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

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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 $^{\circ}$C decade^{-}

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 ^{o}C

71   to 25-35 ^{o}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 km^2) 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 km^2), 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 $$\Delta X/\Delta t = (r' - S - G - D)X, \qquad (1)$$

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

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 $20\mu V/W/m^2$) 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 (m^3 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 $$y = 0.0076x^{1.253}, \qquad\qquad (3)$$

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).

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,

11

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

259

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 ith 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 ± 2.8 mg m^{-3}, observed = 2.0 ± 3.2 mg m^{-3}), R (modelled = 9.1

280   ± 7.1 mg m^{-3}, observed = 8.9 ± 8.0 mg m^{-3}) and CS (modelled = 3.2 ± 4.2 mg m^{-3}, observed =

281   3.1 ± 6.0 mg m^{-3}) strategists were very similar (Fig. 2). The model performed less well for S

282   strategists (modelled=1.2 ± 0.6 mg m^{-3}, observed= 4.2 ± 7.9 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 mg m^{-3} $^{\circ}$C^{-1}, leading to elevated concentrations at higher temperatures (17.5 mg m^{-3} at +6

288    $^{\circ}$C compared to 9.6 mg m^{-3} at +0 $^{\circ}$C) (Fig. 3a). Post-stratfication, in autumn, chlorophyll *a*

289   concentrations remained slightly higher at the highest temperature increases (12.8 mg m^{-3} at

290   +6 $^{\circ}$C, cf. 10.6 mg m^{-3} at -2 $^{\circ}$C) (Fig. 3a). Higher temperatures also advanced the onset of the

291   spring bloom; at +6 $^{\circ}$C chlorophyll *a* concentrations reached 5 mg m^{-3} eleven days earlier

292   than at -2 $^{\circ}$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 $^{\circ}$C compared to -2 $^{\circ}$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 $^{\circ}$C to + 6 $^{\circ}$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 $^{\circ}$C to H' = 2.3

300   at +6 $^{\circ}$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 $^{\circ}$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 ºC 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 +2ºC) 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).

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; Selmeczy *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.

472 **Acknowledgements**

479 would also like to thank the two anonymous reviewers for their constructive feedback on

480 draft versions of this work.

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 (µm²)	Volume (µm³)	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

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

695   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

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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 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

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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 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

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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

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

729 respectively.

730 Figure 8. Percentage of total cyanobacteria at each mixed depth and temperature change for

731 (a) *Dolichospermum* in stratified summer (b) *Planktothrix* in stratified summer, (c)

732 *Dolichospermum* in stratified autumn and (d) *Planktothrix* in stratified autumn, dashed

733 vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham

734 Tarn, respectively.

735 Figure 9. Shannon diversity index for each mixed depth and temperature change for (a)

736 annual average (b) stratified spring (c) stratified summer, (d) stratified autumn dashed

737 vertical and horizontal lines mark the baseline mixed depth and temperature for Blelham

738 Tarn, respectively.

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755   **Figure 1**
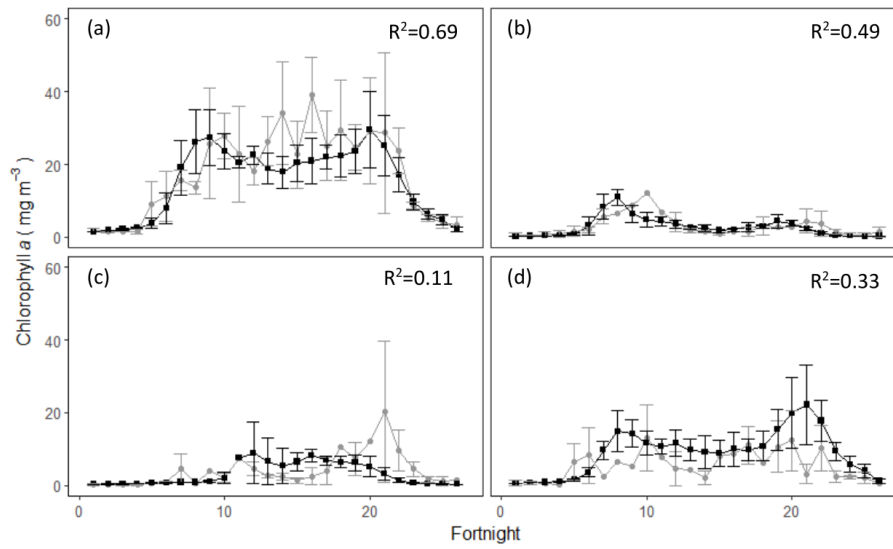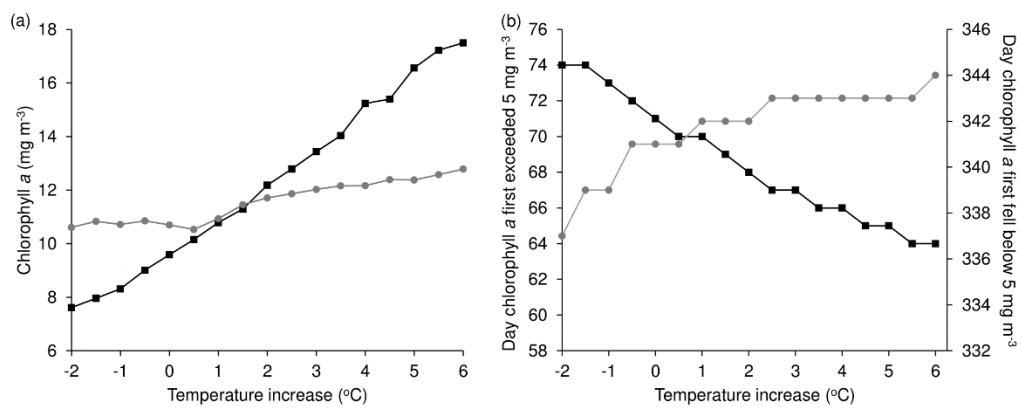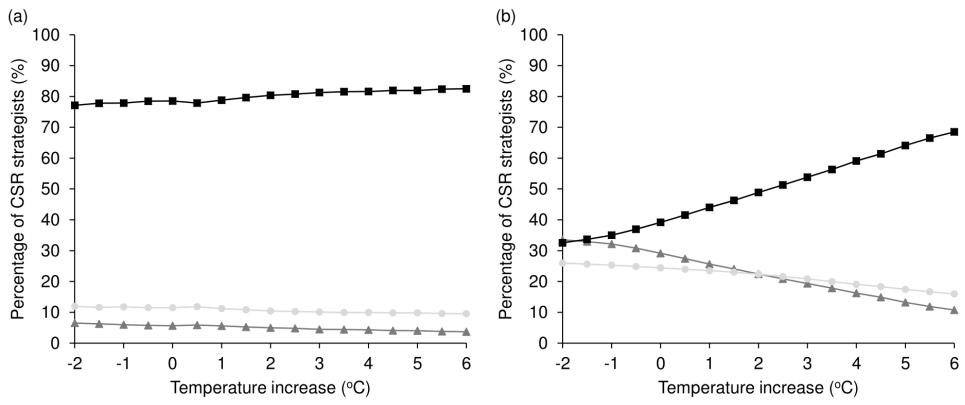
Figure 2

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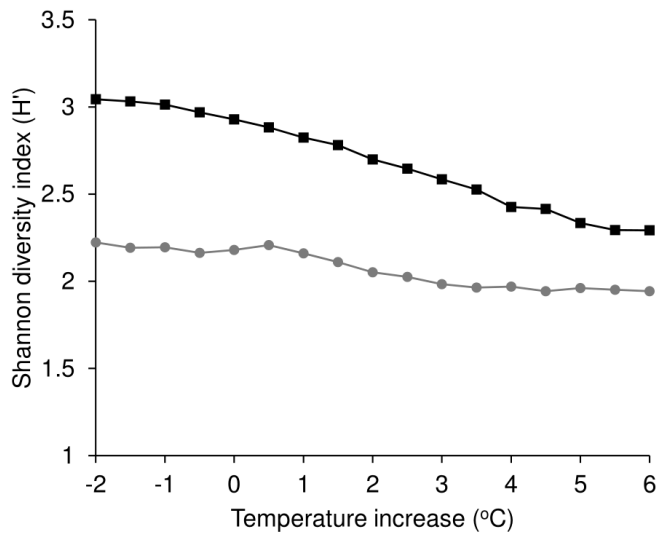
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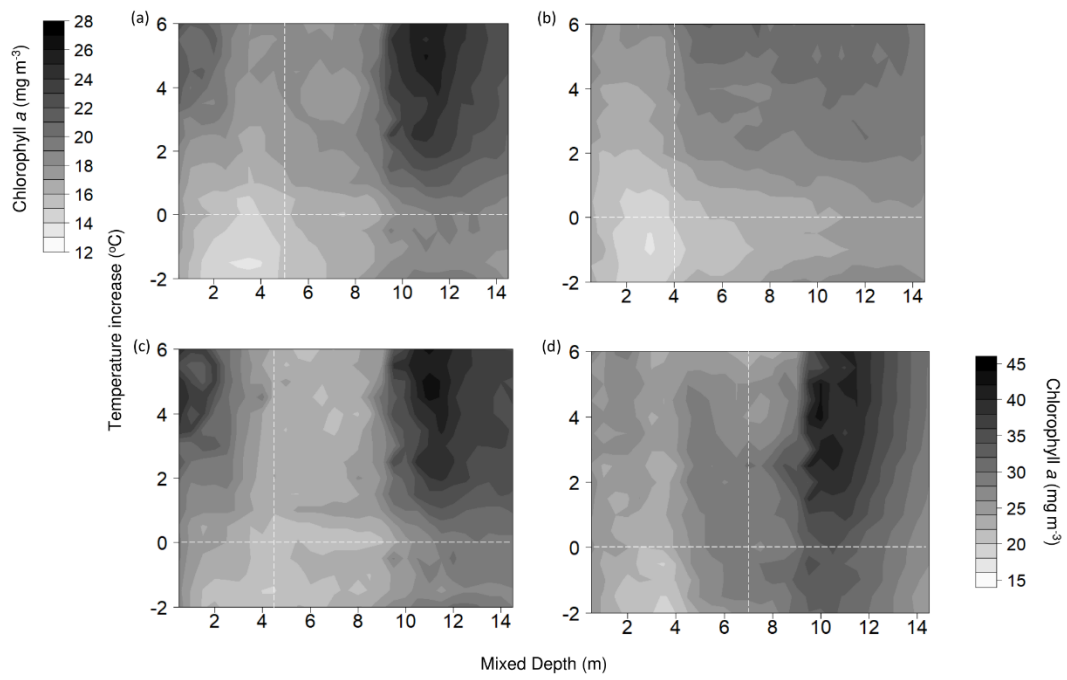775

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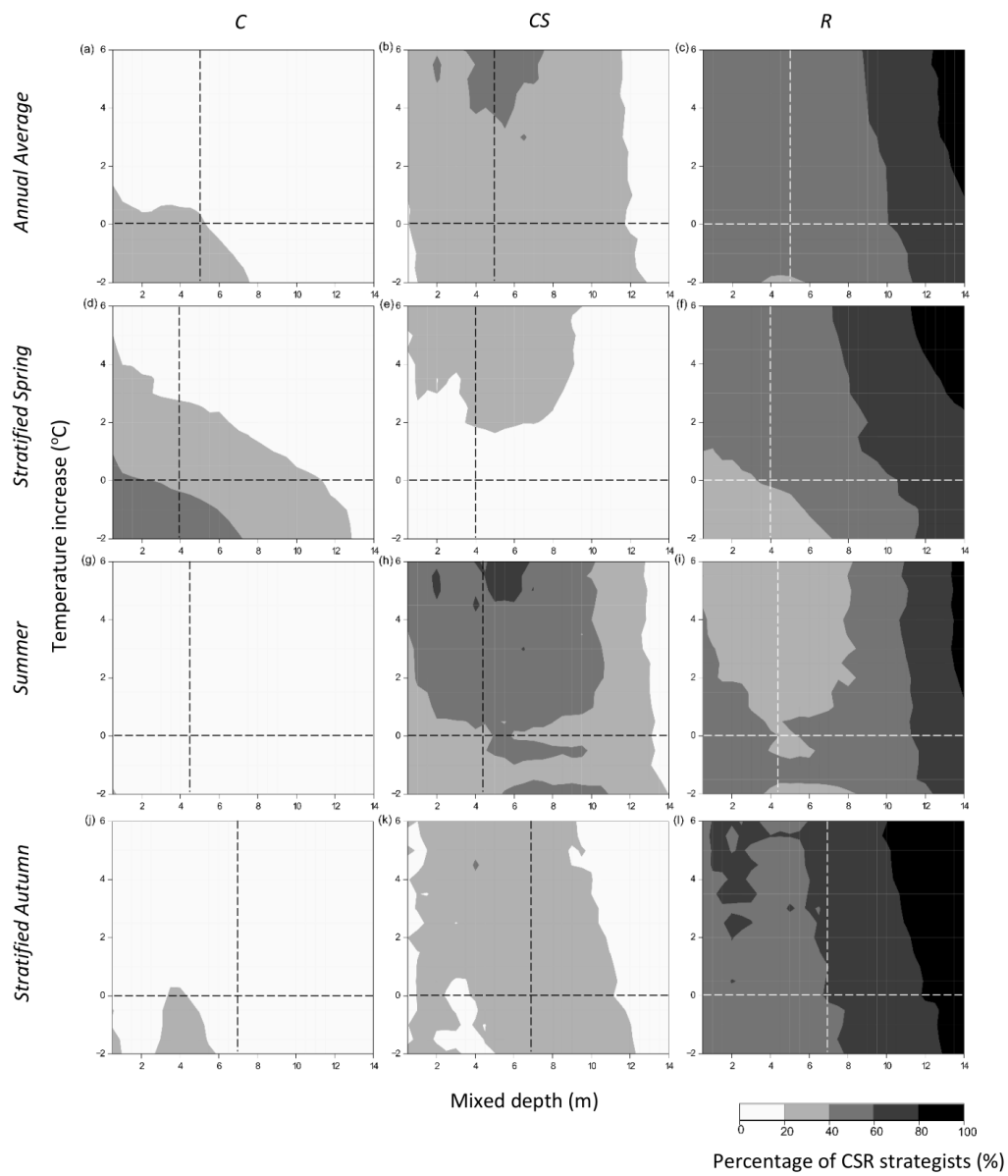
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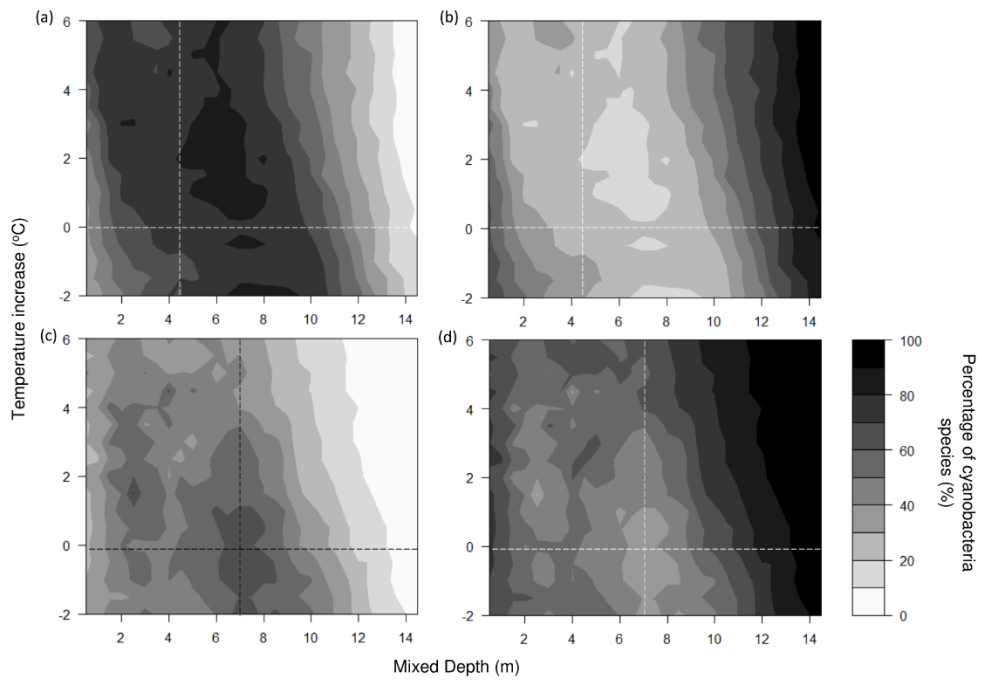
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792 **Figure 6**

Figure 7

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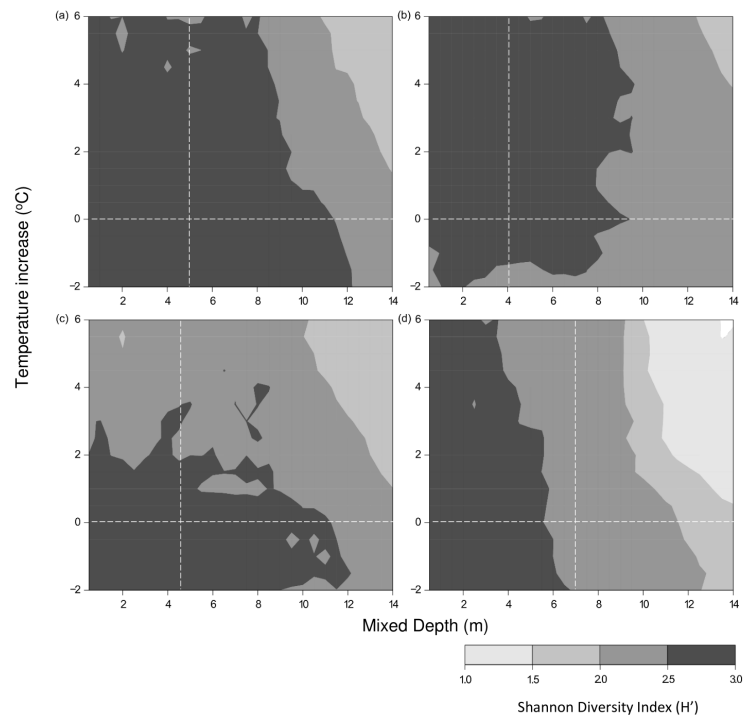
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805   **Figure 8**

Figure 9

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