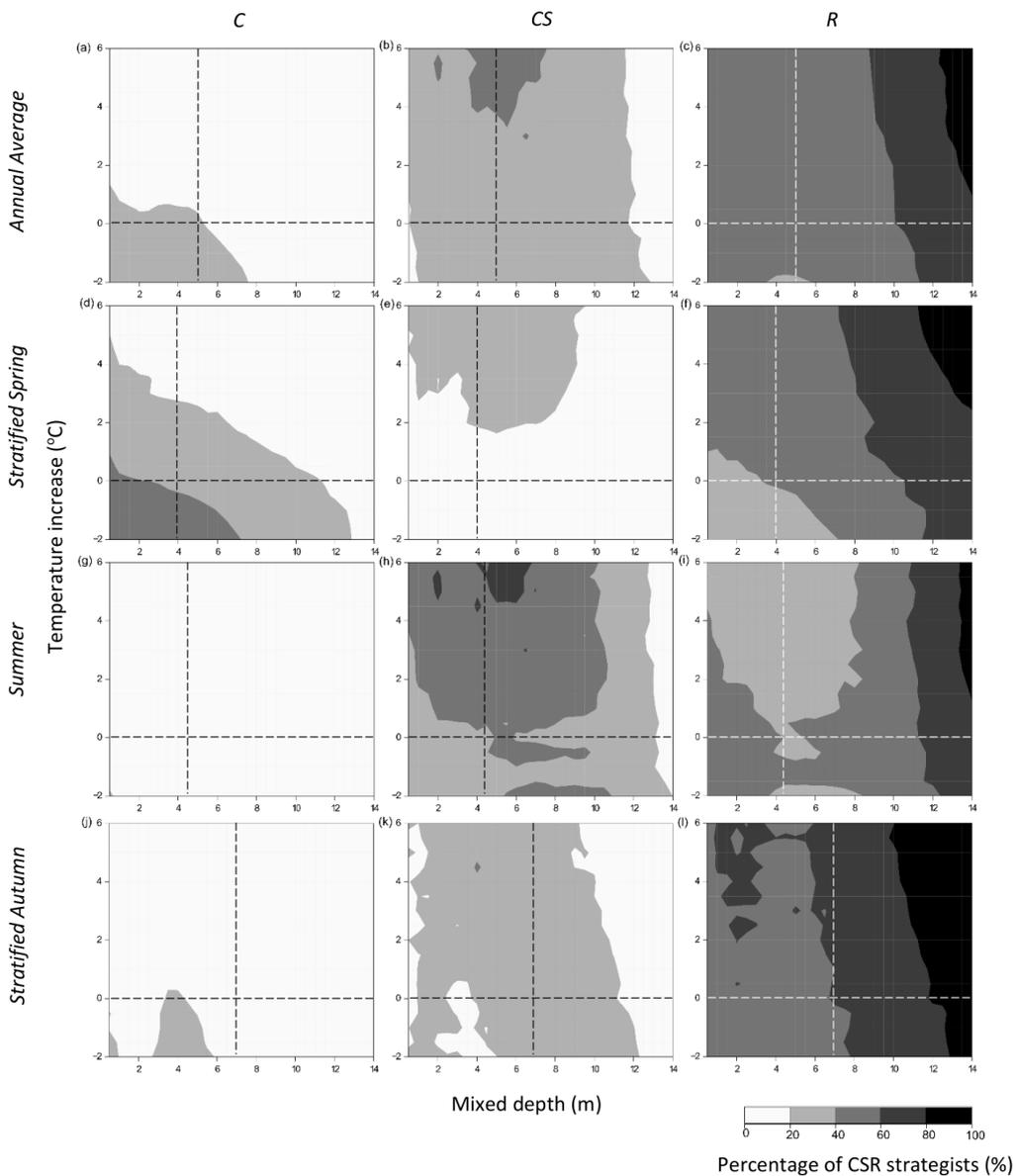
730 Figure 6. Mean chlorophyll *a* concentrations at each mixed depth and temperature change for
731 (a) annual mean (note different scale for chlorophyll *a*) (b) stratified spring, (c) stratified
732 summer and (d) stratified autumn, dashed vertical and horizontal lines mark the baseline
733 mixed depth and temperature for Blelham Tarn, respectively.



734

735

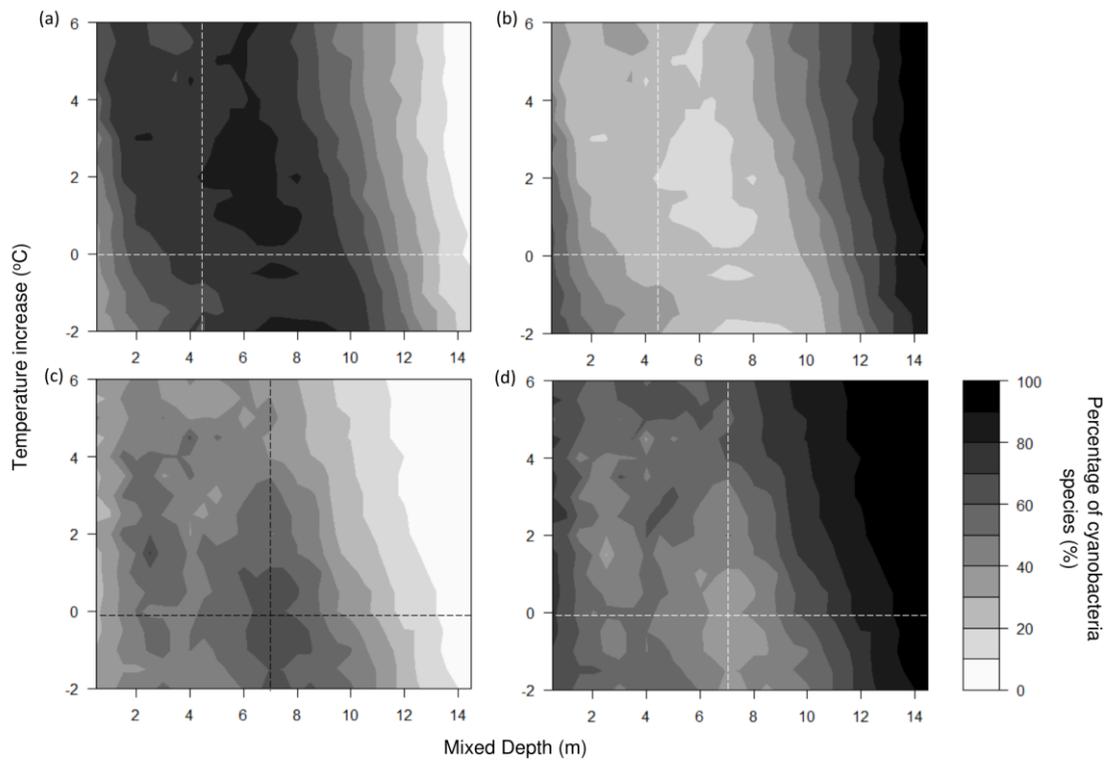
736 Figure 7. Percentage of (a,d,g,j) *C* (b,e,h,k) *CS* (c,f,i,l) and *R* strategists in (a,b,c) annual
 737 average, (d,e,f) stratified spring, (g,h,i) summer, (j,k,l) stratified autumn, dashed vertical and
 738 horizontal lines mark the baseline mixed depth and temperature for Blelham Tarn,
 739 respectively.



740

741

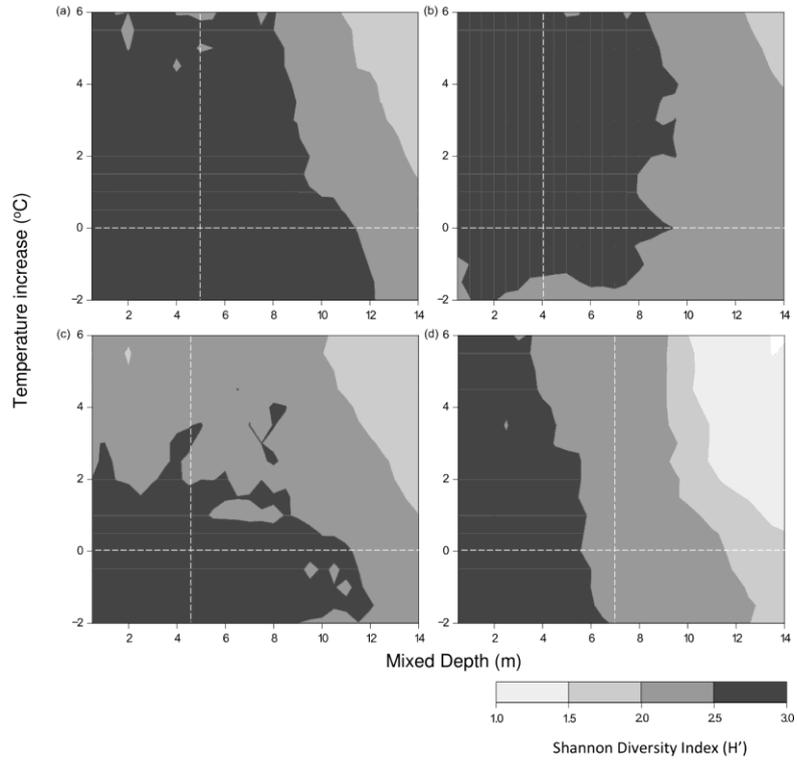
742 Figure 8. Percentage of total cyanobacteria at each mixed depth and temperature change for
743 (a) *Dolichospermum* in stratified summer (b) *Planktothrix* in stratified summer, (c)
744 *Dolichospermum* in stratified autumn and (d) *Planktothrix* in stratified autumn, dashed
745 vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham
746 Tarn, respectively.



747

748

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



753