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IS THE FUTURE BLUE-GREEN? A REVIEW OF THE CURRENT MODEL

PREDICTIONS OF HOW CLIMATE CHANGE COULD AFFECT PELAGIC

FRESHWATER CYANOBACTERIA

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ABSTRACT

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

KEYWORDS:

lake modelling, nitrogen limitation, phenology, water quality, eutrophication
1. INTRODUCTION

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

Cyanobacteria are photosynthetic prokaryotes that used to be referred to as blue-green algae. In lakes, they generally form large colonies or filaments and many species possess the ability to be buoyant through intracellular gas vesicles (Reynolds, 2006). Although this property can in itself lead to unsightly blooms forming near the lake surface, the so-called algal scums, it is their ability to produce toxins that concerns humans the most. There are several types of toxins produced including hepatotoxins, neurotoxins and cytotoxins (Codd, Morrison and Metcalf, 2005). Hepatotoxic microcystins damage the digestive tract and liver, and in humans can cause pneumonia-like symptoms, whereas neurotoxins affect the nervous system. Cytotoxins cause widespread necrotic injury in mammals (e.g. liver, kidneys, lungs, spleen, intestine) and are also genotoxic, causing chromosome loss and DNA strand breakage (Codd, Morrison and Metcalf, 2005) (for more information, see Chapter 3 in Chorus and Bartram, 1999). Such has been the recognition in recent decades of the threat posed by these toxins, the World Health Organisation (WHO) has produced a specific report on the topic (Chorus and Bartram, 1999).
The general view held for Cyanobacteria is that they grow better at higher temperatures (>25 °C), although there are exceptions at lower temperatures (see Reynolds and Walsby, 1975) and in lakes that experience low winter flushing (Hendry et al. 2006). Of course, in the field such high temperatures usually occur in lakes at the same time as increasing stratification which allows Cyanobacteria with buoyancy regulating properties to appear in near-surface waters. Therefore discerning whether temperature or stratification (or both) are the key driver to the formation of a large Cyanobacteria bloom can be difficult (Reynolds and Walsby, 1975). Regardless, the positive connection between higher temperatures and increased Cyanobacteria success (e.g. biomass and/or dominance of the phytoplankton community) would seem to mean that the predicted warmer world of the late 21st century (IPCC, 2007) will be more suitable for these phytoplankton. However, in order to test such a prediction we need to subject lakes to future conditions and one of the best ways to do that is through using computer models.

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

2. PREDICTING CLIMATE CHANGE IMPACTS
   2.1 Using Regional Climate Models (RCMs)

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

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

A more comprehensive study was conducted by Elliott et al. (2005), where the outputs of HADCM2 were used to drive a smaller scale RCM and, after suitable
downscaling, provide weather drivers for the PROTECH model. PROTECH (Phytoplankton RespOnses To Environment CHange) is a process-based lake phytoplankton community model that can simulate 8-10 taxa (genus or species) and can include numerous types of Cyanobacteria (see Reynolds et al., 2001 and Elliott et al., 2010 for details). In this study of the phytoplankton community of Bassenthwaite Lake (UK), *Anabaena*, *Aphanizomenon* and *Planktothrix* made up the Cyanobacteria element. The simulations first validated that using 20 years of the downscaled weather from a present (1970-1990) day climate scenario produced the observed phytoplankton community and then tested the effect that 20 years of future (2080-2100) climate had on the phytoplankton. Surface water temperature increased on average 2.7 °C but the mixed depth was relatively unaffected. The Cyanobacteria response was to grow earlier in the year (spring time) but there was a decline in their mean biomass later in the year when they had previously been more abundant (Fig. 1). This effect was due to nutrient limitation caused by an increased uptake of nutrients when growth was enhanced in the spring; thus, as the nutrient-defined carrying capacity of the lake had not been changed by the scenarios, the overall annual Cyanobacteria biomass produced remained fairly constant and only the timing of its production was altered.

Of course, climate change is likely to affect the catchment that any given lake resides in and two Swedish studies have sought to link climate, catchment and lake models. The first (Arhiemer et al., 2005) examined the impact of several downscaled climate scenarios on the Rönneå catchment and the eutrophic Lake Ringsjön (Sweden). The catchment part of the study mainly focused on nitrogen export to the lake which increased under all of the future scenarios. The impact of this upon the lake was modelled using PROBE (PROgram for Boundary layers in the Environment; Svensson, 1998) to simulate the lake physics coupled to BIOLA (BIOgeochemical LAke model; Pers 2002) which includes Cyanobacteria as a whole group rather than individual species. As in Elliott et al. (2005), the authors validated the
simulated phytoplankton driven by the present day climate against observed data, which produced a reasonable fit for the main summer bloom but simulated a spring bloom when none was observed. Despite thus, the relative differences between the present climate and future climates suggested a huge increase in Cyanobacteria biomass produced (>80% increase). The cause behind this response was mainly raised water temperatures (by 1-5 °C) stimulating an increase in nutrient mineralization and Cyanobacteria growth rates coupled to a higher nutrient load to the lake.

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

A study of three lakes in New Zealand of different trophic status using the lake model DYRESM-CAEDYM (DYnamic REservoir Simulation Model – Computational Aquatic Ecosystem DYnamic Model; Hamilton and Schladow, 1997) also used this A2 scenario but only the air temperature element (Trolle et al., 2011). After initial calibration and validation against recent observations, only the eutrophic Lake Rotoehu was run with a Cyanobacteria
state variable. Under the future scenario, the Cyanobacteria showed an increase of $>15\%$ in dominance due to an increase in water temperature and/or nutrient load to the lake. What was especially interesting about this study, however, was that the future scenario was tested under a range of nutrient loads which showed that, at least in terms of total chlorophyll $a$, the tested climate scenario caused effects equivalent to increasing the nitrogen and phosphorus load to the lake by $25-50\%$.

2.2 Using the sensitivity approach

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

The first modelling study to use this method in relation to climate change and Cyanobacteria was Elliott et al. (2006). They examined the impact of changing nutrient (phosphorus and nitrate) loads and water temperature upon the phytoplankton community of Bassenthwaite Lake (UK). Focussing on just the Cyanobacteria part of the simulated community, the impact of increased water temperature was clear. It caused the bloom to become earlier (by 2 days per $1{\degree}C$ increase) and increasing the maximum percentage dominance of Cyanobacteria (by $7.6\%$ per $1{\degree}C$ increase) from a present day level of $17.3\%$ to $56.3\%$ at $+5{\degree}C$ (Fig. 2). Importantly, the factorial nature of the study also showed that these responses to temperature were enhanced by higher nutrient loads to the lake and, conversely, suppressed by the lower nutrient scenarios.
Mooij et al. (2007) also used this factorial approach to test the effect of a wide range of nutrient loadings and water temperature patterns upon a conceptual shallow lake using the lake ecosystem model PCLake (e.g. Janse and Van Liere, 1995). The study found that the Cyanobacteria part of PCLake responded favourably (e.g. % Cyanobacteria abundance rising from 21 to 79%) to increasing temperature (particularly in the winter) but only if the nutrient supply to the lake was above a critical threshold. More importantly, they concluded that this threshold was lower under the warmer water scenarios compared to the control run under present day temperatures. Furthermore, the model was run in two different states: macrophyte-dominated clear state and phytoplankton dominated turbid state. Unsurprisingly, Cyanobacteria dominated the latter state even under present day conditions and their dominance was enhanced with the warming scenario. However, in the clear state this response by the Cyanobacteria was greatly reduced, with little change in biomass and a 3-4 week shift in their bloom formation to earlier in the year. In general, though, the consequence of this increased dominance by Cyanobacteria to the modelled food web was that, because of their poor edibility, the flow of energy to higher trophic levels was reduced.

In another study, Loch Leven (UK) was examined using the PROTECH model to test the response of its phytoplankton community to changes in water temperature and nutrient supply (Elliott and May, 2008). The effect of increased water temperature upon annual mean Cyanobacteria percentage abundance was very small (+1-2% per 1 °C increase) and generally enhanced at the lower nutrient scenarios (which tested changing only phosphorus and phosphorus and nitrogen together). The complex nature of this response was caused by the lake experiencing low nitrate levels during the prime growing period for Cyanobacteria (July-September). As the dominant Cyanobacteria was the nitrogen-fixing taxon *Anabaena*, this meant that they actually performed better under the lower nitrate/SRP scenarios because they were the only phytoplankton in the simulations that could utilise the phosphorus from the
spring bloom that carried over to later in the year. However, the warmer scenarios also
caused more of the nutrients to be used earlier in the year by non-Cyanobacteria taxa, leading
to less phosphorus being available and thus a decline in annual mean *Anabaena* abundance
(although their percentage abundance actually increasing). This study again emphasises the
complex coupling of climate-change driven responses to nutrient availability.

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

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

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

3.1 Water temperature

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

Despite the obvious close relationship between stratification and temperature, some studies had either controlled for the effect of stratification (e.g. Elliott et al., 2006 where the present day pattern of stratification was forced for the warmer scenarios), stratification did not change greatly (Elliott et al., 2005) or the model used assumed a continuously mixed water column (e.g. Mooij et al., 2007). These studies allowed the direct effects caused by the elevated water temperature to be tested and seemed to cause an alteration in the timing of Cyanobacteria growth (usually an advancement e.g. Elliott et al., 2005; Mooij et al., 2007)
and an increase in their dominance of the phytoplankton biomass (Elliott et al., 2006; Mooij et al., 2007). The latter is of concern, because it shows that a lake under a future climate may not necessarily be more productive but a greater proportion of the phytoplankton produced could be Cyanobacteria, thus reducing water quality with little or no change in trophic status.

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

3.2 Stratification

Some of the modelling studies reviewed simulated lake stratification and examined the effect the scenarios had on it. Stratification was not always affected by increased air temperature (Elliott et al., 2005) but where it was, it generally led to an increase in the number of days stratified and/or a stronger stratification (Markensten et al., 2010; Elliott, 2012). Markensten et al. (2010) concluded that despite an increase in stratification duration, its impact on the Cyanobacteria was small compared to catchment influences (e.g. nutrient load). In Elliott (2012), the effect of changing stratification period in the autumn was to disrupt the general relationship of increasing Cyanobacteria biomass with warmer surface temperatures, and was related to reduced nutrient availability at the end of the phytoplankton growing season. Such a strong relationship between stratification, nutrient availability and Cyanobacteria
abundance has been seen in other studies (Wagner and Adrian, 2009) and warrants greater consideration in future modelling studies, especially given that there is evidence that phytoplankton biomass in surface waters can enhance stratification (e.g. Jones et al., 2005; Rinke et al., 2010).

3.3 Nutrient load

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

3.4 Nitrogen fixation

This relationship between the climate-driven response and nutrients is further complicated by the influence of nitrogen-fixing Cyanobacteria, a property simulated in some of the models in this review (e.g. PROTECH, PROTBAS). This ability allows these Cyanobacteria to effectively circumvent nitrogen limitation, making the nutrient that is limiting growth important. The effects of this were particularly evident in the Loch Leven (Elliott and May, 2008) and Esthwaite Water (Elliott, 2010) studies. In the former, the warmer scenarios
produced less biomass due to increased nutrient consumption earlier in the year, but increased the Cyanobacteria dominance of the phytoplankton because of the modelled ability of *Anabaena* to utilise the phosphorus in the lake despite nitrogen concentrations being limiting. The same mechanism was evident in the Esthwaite Water simulations, where the reduced flow scenarios restricted nutrient supply to the lake and caused less nitrogen to be available later in the year, leading to increased Cyanobacteria dominance. Therefore, both of these examples show how increased water temperature can cause Cyanobacteria to experience an indirect advantage through a general raising of growth rates earlier in the year, leading to greater nutrient uptake and therefore an increased likelihood of nitrogen limitation later in the year.

3.5 Other consequences

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

3.6 The future for Cyanobacteria lake modelling

In writing this review, it was surprising how few published studies there were that looked specifically at the potential impact of climate change on lake Cyanobacteria populations.
One possible answer could be that that many modellers have a low level of confidence in the ability of their lake model to capture the dynamics of these important phytoplankton. Most of the models included in this review treated Cyanobacteria as a generic group whereas only PROTECH and PROTBAS tried to model individual taxa of Cyanobacteria at a scale analogous to the species level which would allow for successional changes within the group to be explored. Furthermore, even these models did not try and model the detailed life cycle of the Cyanobacteria that some models have attempted to capture (e.g. Hense and Beckmann, 2006). Given these issues, what would be the best approach to take the modelling of lake Cyanobacteria forward?

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

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

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

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

- Finally, it is possible that an increase in Cyanobacteria dominance of the phytoplankton biomass will lead to poorer energy flow to higher trophic levels due to their relatively poor edibility for zooplankton.
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Table 1 Summary of the main climate drivers and their affect on Cyanobacteria in the studies reviewed. Note: RCM? Y = Driven by Regional Climate Model, N = sensitivity method (see text for details).

<table>
<thead>
<tr>
<th>Lake (country) Model(s) used</th>
<th>Trophic status</th>
<th>Depth (m) (mean/max)</th>
<th>Volume (10⁶ m³)</th>
<th>RCM?</th>
<th>Driver</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Farmoor Reservoir (UK)¹ CLAMM</td>
<td>Eutrophic</td>
<td>9.2 / 11</td>
<td>4.5</td>
<td>Y</td>
<td>Reduced short-wave radiation</td>
<td>None</td>
</tr>
<tr>
<td>Bassenthwaite Lake (UK)² PROTECH</td>
<td>Eutrophic</td>
<td>5.3 / 19</td>
<td>27.9</td>
<td>Y</td>
<td>Higher temperature</td>
<td>No change in overall biomass, earlier growth</td>
</tr>
<tr>
<td>Ringsjön (Sweden)³ PROBE &amp; BIOLA</td>
<td>Eutrophic</td>
<td>5 / 17.5</td>
<td>184.2</td>
<td>Y</td>
<td>Higher temperature</td>
<td>Increase in overall biomass (via nutrients)</td>
</tr>
<tr>
<td>Galten basin of Lake Mälaren (Sweden)⁴ PROTBAS</td>
<td>Eutrophic</td>
<td>3.4 / 19</td>
<td>210</td>
<td>Y</td>
<td>Higher temperature</td>
<td>Increase in dominance (via nutrients)</td>
</tr>
<tr>
<td>Lake Rotoehu (New Zealand)⁵ DYRESM-CAEDYM</td>
<td>Eutrophic</td>
<td>8.2 / 13.5</td>
<td>60</td>
<td>Y</td>
<td>Higher temperature/nutrients</td>
<td>Increase in dominance</td>
</tr>
<tr>
<td>Bassenthwaite Lake (UK)⁶ PROTECH</td>
<td>Eutrophic</td>
<td>5.3 / 19</td>
<td>27.9</td>
<td>N</td>
<td>Higher temperature</td>
<td>Increase in dominance</td>
</tr>
<tr>
<td>Generic shallow lake⁷ PCLake</td>
<td>Varies</td>
<td>N/A</td>
<td>N/A</td>
<td>N</td>
<td>Higher temperature</td>
<td>Increase in dominance if nutrients high and/or lake turbid</td>
</tr>
<tr>
<td>Loch Leven (UK)⁸ PROTECH</td>
<td>Eutrophic</td>
<td>3.9 / 25.5</td>
<td>52.4</td>
<td>N</td>
<td>Higher temperature</td>
<td>None</td>
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<tr>
<td>Esthwaite Water (UK)⁹ PROTECH</td>
<td>Eutrophic</td>
<td>6.4 / 15.5</td>
<td>6.4</td>
<td>N</td>
<td>Higher temperature Lower flushing</td>
<td>Increase in dominance</td>
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<tr>
<td>Windermere (UK)¹⁰ PROTECH</td>
<td>Mesotrophic</td>
<td>21.3 / 64</td>
<td>314.5</td>
<td>N</td>
<td>Higher temperature</td>
<td>Increase in dominance</td>
</tr>
</tbody>
</table>

Figure legends

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

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

Fig. 3 - Response of annual maximum percentage Cyanobacteria abundance in Esthwaite Water to changing water temperature ($^\circ$C) and flushing rate for (a) the whole year, (b) spring, (c) summer and (d) number of days exceeding the lower WHO (World Health Organisation) Cyanobacteria concentration threshold of $> 10$ chlorophyll $a$ mg m$^{-3}$ (After Elliott, 2010).
Fig. 1

Chlorophyll a (mg m$^{-3}$)

Fortnightly means
Fig. 2

Proportional change in nutrient load

Temperature difference (°C)

Maximum percentage cyanobacterial abundance

30

40

50