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1 **IS THE FUTURE BLUE-GREEN? A REVIEW OF THE CURRENT MODEL**
2 **PREDICTIONS OF HOW CLIMATE CHANGE COULD AFFECT PELAGIC**
3 **FRESHWATER CYANOBACTERIA**

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9 **ABSTRACT**

10 There is increasing evidence that recent changes in climate have had an effect on lake
11 phytoplankton communities and it has been suggested that it is likely that Cyanobacteria will
12 increase in relative abundance under the predicted future climate. However, testing such a
13 qualitative prediction is challenging and usually requires some form of numerical computer
14 model. Therefore, the lake modelling literature was reviewed for studies that examined the
15 impact of climate change upon Cyanobacteria. These studies, taken collectively, generally
16 show an increase in relative Cyanobacteria abundance with increasing water temperature,
17 decreased flushing rate and increased nutrient loads. Furthermore, they suggest that whilst
18 the direct effects of climate change on the lakes can change the timing of bloom events and
19 Cyanobacteria abundance, the amount of phytoplankton biomass produced over a year is not
20 enhanced directly by these changes. Also, warmer waters in the spring increased nutrient
21 consumption by the phytoplankton community which in some lakes caused nitrogen
22 limitation later in the year to the advantage of some nitrogen-fixing Cyanobacteria. Finally, it
23 is also possible that an increase in Cyanobacteria dominance of the phytoplankton biomass
24 will lead to poorer energy flow to higher trophic levels due to their relatively poor edibility
25 for zooplankton.

26

27 **KEYWORDS:**

28 lake modelling, nitrogen limitation, phenology, water quality, eutrophication

29

30 1. INTRODUCTION

31 In recent years, there has been increased concern in the field of limnology about how climate
32 change may affect phytoplankton populations. This is a logical area of interest, given the
33 way that climate affects the temperature and physical structure of a lake, as well as numerous
34 in-lake chemical (e.g. dissolved oxygen concentrations) and biological processes (e.g.
35 through water temperature) (Kalff 2002). However, out of all the phytoplankton species that
36 make up the lake communities of the world, it is perhaps those species that fall under the
37 phylum Cyanobacteria that have caused the greatest amount of concern and speculation about
38 how climate change may affect them (Paerl and Huisman, 2008).

39 Cyanobacteria are photosynthetic prokaryotes that used to be referred to as blue-green
40 algae. In lakes, they generally form large colonies or filaments and many species possess the
41 ability to be buoyant through intracellular gas vesicles (Reynolds, 2006). Although this
42 property can in itself lead to unsightly blooms forming near the lake surface, the so-called
43 algal scums, it is their ability to produce toxins that concerns humans the most. There are
44 several types of toxins produced including hepatoxins, neurotoxins and cytotoxins (Codd,
45 Morrison and Metcalf, 2005). Hepatotoxic microcystins damage the digestive tract and liver,
46 and in humans can cause pneumonia-like symptoms, whereas neurotoxins affect the nervous
47 system. Cytotoxins cause widespread necrotic injury in mammals (e.g. liver, kidneys, lungs,
48 spleen, intestine) and are also genotoxic, causing chromosome loss and DNA strand breakage
49 (Codd, Morrison and Metcalf, 2005) (for more information, see Chapter 3 in Chorus and
50 Bartram, 1999). Such has been the recognition in recent decades of the threat posed by these
51 toxins, the World Health Organisation (WHO) has produced a specific report on the topic
52 (Chorus and Bartram, 1999).

53 The general view held for Cyanobacteria is that they grow better at higher
54 temperatures (>25 °C), although there are exceptions at lower temperatures (see Reynolds
55 and Walsby, 1975) and in lakes that experience low winter flushing (Hendry et al. 2006). Of
56 course, in the field such high temperatures usually occur in lakes at the same time as
57 increasing stratification which allows Cyanobacteria with buoyancy regulating properties to
58 appear in near-surface waters. Therefore discerning whether temperature or stratification (or
59 both) are the key driver to the formation of a large Cyanobacteria bloom can be difficult
60 (Reynolds and Walsby, 1975). Regardless, the positive connection between higher
61 temperatures and increased Cyanobacteria success (e.g. biomass and/or dominance of the
62 phytoplankton community) would seem to mean that the predicted warmer world of the late
63 21st century (IPCC, 2007) will be more suitable for these phytoplankton. However, in order
64 to test such a prediction we need to subject lakes to future conditions and one of the best
65 ways to do that is through using computer models.

66 Given their importance in affecting water quality, it is unsurprising the many lake
67 models include a Cyanobacteria component. However, given the interest in climate change
68 in recent years, it is surprising how few studies have used models to examine the potential
69 effect climate change could have on Cyanobacteria; perhaps this reflects the complexity of
70 modelling phytoplankton sub-groups and the confidence of modellers. Nevertheless, this
71 review collects together the published modelling evidence so far (Table 1) in order to gain a
72 collective synthesis of how climate change could affect Cyanobacteria, moving beyond
73 speculation based on present day observations and trying to predict the future responses of
74 these phytoplankton. The studies included had to meet the strict criteria of having used a
75 computer lake model, which included a Cyanobacteria component, and directly tested climate
76 change scenarios or the sensitivity of climate drivers (e.g. changing water temperature). The

77 review is structured by the approach used in the studies which fall into two broad categories
78 detailed below.

79

80

81 2. PREDICTING CLIMATE CHANGE IMPACTS

82 2.1 Using Regional Climate Models (RCMs)

83 This method involves taking the future predictions of a climate model and using them to
84 drive a lake model that includes a Cyanobacteria element (e.g. species, taxonomic group).
85 However, usually the daily weather prediction covers an area much bigger than the lake
86 system being modelled (e.g. > 50-100km grids) and therefore some kind of downscaling is
87 required. Also, any predictions are limited to the particular climate scenario model used,
88 even when groups of different models are applied, giving only limited scope for examining
89 where key thresholds of change might occur or how changes in other stressors unrelated to
90 the climate scenario may affect the response.

91 One of the earliest applications of this method for Cyanobacteria response predictions
92 was conducted by Howard and Easthope (2002) using CLAMM (Cyanobacteria Lake Mixing
93 Model). In this study, *Microcystis* growth in Farmoor reservoir (UK) was simulated using 90
94 years of future predicted output from the HADCM2 (see Jones et al., 1997) climate model.
95 Curiously, the key drivers used were wind speed, incoming solar radiation and cloud cover;
96 air temperature was not used. Consequently, as the main trend of change in the climatic
97 variables tested was only a slight decline in solar radiation due to an increase in cloud cover,
98 there was little forecasted change in *Microcystis* growth.

99 A more comprehensive study was conducted by Elliott et al. (2005), where the
100 outputs of HADCM2 were used to drive a smaller scale RCM and, after suitable

101 downscaling, provide weather drivers for the PROTECH model. PROTECH (Phytoplankton
102 RespOnses To Environment CHange) is a process-based lake phytoplankton community
103 model that can simulate 8-10 taxa (genus or species) and can include numerous types of
104 Cyanobacteria (see Reynolds et al., 2001 and Elliott et al., 2010 for details). In this study of
105 the phytoplankton community of Bassenthwaite Lake (UK), *Anabaena*, *Aphanizomenon* and
106 *Planktothrix* made up the Cyanobacteria element. The simulations first validated that using
107 20 years of the downscaled weather from a present (1970-1990) day climate scenario
108 produced the observed phytoplankton community and then tested the effect that 20 years of
109 future (2080-2100) climate had on the phytoplankton. Surface water temperature increased
110 on average 2.7 °C but the mixed depth was relatively unaffected. The Cyanobacteria
111 response was to grow earlier in the year (spring time) but there was a decline in their mean
112 biomass later in the year when they had previously been more abundant (Fig. 1). This effect
113 was due to nutrient limitation caused by an increased uptake of nutrients when growth was
114 enhanced in the spring; thus, as the nutrient-defined carrying capacity of the lake had not
115 been changed by the scenarios, the overall annual Cyanobacteria biomass produced remained
116 fairly constant and only the timing of its production was altered.

117 Of course, climate change is likely to affect the catchment that any given lake resides
118 in and two Swedish studies have sought to link climate, catchment and lake models. The first
119 (Arheimer et al., 2005) examined the impact of several downscaled climate scenarios on the
120 Rönneå catchment and the eutrophic Lake Ringsjön (Sweden). The catchment part of the
121 study mainly focussed on nitrogen export to the lake which increased under all of the future
122 scenarios. The impact of this upon the lake was modelled using PROBE (PROgram for
123 Boundary layers in the Environment; Svensson, 1998) to simulate the lake physics coupled to
124 BIOLA (BIOgeochemical LAke model; Pers 2002) which includes Cyanobacteria as a whole
125 group rather than individual species. As in Elliott et al. (2005), the authors validated the

126 simulated phytoplankton driven by the present day climate against observed data, which
127 produced a reasonable fit for the main summer bloom but simulated a spring bloom when
128 none was observed. Despite thus, the relative differences between the present climate and
129 future climates suggested a huge increase in Cyanobacteria biomass produced (>80%
130 increase). The cause behind this response was mainly raised water temperatures (by 1-5 °C)
131 stimulating an increase in nutrient mineralization and Cyanobacteria growth rates coupled to
132 a higher nutrient load to the lake.

133 The second Swedish study (Markensten et al., 2010) coupled the catchment model,
134 GWLF (Generalised Watershed Loading Functions; Haith and Shoemaker, 1987) to PROBE
135 (Svensson, 1998) and PROTBAS (PROTech Based Algal Simulations; Markensten and
136 Pierson, 2007). The Galten basin of western Lake Mälaren (Sweden) was the study site and,
137 after validating the lake models against present day observations, a 21 year A2 climate
138 change scenario (assumes doubling of present CO₂ concentrations; IPCC 2001) was used to
139 test the potential climate change impacts. The effect of this scenario was to increase the
140 period of stratification (by >25%), reduce ice-cover and increase surface water temperatures.
141 The impact of this on the phytoplankton was to slightly increase the total biomass (+9%) and
142 Cyanobacteria dominance. The drivers identified for this change were the altered timing of
143 nutrient delivery to the lake rather than changes in water temperature and stratification. The
144 former, coupled to an extended growing season, increased the likelihood of nitrogen
145 limitation later in the year, to the advantage of the nitrogen-fixing Cyanobacteria.

146 A study of three lakes in New Zealand of different trophic status using the lake model
147 DYRESM-CAEDYM (DYnamic REservoir Simulation Model – Computational Aquatic
148 Ecosystem DYnamics Model; Hamilton and Schladow, 1997) also used this A2 scenario but
149 only the air temperature element (Trolle et al., 2011). After initial calibration and validation
150 against recent observations, only the eutrophic Lake Rotoehu was run with a Cyanobacteria

151 state variable. Under the future scenario, the Cyanobacteria showed an increase of >15% in
152 dominance due to an increase in water temperature and/or nutrient load to the lake. What
153 was especially interesting about this study, however, was that the future scenario was tested
154 under a range of nutrient loads which showed that, at least in terms of total chlorophyll *a*, the
155 tested climate scenario caused effects equivalent to increasing the nitrogen and phosphorus
156 load to the lake by 25-50%.

157

158 2.2 Using the sensitivity approach

159 Studies that use a sensitivity procedure take a present day simulation of a lake system and
160 then run it again altering, for example, temperature and nutrient loading in a factorial design.
161 This produces a range of “what if...?” scenarios and allows the exploration of two key
162 drivers simultaneously. The outputs from the model runs can then be plotted on an X-Y-Z
163 plot to reproduce a response surface for the variable concerned. The method also allows the
164 identification of non-linear changes and thresholds.

165 The first modelling study to use this method in relation to climate change and
166 Cyanobacteria was Elliott et al. (2006). They examined the impact of changing nutrient
167 (phosphorus and nitrate) loads and water temperature upon the phytoplankton community of
168 Bassenthwaite Lake (UK). Focussing on just the Cyanobacteria part of the simulated
169 community, the impact of increased water temperature was clear. It caused the bloom to
170 become earlier (by 2 days per 1 °C increase) and increasing the maximum percentage
171 dominance of Cyanobacteria (by 7.6% per 1 °C increase) from a present day level of 17.3%
172 to 56.3% at +5 °C (Fig. 2). Importantly, the factorial nature of the study also showed that
173 these responses to temperature were enhanced by higher nutrient loads to the lake and,
174 conversely, suppressed by the lower nutrient scenarios.

175 Mooij et al. (2007) also used this factorial approach to test the effect of a wide range
176 of nutrient loadings and water temperature patterns upon a conceptual shallow lake using the
177 lake ecosystem model PCLake (e.g. Janse and Van Liere, 1995). The study found that the
178 Cyanobacteria part of PCLake responded favourably (e.g. % Cyanobacteria abundance rising
179 from 21 to 79%) to increasing temperature (particularly in the winter) but only if the nutrient
180 supply to the lake was above a critical threshold. More importantly, they concluded that this
181 threshold was lower under the warmer water scenarios compared to the control run under
182 present day temperatures. Furthermore, the model was run in two different states:
183 macrophyte-dominated clear state and phytoplankton dominated turbid state. Unsurprisingly,
184 Cyanobacteria dominated the latter state even under present day conditions and their
185 dominance was enhanced with the warming scenario. However, in the clear state this
186 response by the Cyanobacteria was greatly reduced, with little change in biomass and a 3-4
187 week shift in their bloom formation to earlier in the year. In general, though, the
188 consequence of this increased dominance by Cyanobacteria to the modelled food web was
189 that, because of their poor edibility, the flow of energy to higher trophic levels was reduced.

190 In another study, Loch Leven (UK) was examined using the PROTECH model to test
191 the response of its phytoplankton community to changes in water temperature and nutrient
192 supply (Elliott and May, 2008). The effect of increased water temperature upon annual mean
193 Cyanobacteria percentage abundance was very small (+1-2% per 1 °C increase) and generally
194 enhanced at the lower nutrient scenarios (which tested changing only phosphorus and
195 phosphorus and nitrogen together). The complex nature of this response was caused by the
196 lake experiencing low nitrate levels during the prime growing period for Cyanobacteria (July-
197 September). As the dominant Cyanobacteria was the nitrogen-fixing taxon *Anabaena*, this
198 meant that they actually performed better under the lower nitrate/SRP scenarios because they
199 were the only phytoplankton in the simulations that could utilise the phosphorus from the

200 spring bloom that carried over to later in the year. However, the warmer scenarios also
201 caused more of the nutrients to be used earlier in the year by non-Cyanobacteria taxa, leading
202 to less phosphorus being available and thus a decline in annual mean *Anabaena* abundance
203 (despite their percentage abundance actually increasing). This study again emphasises the
204 complex coupling of climate-change driven responses to nutrient availability.

205 The above studies focussed on the interaction of nutrient load and water temperature,
206 but a study by Elliott (2010) used the PROTECH model to test the sensitivity of
207 Cyanobacteria to changing flushing rate and water temperature. Esthwaite Water (UK) was
208 the lake studied and a new response metric was used that recorded the number of days that
209 Cyanobacteria chlorophyll *a* concentrations exceeded thresholds defined by the World Health
210 Organisation (WHO; Chorus and Bartram, 1999). Annual mean percentage Cyanobacteria
211 abundance increased with higher temperatures and lower flushing rates (Fig. 3a), although the
212 present day level of dominance was very high (annual mean: 41%, annual max: 93%)
213 meaning the actual change was relatively small. However, the seasonal responses were
214 different: in the spring, mean percentage Cyanobacteria increased with temperature but
215 showed little response to changing flushing rate (Fig. 3b) whereas in the summer, the pattern
216 was similar to that seen in the annual means i.e. high percentage abundance with increased
217 temperatures and decreased flushing (Fig. 3c). However, in terms of absolute concentration,
218 as indicated by the number of days exceeding the WHO thresholds, the response was quite
219 different (Fig. 3d); low flushing rates increased the number of days above the threshold
220 whereas higher temperatures generally reduced the number. The mechanisms behind all
221 these responses were that the blooms were less prolonged and collapsed earlier due to the
222 increase in the community growth rate caused by the raised temperatures throughout the year.
223 Furthermore, under decreased flushing, nutrient load (i.e. of phosphorus, nitrogen and silica)
224 via the inflowing rivers was reduced leading to increasing reliance of internally released

225 phosphorus to support the summer and autumn growth, which, again, gave the nitrogen-
226 fixing Cyanobacteria an advantage.

227 The final study in this review concerns PROTECH simulations of England's largest
228 lake, Windermere (Elliott, 2012). The lake consists of two interconnected basins (North and
229 South) and, using a present day simulation of both, the effect of changing air temperature and
230 nutrient load was examined. In both basins, the annual mean Cyanobacteria biomass
231 increased with temperature but the effect from nutrient load changes was more pronounced
232 and enhanced the temperature effect. This response was also echoed in the number of days
233 on which the WHO Cyanobacteria chlorophyll *a* threshold of 10 mg m⁻³ was exceeded,
234 although there was a striking dependence on nutrients. For example under the baseline
235 nutrient load, the increase in days averaged 2 days per 1°C increase, whereas under the +50%
236 phosphorus load scenarios the increase was 7 days per 1°C.

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238

239

240 3. DISCUSSION

241 In the studies covered in this review, a range of scenarios were tested which allowed the
242 importance of different drivers to be assessed. The key factors were changing water
243 temperature, stratification and nutrient loading. Therefore, the influence of these factors is
244 discussed below separately, drawing together the results of the different models and studies.

245 *3.1 Water temperature*

246 Across most of the studies there was a general trend of enhanced Cyanobacteria biomass
247 and/or dominance with increasing water temperature, although, interestingly both of the
248 Swedish studies reviewed showed the least effect (Arheimer et al., 2005; Markensten et al.,
249 2010). This overall result fits the common speculation, advanced by studies of current
250 observations (e.g. Paerl and Huisman, 2008), whereby it is assumed that Cyanobacteria
251 biomass will increase with a future warmer climate. However, just as has been observed in
252 studies of current climate change impacts on phytoplankton (e.g. Staehr & Sand-Jensen,
253 2006; Huber *et al.*, 2008; Tadonl  k  , 2010), the strength of this response to a changing
254 climate appears to be greatly influenced by the nutrient resource base of the system i.e. the
255 trophic status of the lake.

256 Despite the obvious close relationship between stratification and temperature, some
257 studies had either controlled for the effect of stratification (e.g. Elliott et al., 2006 where the
258 present day pattern of stratification was forced for the warmer scenarios), stratification did
259 not change greatly (Elliott et al., 2005) or the model used assumed a continuously mixed
260 water column (e.g. Mooij et al., 2007). These studies allowed the direct effects caused by the
261 elevated water temperature to be tested and seemed to cause an alteration in the timing of
262 Cyanobacteria growth (usually an advancement e.g. Elliott et al., 2005; Mooij et al., 2007)

263 and an increase in their dominance of the phytoplankton biomass (Elliott et al., 2006; Mooij
264 et al., 2007). The latter is of concern, because it shows that a lake under a future climate may
265 not necessarily be more productive but a greater proportion of the phytoplankton produced
266 could be Cyanobacteria, thus reducing water quality with little or no change in trophic status.

267 Interestingly, whilst the study using PCLake (Mooij et al., 2007) parameterized the
268 Cyanobacteria group in the model to have a stronger temperature dependency than the other
269 two simulated groups (diatoms and green algae), no such method was used for the
270 Cyanobacteria taxa modelled in the PROTECH simulations (Elliott et al., 2005; Elliott et al.,
271 2006) where the growth rate of the taxa is dependent on its morphology. Subsequent testing
272 of PROTECH has shown that it is the movement characteristics and other abilities (nitrogen
273 fixation) of the Cyanobacteria taxa in the model that seems to give them their advantage
274 during the typical period of Cyanobacteria seasonal dominance (i.e. late summer) (Elliott et
275 al., 2010). This would suggest that the stratification pattern of the lake could be influential.

276 *3.2 Stratification*

277 Some of the modelling studies reviewed simulated lake stratification and examined the effect
278 the scenarios had on it. Stratification was not always affected by increased air temperature
279 (Elliott et al., 2005) but where it was, it generally led to an increase in the number of days
280 stratified and/or a stronger stratification (Markensten et al., 2010; Elliott, 2012). Markensten
281 et al. (2010) concluded that despite an increase in stratification duration, its impact on the
282 Cyanobacteria was small compared to catchment influences (e.g. nutrient load). In Elliott
283 (2012), the effect of changing stratification period in the autumn was to disrupt the general
284 relationship of increasing Cyanobacteria biomass with warmer surface temperatures, and was
285 related to reduced nutrient availability at the end of the phytoplankton growing season. Such
286 a strong relationship between stratification, nutrient availability and Cyanobacteria

287 abundance has been seen in other studies (Wagner and Adrian, 2009) and warrants greater
288 consideration in future modelling studies, especially given that there is evidence that
289 phytoplankton biomass in surface waters can enhance stratification (e.g. Jones et al., 2005;
290 Rinke et al., 2010).

291 3.3 *Nutrient load*

292 Most of the modelling studies that included a change in nutrients showed an enhancement
293 under the higher nutrient scenarios of the Cyanobacteria response to the climate drivers (e.g.
294 Fig. 2). This draws out the interesting point that in most lake systems, even eutrophic ones,
295 nutrients ultimately restrain the annual biomass of phytoplankton produced and that direct
296 effects of climate change on the lake are unlikely to change the annual carrying capacity.
297 However, the studies in this review (Arheimer et al., 2005; Markensten et al., 2010) that
298 included catchment models, highlighted that climate change could affect the nutrient load to
299 the lake via the catchment, complicating the response of the phytoplankton. Therefore, the
300 importance of nutrient availability also shows that it is possible to try and alleviate climate-
301 driven effects through reducing the nutrient load to the lake. Therefore, whilst demanding,
302 local solutions via nutrient load reduction to the lake are available to solve the added
303 complications that climate change could cause regarding Cyanobacteria.

304 3.4 *Nitrogen fixation*

305 This relationship between the climate-driven response and nutrients is further complicated by
306 the influence of nitrogen-fixing Cyanobacteria, a property simulated in some of the models in
307 this review (e.g. PROTECH, PROTBAS). This ability allows these Cyanobacteria to
308 effectively circumvent nitrogen limitation, making the nutrient that is limiting growth
309 important. The effects of this were particularly evident in the Loch Leven (Elliott and May,
310 2008) and Esthwaite Water (Elliott, 2010) studies. In the former, the warmer scenarios

311 produced less biomass due to increased nutrient consumption earlier in the year, but increased
312 the Cyanobacteria dominance of the phytoplankton because of the modelled ability of
313 *Anabaena* to utilise the phosphorus in the lake despite nitrogen concentrations being limiting.
314 The same mechanism was evident in the Esthwaite Water simulations, where the reduced
315 flow scenarios restricted nutrient supply to the lake and caused less nitrogen to be available
316 later in the year, leading to increased Cyanobacteria dominance. Therefore, both of these
317 examples show how increased water temperature can cause Cyanobacteria to experience an
318 indirect advantage through a general raising of growth rates earlier in the year, leading to
319 greater nutrient uptake and therefore an increased likelihood of nitrogen limitation later in the
320 year.

321 *3.5 Other consequences*

322 If climate change does increase the dominance of Cyanobacteria amongst the phytoplankton
323 of lakes, there is another potential impact to the whole food-web that was highlighted by
324 Mooij et al. (2007). As PCLAKE modelled the whole lake system, it showed that the
325 presence of large quantities of essentially inedible Cyanobacteria could reduce the amount of
326 energy that can flow up to the higher trophic levels. This would see negative and disruptive
327 impacts upon the zooplankton and fish populations within the lake community. Of course, as
328 Mooij et al. (2007) suggest themselves, this is an area of impact that warrants further
329 consideration by other studies and models before it is known how universal an effect it could
330 be, nevertheless, it is another result from these modelling studies that is a cause of concern
331 for lake ecosystem function.

332 *3.6 The future for Cyanobacteria lake modelling*

333 In writing this review, it was surprising how few published studies there were that looked
334 specifically at the potential impact of climate change on lake Cyanobacteria populations.

335 One possible answer could be that that many modellers have a low level of confidence in the
336 ability of their lake model to capture the dynamics of these important phytoplankton. Most of
337 the models included in this review treated Cyanobacteria as a generic group whereas only
338 PROTECH and PROTBAS tried to model individual taxa of Cyanobacteria at a scale
339 analogous to the species level which would allow for successional changes within the group
340 to be explored. Furthermore, even these models did not try and model the detailed life cycle
341 of the Cyanobacteria that some models have attempted to capture (e.g. Hense and Beckmann,
342 2006). Given these issues, what would be the best approach to take the modelling of lake
343 Cyanobacteria forward?

344 Perhaps the first step would be to try and apply the models we already have, despite
345 our confidence in them. Obviously, models can be developed and further complicated almost
346 indefinitely in the search of perfection (or at least something close to it) but there should
347 come a time when they are used to investigate science questions and contribute to our
348 understanding of lake ecology. For example, PROTECH is a far from perfect model and
349 carries many simplifications (e.g. no Cyanobacteria life-cycle mechanics, assumes that
350 nitrogen-fixing taxa growth rates can never be limited by nitrogen availability) and yet it has
351 been used in five of the eleven studies presented here. Furthermore, despite these
352 simplifications, the general results from those studies are supported by the results produced
353 by the other models reviewed as well as the speculations derived from analysis of observed
354 data (e.g. Paerl and Huisman, 2008). This shows how models, regardless of their complexity,
355 can, and should be, used to help the lake phytoplankton community understand and predict
356 how climate change may impact upon these systems and particularly Cyanobacteria.

357

358 4. CONCLUSION

359 Despite the importance of knowing how Cyanobacteria may be influenced by climate change,
360 surprisingly few lake modelling studies have tackled the issue. However, from the few
361 studies that have, it seems clear that a number of important deductions can be drawn which,
362 whilst not totally conclusive, do have some merit worthy of further consideration.

363 - Firstly, the direct effect of climate change via water temperature appears to affect the
364 timing and proportional dominance of the Cyanobacteria, but not the amount of annual
365 biomass of the phytoplankton community. Furthermore, the more nutrient rich the lake and
366 greater the response of the Cyanobacteria populations modelled. There is also some evidence
367 that climate change could increase this loading to lakes.

368 - Secondly, due to the ability of some Cyanobacteria to utilise nitrogen-fixing, these
369 phytoplankters can gain an advantage later in the growing season through nitrogen limitation
370 caused by warmer waters in the spring increasing growth rates and nutrient consumption.

371 - Finally, it is possible that an increase in Cyanobacteria dominance of the
372 phytoplankton biomass will lead to poorer energy flow to higher trophic levels due to their
373 relatively poor edibility for zooplankton.

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458

459

460 Table 1 Summary of the main climate drivers and their affect on Cyanobacteria in the studies reviewed. Note: RCM? Y = Driven by Regional
 461 Climate Model, N = sensitivity method (see text for details).

Lake (country) <i>Model(s) used</i>	Trophic status	Depth (m) (mean/max)	Volume (10 ⁶ m ³)	RCM?	Driver	Response
Farmoor Reservoir (UK) ¹ <i>CLAMM</i>	Eutrophic	9.2 / 11	4.5	Y	Reduced short-wave radiation	None
Bassenthwaite Lake (UK) ² <i>PROTECH</i>	Eutrophic	5.3 / 19	27.9	Y	Higher temperature	No change in overall biomass, earlier growth
Ringsjön (Sweden) ³ <i>PROBE & BIOLA</i>	Eutrophic	5 / 17.5	184.2	Y	Higher temperature	Increase in overall biomass (via nutrients)
Galten basin of Lake Mälaren (Sweden) ⁴ <i>PROTBAS</i>	Eutrophic	3.4 / 19	210	Y	Higher temperature	Increase in dominance (via nutrients)
Lake Rotoehu (New Zealand) ⁵ <i>DYRESM-CAEDYM</i>	Eutrophic	8.2 / 13.5	60	Y	Higher temperature/nutrients	Increase in dominance
Bassenthwaite Lake (UK) ⁶ <i>PROTECH</i>	Eutrophic	5.3 / 19	27.9	N	Higher temperature	Increase in dominance
Generic shallow lake ⁷ <i>PCLake</i>	Varies	N/A	N/A	N	Higher temperature	Increase in dominance if nutrients high and/or lake turbid
Loch Leven (UK) ⁸ <i>PROTECH</i>	Eutrophic	3.9 / 25.5	52.4	N	Higher temperature	None
Esthwaite Water (UK) ⁹ <i>PROTECH</i>	Eutrophic	6.4 / 15.5	6.4	N	Higher temperature Lower flushing	Increase in dominance Increase in dominance
Windermere (UK) ¹⁰ <i>PROTECH</i>	Mesotrophic	21.3 / 64	314.5	N	Higher temperature	Increase in dominance

462 ¹Howard and Easthope (2002), ²Elliott et al. (2005), ³Arheimer et al. (2005), ⁴Markensten et al. (2010), ⁵Trolle et al. (2011), ⁶Elliott et al. (2006), ⁷Mooij et al. (2007), ⁸Elliott
 463 and May (2008), ⁹Elliott (2010), ¹⁰Elliott (2012)

465 Figure legends

466 Fig. 1 - Comparison of modelled Cyanobacteria chlorophyll *a* (fortnightly means) based on
467 present climate (solid line) and future climate (dotted line) in Bassenthwaite Lake (After
468 Elliott et al., 2005).

469 Fig. 2 - The maximum annual percentage abundance of Cyanobacteria in the simulated
470 phytoplankton communities of Bassenthwaite Lake (After Elliott et al., 2006).

471 Fig. 3 - Response of annual maximum percentage Cyanobacteria abundance in Esthwaite
472 Water to changing water temperature (°C) and flushing rate for (a) the whole year, (b) spring,
473 (c) summer and (d) number of days exceeding the lower WHO (World Health Organisation)
474 Cyanobacteria concentration threshold of > 10 chlorophyll *a* mg m⁻³ (After Elliott, 2010).

Fig. 1

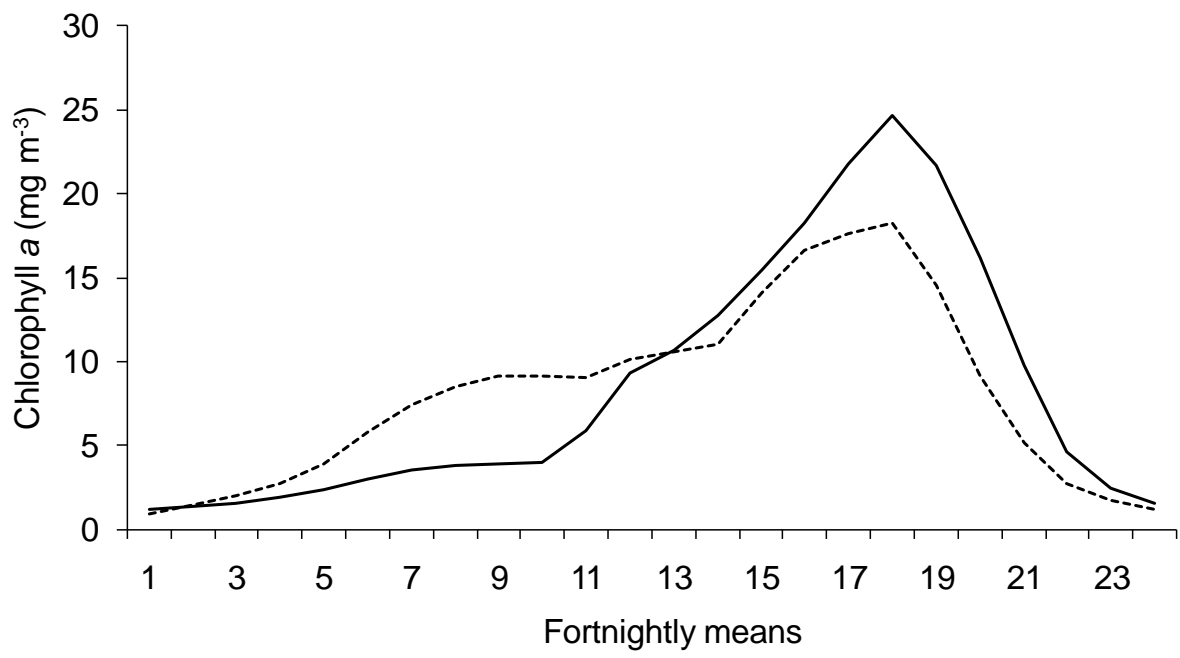


Fig. 2

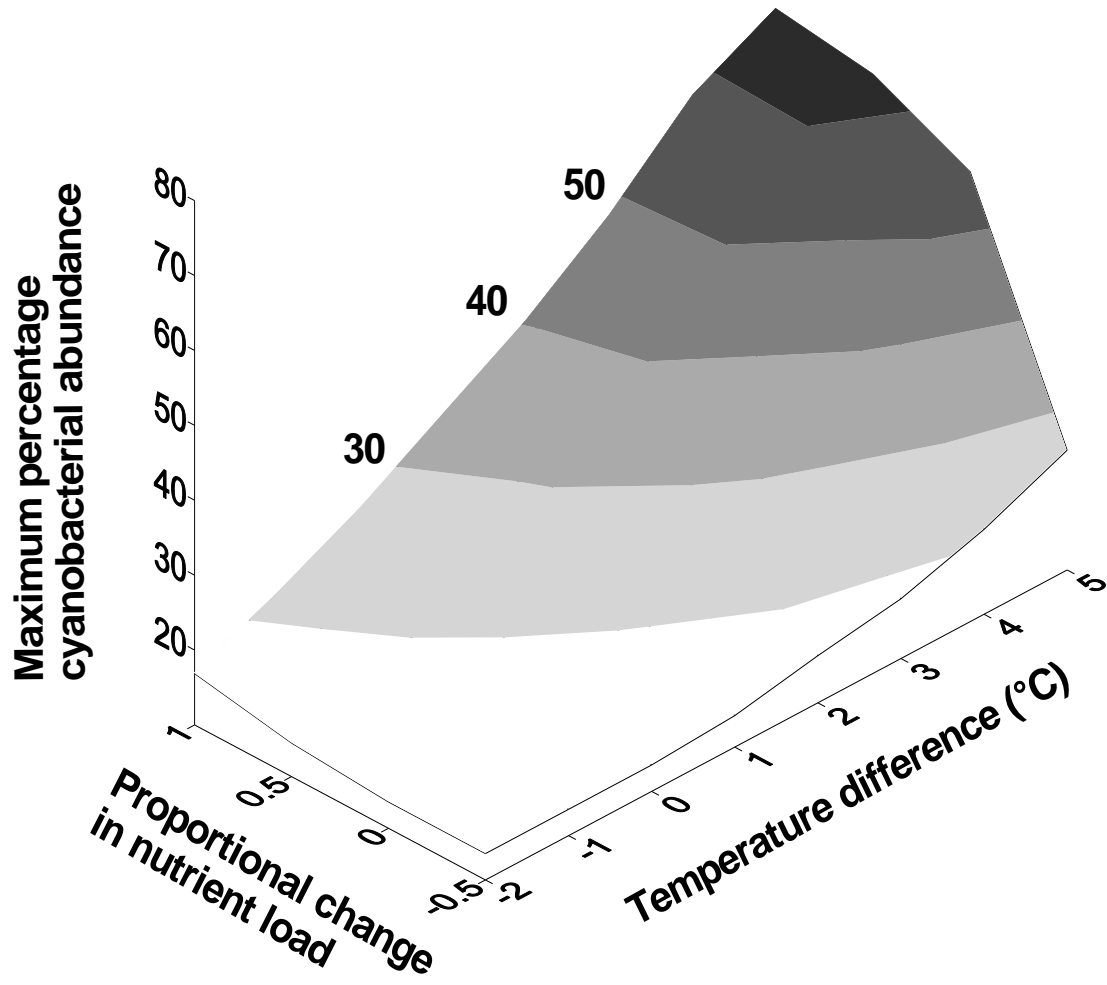


Fig. 3.

