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The seasonal sensitivity of Cyanobacteria and other phytoplankton to changes in flushing rate and water temperature

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Abstract

The phytoplankton lake community model PROTECH (Phytoplankton RespOnses To Environmental CHange) was applied to the eutrophic lake, Esthwaite Water (United Kingdom). It was validated against monitoring data from 2003 and simulated well the seasonal pattern of total chlorophyll, diatom chlorophyll and Cyanobacteria chlorophyll with respective R^2-values calculated between observed and simulated of 0.68, 0.72 and 0.77 (all $P<0.01$). This simulation was then rerun through various combinations of factorized changes covering a range of half to double the flushing rate and from −1 to + 4 °C changes in water temperature. Their effect on the phytoplankton was measured as annual, spring, summer and autumn means of the total and species chlorophyll concentrations. In addition, Cyanobacteria mean percentage abundance (%Cb) and maximum percentage abundance (Max %Cb) was recorded, as were the number of days that Cyanobacteria chlorophyll concentration exceed two World Health Organization (WHO) derived risk thresholds (10 and 50 mg m^{-3}). The phytoplankton community was dominated in the year by three of the eight phytoplankton simulated. The vernal bloom of the diatom *Asterionella* showed little annual or seasonal response to the changing drivers but this was not the case for the two Cyanobacteria that also dominated, *Anabaena* and *Aphanizomenon*. These Cyanobacteria showed enhanced abundance, community dominance and increased duration above the highest WHO risk threshold with increasing water temperature and decreasing flushing rate: this effect was greatest in the summer period. However, the response was ultimately controlled by the availability of nutrients, particularly phosphorus and nitrogen, with occasional declines in the latter's concentration helping the dominance of these nitrogen-fixing phytoplankton.

Keywords: blue–green algae, climate change, eutrophication, phytoplankton, PROTECH, retention time

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Introduction

In assessing the impact of climate change on organisms, there has been much focus on the threats to species (e.g. Visser, 2008), but the reverse is also true in that some species will inevitably be more successful under such conditions (e.g. Cumming & Van Vuuren, 2006). Cyanobacteria (also referred to as blue–green algae) are a phytoplankton phylum that can deteriorate water quality through the production of toxins that are harmful to birds and mammals, including humans (Chorus & Bartram, 1999). In recent years, there has been increasing interest in how climate change could potentially affect the proliferation of harmful Cyanobacteria blooms in water bodies (e.g. Paerl & Huisman, 2008). This has mainly focused on the direct effects of increased water temperature, but some studies have also highlighted the importance of changes in stratification strength and duration (e.g. Jones & Elliott, 2007; Jöhnk *et al.*, 2008). However, there is also a close relationship between the hydraulic retention time of the lake (flushing rate) and Cyanobacteria bloom formation (Paerl & Huisman, 2008). Significantly, there appears to

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have been no study that has attempted to evaluate the relative importance of temperature and flushing rate when applied simultaneously. Therefore, this work aims to address precisely this question.

The projected changes for air temperature and river flow across the United Kingdom in general are for an overall increase in temperature (2–3.5 °C by the 2080s) and winter flow, with increased likelihood of lower summer flow (Hulme *et al*., 2002). However, many UK catchment level studies using Regional Climate Models (RCMs) have shown that predicting impacts at such a detailed scale is particularly challenging given the levels of uncertainty in the modelled climate drivers (e.g. rainfall) and the heavy influence catchment topography (e.g. Reynard *et al*., 2005; Kay *et al*., 2006). Therefore, this study uses a method that tests the *sensitivity* of a lake's phytoplankton community to such climatic changes by perturbing observed weather data over a range of values. Thus, the sensitivity of the lake to a wide range of different climatic conditions can be observed, rather than for just one modelled outcome, with all its associated uncertainties (i.e. the 'cascade of uncertainty'; Henderson-Sellers, 1993).

Therefore, the aim of this article is to identify, through simulation using a phytoplankton lake community computer model, the sensitivity of the Cyanobacteria and other phytoplankton to changing flushing rate and water temperature. This sensitivity is measured at the annual and seasonal level (spring, summer and autumn) and of particular interest is the response of the Cyanobacteria, both in terms of the seasonal means but also their maximum abundance (i.e. the worst day in terms of related water quality) and World Health Organization (WHO) abundance thresholds.

It is predicted, in accordance with the perceived view on factors favourable to Cyanobacteria (Reynolds, 2006; Paerl & Huisman, 2008) that

(i) higher water temperatures and/or
(ii) lower flushing rates will promote Cyanobacteria dominance, particularly in the summer/autumn.

Methods

Site description

Esthwaite Water is a small (surface area 1.0 km^2, mean depth 6.4 m, maximum depth 15.5 m (Ramsbottom, 1976)), eutrophic lake [mean annual phytoplankton chlorophyll concentration 13.5 $mg\,m^{-3}$ (Maberly *et al*., 2006)] situated in northwest England [54°21′N, 3°0′W (Reynolds, 1984)] and classed as a Site of Special Scientific Interest (SSSI) (Talling, 1999). The lake has undergone persistent eutrophication since the late 1960s (Bennion *et al*., 2000) and regularly produces Cyanobacteria blooms in the summer to early autumn consisting mainly of *Anabaena* and *Aphanizomenon* (Heaney *et al*., 1992).

The historic source of much of the nutrient enrichment has been point derived, with >60% of the total phosphorus load originating from the local sewage works before stripping was added in 1986 (Talling & Heaney, 1988). However, recovery has been complicated by the addition of a fish farm and internal phosphorus fluxes (Heaney *et al*., 1992). The estimated annual mean hydraulic retention time is ca.90 days (Talling & Heaney, 1988).

Data

The driving and validation data for the simulations were all taken from 2003 as this year provided a good set of data for both driving and validating the model, as well as shown the typical patterns of thermal structure and phytoplankton development for this lake. Daily measurements of the outflow (Cunsey Beck) and the main inflow (Black Beck) discharges were available (annual retention time for 2003 of 104 days) and, for Black Beck, fortnightly soluble reactive phosphorus (SRP), nitrate-nitrogen and silica concentrations were available. Fortnightly in-lake water temperature, SRP, nitrate-nitrogen, silica and chlorophyll *a* concentrations (integrated over the top 5 m), including phytoplankton species counts, were also available for the same period.

The latter count data were converted to chlorophyll *a* estimates using cell volume to chlorophyll *a* relationships given by Reynolds (1984). This method, while being potentially a considerable source of error, was necessary for comparison with the model output and the data should be regarded as a rough, semiquantitative estimate of the relative importance of certain taxa during the year.

Daily meteorological data were drawn from two sources: wind speed and air temperature were measured on site at a shore meteorological station, while cloud cover (oktas) estimates were from a meteorological station situated 7 km away.

PROTECH model description

The phytoplankton community model used is called Phytoplankton RespOnses To Environmental CHange (PROTECH); (Reynolds *et al*., 2001). It is a process-based model that simulates the daily growth of multiple phytoplankton types throughout the water column. The model has been developed and tested on a wide range of lakes and reservoirs around the world over the last two decades (e.g. Elliott *et al*., 2000, 2005, 2007; Lewis *et al*., 2002; Elliott & Thackeray, 2004; Bernhardt *et al*., 2008).

The biological component of PROTECH (see Reynolds *et al*., 2001 for a full description) has at its heart

a simple equation that determines the daily change in the chlorophyll *a* concentration ($\Delta X/\Delta t$, mg m^{-3} day^{-1}) of each phytoplankton:

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

where r' is the growth rate defined as a proportional increase over 24 h, S is the loss due to settling out of the water column, G is the loss due to *Daphnia* grazing (phytoplankton $>50\,\mu$m are not grazed) and D is the loss due to dilution. The growth rate (r', day^{-1}) is further defined by

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

where $r'_{(\theta,\,I)}$ is the growth rate due to temperature and daily photoperiod and r'_{P}, r'_{N}, r'_{Si} are the growth rates determined by phosphorus, nitrogen and silicon if their concentrations are <3.0, 80.0 and 500.0 mg m^{-3}, respectively (Reynolds, 1984). The r' values are phytoplankton dependent (e.g. nondiatoms are not limited by silica concentrations below 500 mg m^{-3}), relating to the morphology of the alga (for $r'_{(\theta,\,I)}$) and, because of the effects of temperature and light, vary with each time-step throughout the simulated water-column. Thus, no one specific summary r' value exists for a given phytoplankton. Therefore, for each alga within the model, the initial starting value of X mg chlorophyll *a* m^{-3} day^{-1} [Eqn (1)] is modified on a daily time-step to predict change in the chlorophyll *a* concentration for each phytoplanker in each layer in the water column (see Reynolds *et al*., 2001, for details). Nutrient concentrations in the water column are modified to reflect uptake due to growth and daily supply and loss via inflow/outflow exchange. For all the phytoplankton simulated, it is assumed that these nutrients are consumed from the water column in the following stoichiometric ratio of 82 g SiO_2 (only if diatom) : 8.3 g nitrogen : 1.2 g phosphorus : 1 g chlorophyll (Stumm & Morgan, 1981).

There is also a phytoplankton-specific movement function that calculates the position of each alga in the column, accounting for the movement of the water and Stoke's Law (movement down the water column), as well as the motile/buoyancy properties of some phytoplankton (positive movement up the water column, dependent upon light intensity for motile phytoplankton).

An initial profile for the water column (containing temperature, nutrient concentrations and inoculum sizes for the selected phytoplankton) is defined for day 1 (equivalent to 1 January in the simulations presented in this investigation). The daily inoculum was defined so that the total chlorophyll *a* for the eight phytoplankton equalled the nearest observed value to the start of the year i.e. 0.225 mg m^{-3} chl *a* for each phytoplankton to make a total chlorophyll *a* of 1.8 mg m^{-3} chl *a*. Daily wind speed, cloud cover, river inflow (including nutrient concentrations) and outflow data are input to the model and daily insolation is adjusted depending upon the time of the year latitude and cloud cover. For each 24 h time-step, the physical structure of the water column is defined over vertical, morphologically dependent 0.1 m slices. The extent of mixing within the water column is calculated by following the Monin–Obukhov length calculation (Imberger, 1985), which gives an instantaneous prediction of the depth at which the buoyancy forces (due to the heat flux) and the opposing dissipative forces (due to wind stress) are equal in magnitude. This point corresponds to the extent of the mixed layer, assuming initial uniformity. To test the resistance to mixing of an existing density structure, it is also necessary to apply a Wedderburn test, which incorporates a term for the accumulated density difference between the water at the surface and at any nominated depth. At each iteration, the model works down the water column, incorporating each slice until the accumulated density difference resists the incorporation: this slice then corresponds to the depth of the thermocline.

Phytoplankton simulations

Examination of the phytoplankton count data revealed the numerically abundant phytoplankton types detected in the lake during 2003. This information was used to select the following PROTECH phytoplankton for the simulations: *Anabaena*, *Aphanizomenon*, *Aphanothece*, *Asterionella*, *Cryptomonas*, *Plagioselmis*, *Peridinium* and *Ceratium* (Tables 1 and 2). For initial calibration, PROTECH output summarized as total, diatom and Cyanobacteria chlorophyll concentration in the upper 5 m of water were compared with the observed data available. This process, in conjunction with additional examination of in-lake water column nutrient profiles, indicated a lack of phosphorus in the simulated lake during the middle of year. PROTECH does not include equations to simulate the release of SRP from sediment which is known to be important in this lake (Drake & Heaney, 1987; Miller *et al*., 2005), therefore extra SRP was added to the water column from 1 June to 31 August. This amounted to an extra 0.44 mg m^{-3} per 0.1 m layer per day [over a total of 155 layers, i.e. 15.5 m deep lake; roughly equating to 2.8 mg m^{-2} day^{-1} and falling within the commonly observed range of 0.5–5 mg m^{-2} day^{-1} (Drake & Heaney, 1987)] to produce hypolimnion concentrations similar to those observed and was the only calibration required to the initial generic model set-up.

For validation of the simulation, visual comparison and regression analysis were used to compare total chlorophyll, as well as the diatom and Cyanobacteria

Table 1 The morphological and phylogenetic characteristics of the eight simulated phytoplankton

Phytoplankton	Surface area (μm^2)	Volume (μm^3)	Maximum dimension (μm)	Diatom	Grazed	Nitrogen fixer
Plagioselmis	108	72	11	F	T	F
Cryptomonas	1030	2710	21	F	T	F
Peridinium	5027	33 510	40	F	F	F
Ceratium	9600	43 700	201	F	F	F
Asterionella	6690	5160	130	T	T	F
Aphanothece	7854	65 450	500	F	F	F
Anabaena	6200	29 000	75	F	F	T
Aphanizomenon	5200	15 400	125	F	F	T

The last three columns denote simple logic statements (True/False) which, if True, activate relevant functions in PROTECH. PROTECH, Phytoplankton RespOnses To Environmental CHange.

Table 2 Summary of Phytoplankton RespOnses To Environmental CHange (PROTECH) instructions governing vertical movements of phytoplankton

Phytoplankton	Light condition ($\mu mol\ photon\ m^{-2}\ s^{-1}$)	Movement ($m\ day^{-1}$)
Nonbuoyant nonmotile diatoms		
Asterionella	≤ 500	Sink 0.2
	>500	Sink 1.0
Buoyancy-regulating Cyanobacteria		
Aphanothece	>30	Sink 0.1
	≤ 30 but >10	No move
	≤ 10	Rise 0.1
Anabaena and	>100	Sink 0.3
Aphanizomenon	≤ 100 but >30	Sink 0.1
	≤ 30 but >10	No move
	≤ 10	Rise 0.1
Swimming flagellates		
Cryptomonas	>100	Rise 0.1
	≤ 100	Rise 2.0
Ceratium and	>100	Sink 1.0
Peridinium	≤ 100	Rise 1.0
Plagioselmis	>150	Sink 0.5
	≤ 100 but >30	No move
	≤ 30	Rise 0.5

In all cases of either moving up or down, if the top or bottom layer (i.e. 0.1 m PROTECH layer) is encountered the movement is stopped; if it is the bottom layer the phytoplankton is lost.

biomass simulated. For the latter two variables, it was necessary to convert the fortnightly observed species count data from cells per mL to mg chlorophyll *a* per m^{-3}. These values were calculated using the cell volume to chlorophyll *a* relationships given in Reynolds (1984) and summed for the dominant taxa in the lake, i.e. diatoms and Cyanobacteria.

Taking this baseline simulation, the combined effect of changing retention time and water temperature was tested by the incremental alteration of these two factors. This was done by forcing the water temperature throughout the water column to be between 1 °C cooler to 4 °C warmer, in 1 °C increments; this provided a realistic range of past to possible future water temperature in northwest England (e.g. Elliott *et al*., 2005; Fowler & Kilsby, 2007). It should be stressed that this change in temperature did not alter the original 2003 pattern of stratification, which was fixed so as to isolate only the direct effect of changing temperature on the phytoplankton populations. In addition, the temperature of the inflow discharge was not allowed to change the lake water temperature. In combination with these temperature changes, the retention time of the lake was changed by altering the observed inflow and outflow discharge by the following factors: 0.5, 1.0, 1.5 and 2.0, thus creating drier and wetter years; inflow nutrient concentration was not changed, mimicking the response of a more diffuse nutrient source. For each permutation, the annual, spring (March–May), summer (June–August) and autumn (September–November) mean chlorophyll was calculated for each species and the total biomass. In addition, the mean and maximum percentage dominance by Cyanobacteria was also measured for both the year and the seasons defined above.

Finally, the WHO guidelines for Cyanobacteria blooms (Chorus & Bartram, 1999) were used to calculate the number of days when key threshold levels were passed. Thus, two levels were set with the first representing number of days with $>10\ mg\ m^{-3}$ Cyanobacteria chlorophyll *a* (low risk) and the second for moderate risk when Cyanobacteria chlorophyll *a* exceeded $50\ mg\ m^{-3}$.

Results

Comparison with observed data

The simulated total chlorophyll *a* matched well to the measured data (Fig. 1a), showing a tendency to reproduce the many bloom peaks; this was reflected in a high R^2 of 0.68 ($P<0.01$). This level of good fit was also replicated at the taxonomic level, producing excellent

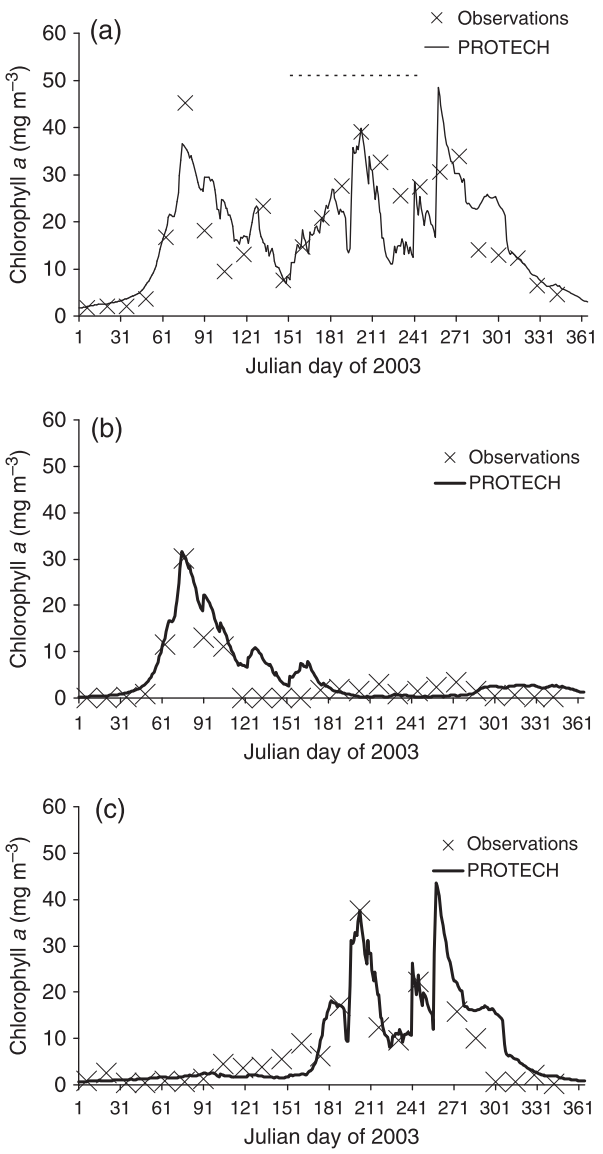

Fig. 1 Comparison between observed (crosses) and PROTECH simulated (solid line) chlorophyll *a* concentrations (mg m^{-3}) for Esthwaite Water, 2003: (a) total chlorophyll *a*, (b) diatoms and (c) Cyanobacteria. *Note*: Dashed line on (a) indicates period of additional internal SRP (see 'Methods'). PROTECH, Phytoplankton RespOnses To Environmental CHange.

simulations of the diatom ($R^2 = 0.72$, $P < 0.01$; Fig. 1b) and Cyanobacteria chlorophyll *a* ($R^2 = 0.77$, $P < 0.01$; Fig. 1c) calculated from the count data. In addition, qualitative validation at the genus level also suggested a good simulation of the phytoplankton community with the simulated bloom in spring being dominated by *Asterionella* and blooms in the late summer by a mix of *Anabaena* and *Aphanizomenon*, which all corresponded well the observed dominance during those respective periods (data not shown). While further years of data for validation purposes would have been desirable, such a pattern of both simulated and observed biomass and dominance is not unusual in temperate lakes in this region (Talling, 1999) and lends some support to the validity of the model, especially given the low level of calibration required.

In addition, it is worth briefly mentioning that, despite 2003 being noted as producing a particularly intense summer heatwave in Europe (Luterbacher *et al.*, 2004) and producing high water temperatures [e.g. 24 °C for Lake Nienue Meer in the Netherlands (Jöhnk *et al.*, 2008)], this was not the case for this lake in the United Kingdom where 2003 was only the 12th warmest year over the period 1947–2005 (2003 maximum observed water temperature 20.3 °C).

Changes in annual means

The response surface for annual mean total chlorophyll (Fig. 2a) showed inconsistent trends of change in response to the simulated variations in temperature and flow. There was a slight tendency for higher biomass means to occur under the lowest flow scenarios, but this was not always the case (i.e. for the 0 °C and +1 °C scenarios). Focussing now on the phytoplankton simulated that contributed the most to the overall phytoplankton biomass, *Asterionella*, the dominant diatom in this study, demonstrated little response to the two drivers tested (Fig. 2b). In contrast, the mean annual chlorophyll of two Cyanobacteria simulated (*Aphanizomenon* and *Anabaena*; Fig. 2c and d, respectively) was enhanced by a combination of low flow and high water temperatures. Both the percentage Cyanobacteria abundance (%Cb) metric and maximum percentage abundance (Max %Cb) reinforced this effect (Fig. 2e and f).

Changes in spring means

In the spring period the dominance by *Asterionella* resulted in little response in both mean total chlorophyll and mean *Asterionella* chlorophyll (Fig. 3a and b, respectively), although there was a hint of a decline in *Asterionella* biomass with increasing temperature. *Aphanizomenon* and *Anabaena* mean biomass levels were very low (data not shown) and this was reflected in the low percentages for %Cb (Fig. 3c) and Max %Cb (Fig. 3d). However, it is important to note that these percentages did increase at higher temperatures, with Max %Cb increasing by ca. 3% per 1 °C increase.

Changes in summer means

In the 3 months of summer, mean total chlorophyll values displayed a clear increase under combined low flow and high temperature scenarios (Fig. 4a), although

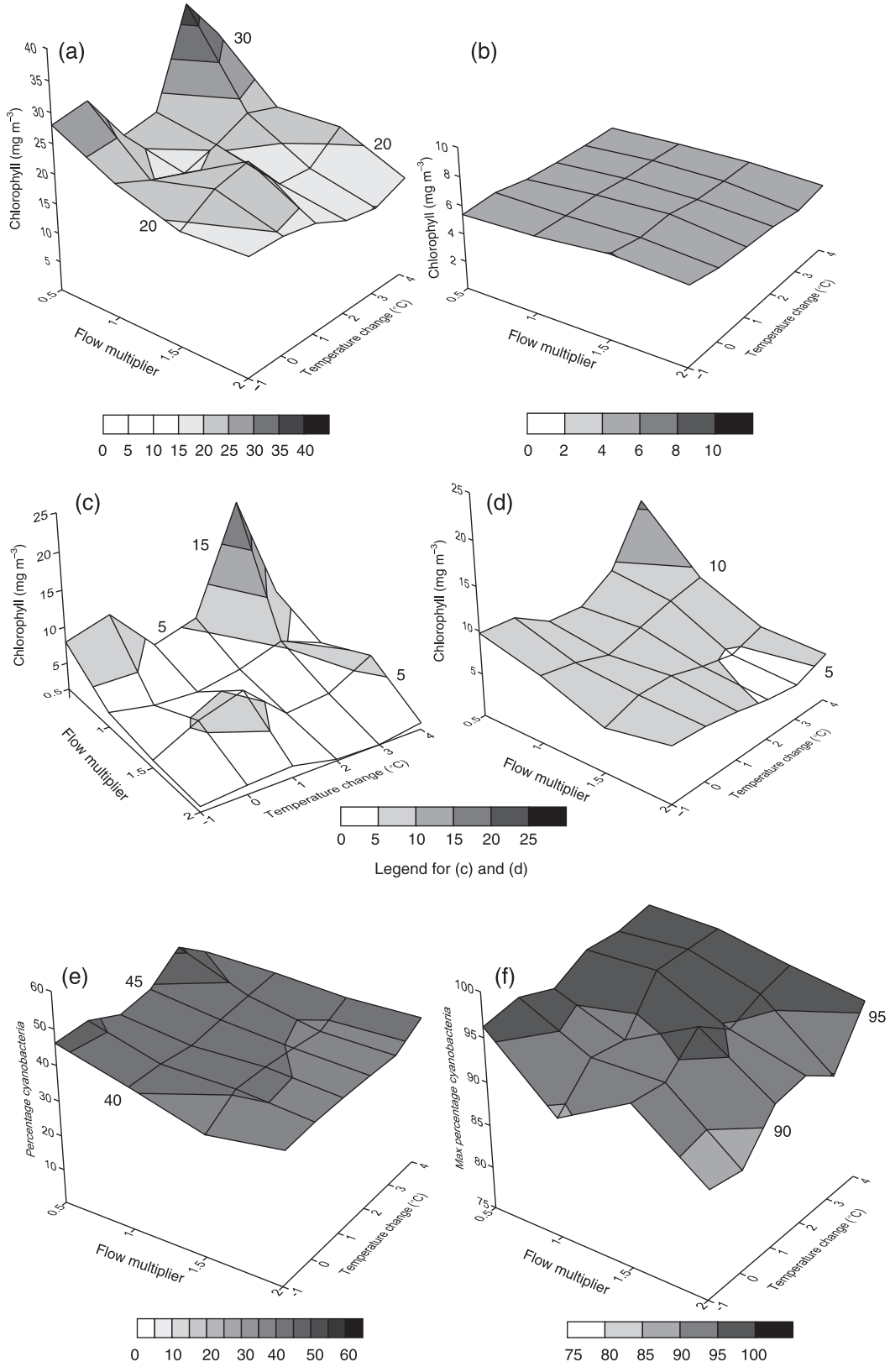

Fig. 2 Response of annual mean chlorophyll *a* concentration (mg m^{-3}), percentage Cyanobacteria abundance (%Cb) and maximum percentage Cyanobacteria abundance (Max %Cb) to changing water temperature (°C) and flushing rate: (a) total chlorophyll *a*, (b) *Asterionella*, (c) *Aphanizomenon*, (d) *Anabaena*, (e) %Cb, (f) Max %Cb.

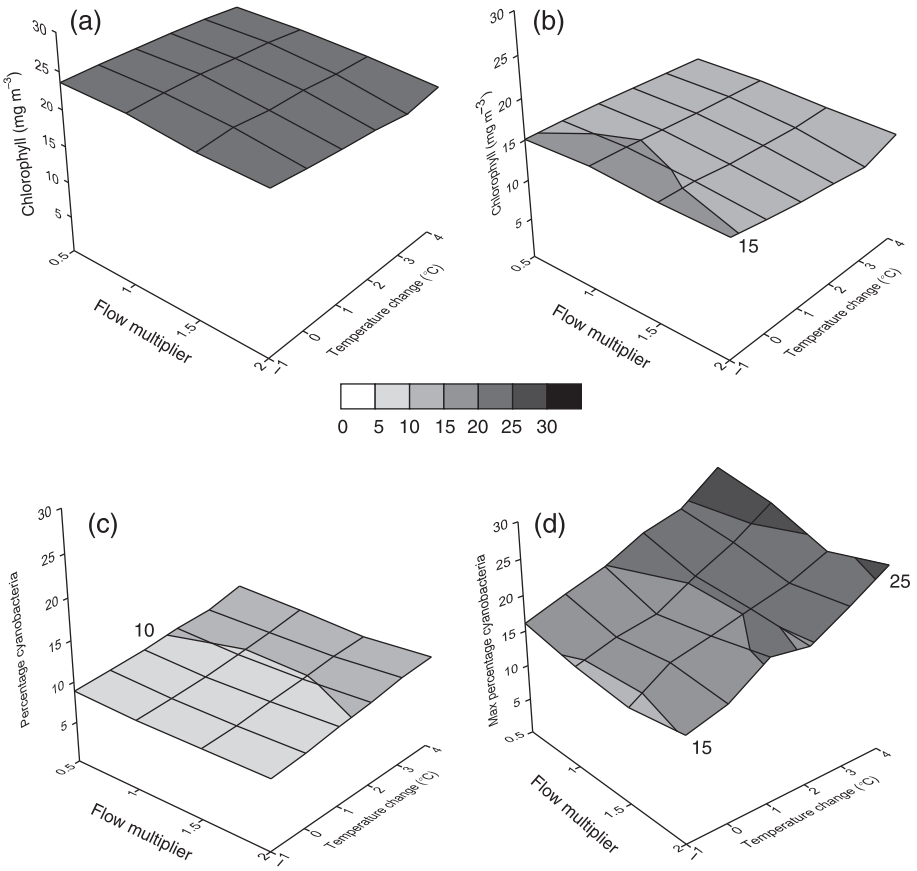

Fig. 3 Response of spring mean chlorophyll *a* concentration (mg m^{-3}), percentage Cyanobacteria abundance (%Cb) and maximum percentage Cyanobacteria abundance (Max %Cb) to changing water temperature (°C) and flushing rate: (a) total chlorophyll *a*, (b) *Asterionella*, (c) %Cb, (d) Max %Cb.

this trend was also induced with low flows and low temperatures. The dominant phytoplankton behind this summer biomass were *Aphanizomenon* (Fig. 4b) and *Anabaena* (Fig. 4c); under most scenario conditions, the mean biomass of the latter Cyanobacteria was slightly higher than that for *Aphanizomenon*. However, for some of the low flow scenarios, this dominance by *Anabaena* was broken by *Aphanizomenon*. The combined dominance by these two phytoplanktons was reflected in the %Cb (Fig. 4d) and Max %Cb (Fig. 4e) values, with both measurements demonstrating again the tendency for higher values with increasing temperature and decreasing flow.

Changes in autumn means

Total chlorophyll in the autumn period proved to be less responsive to the changing physical drivers (Fig. 5a), with the exception of one scenario at $+3\,^{\circ}$C with lowest flow. As in the summer, the main contributors to the overall biomass were *Aphanizomenon* (Fig. 5b) and *Anabaena* (Fig. 5c). Both Cyanobacteria means showed little response except for *Aphanizomenon* in the previously noted scenario. The mean %Cb again showed the tendency for higher values under low flow and higher temperatures (Fig. 5d) but the mean Max %Cb response, while hinting at this trend, was far less smooth and inconsistent for the higher flow/lower temperature scenarios (Fig. 5e).

Days exceeding WHO Cyanobacteria thresholds

Examining first the number of days where Cyanobacteria biomass was $>10\,\mathrm{mg\,m^{-3}}$, it is clear than low flows enhanced the frequency of this occurring more so than changing temperature (Fig. 6a). In fact, increasing temperature generally reduced the number of days when this threshold was passed, particularly with the higher flow scenarios. However, the actual number of days was still large, ranging from between just over 100 to over 150 days.

The higher WHO threshold tested ($>50\,\mathrm{mg\,m^{-3}}$) was exceeded less frequently, ranging from 0 to just under 80 days (Fig. 6b). The three-dimensional response surface for this metric was similar in pattern to that for *Aphanizomenon* in the summer (Fig. 4b) and autumn

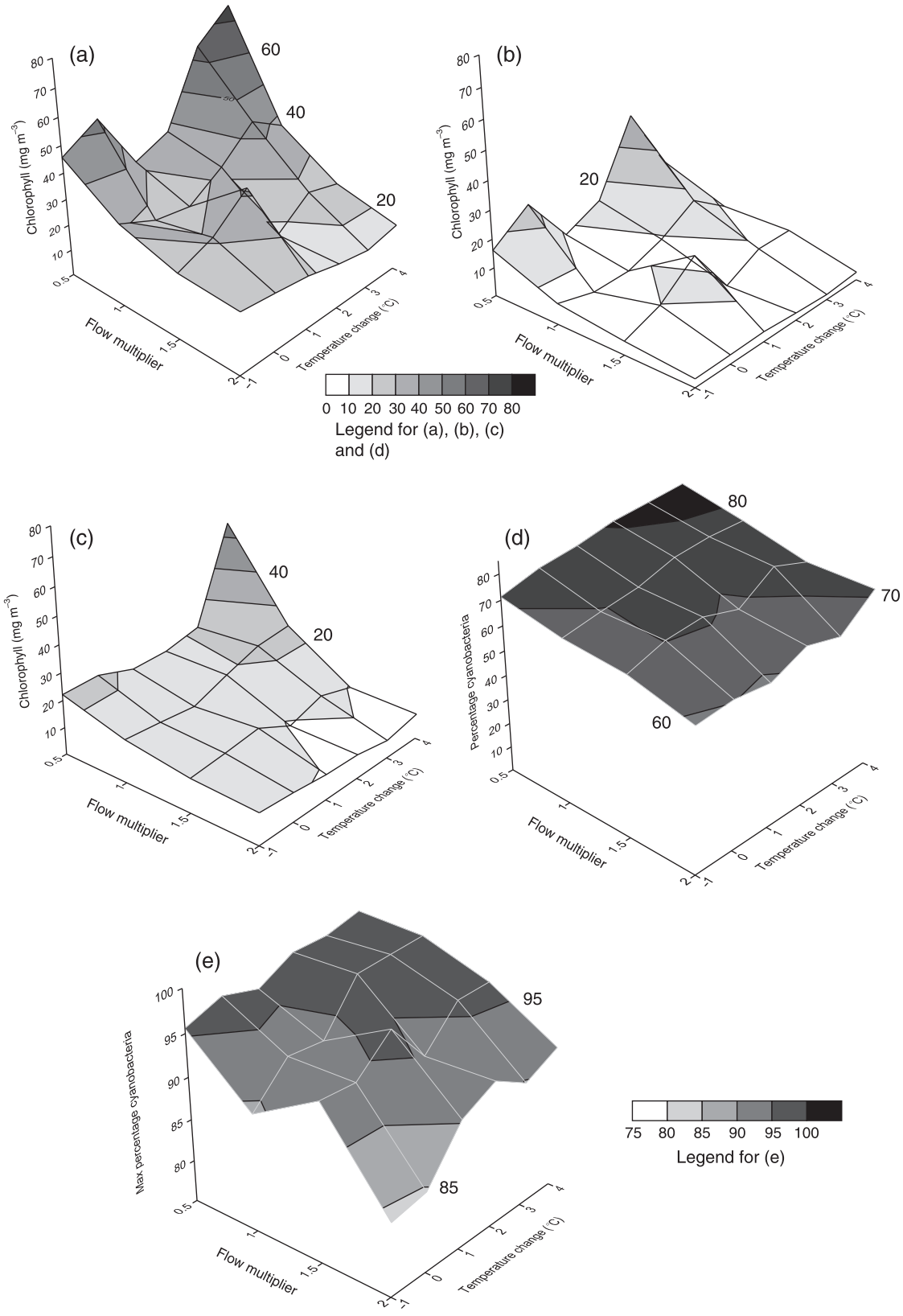

Fig. 4 Response of summer mean chlorophyll *a* concentration (mg m^{-3}), percentage Cyanobacteria abundance (%Cb) and maximum percentage Cyanobacteria abundance (Max %Cb) to changing water temperature (°C) and flushing rate: (a) total chlorophyll *a*, (b) *Aphanizomenon*, (c) *Anabaena*, (d) %Cb, (e) Max %Cb.

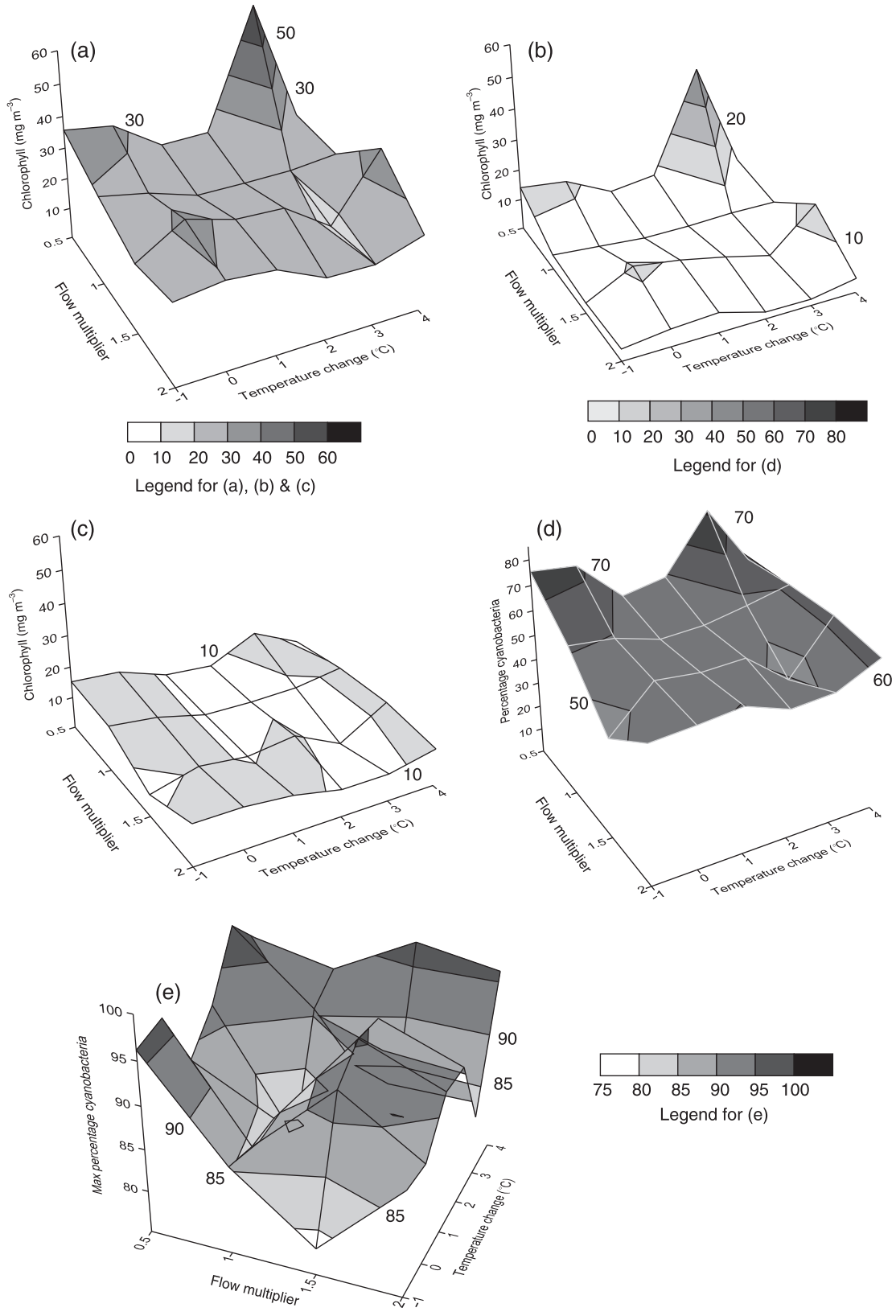

Fig. 5 Response of autumn mean chlorophyll *a* concentration (mg m^{-3}), percentage Cyanobacteria abundance (%Cb) and maximum percentage Cyanobacteria abundance (Max %Cb) to changing water temperature (°C) and flushing rate: (a) total chlorophyll *a*, (b) *Aphanizomenon*, (c) *Anabaena*, (d) %Cb, (e) Max %Cb.

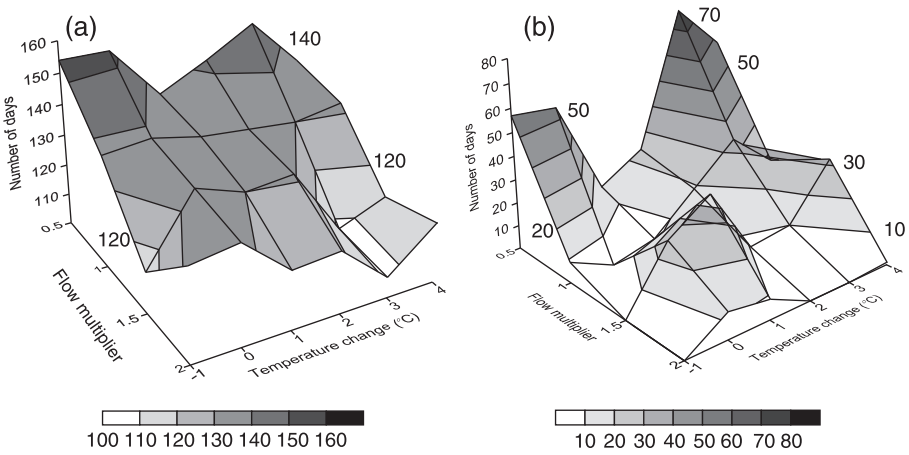

Fig. 6 Response of the number of days above the World Health Organization (WHO) Cyanobacteria concentration thresholds (chlorophyll *a*, mg m^{-3}) to changing water temperature (°C) and flushing rate: (a) >10 mg m^{-3}, (b) >50 mg m^{-3}.

(Fig. 5b), confirming that it was this simulated phytoplankton that was mainly responsibly for these larger Cyanobacteria blooms. Thus the pattern showed a tendency for increased frequency in days exceeding the threshold with increasing temperature and low flow, although this pattern was could be quite variable.

Discussion

Cyanobacteria seem to dominate most eutrophic temperate lake ecosystems in the summer/autumn (Watson *et al*., 1997) and the lake modelled in this study is no exception. However, while the mechanisms behind such dominance have sparked much debate, it has been observed that Cyanobacteria tend to be favoured by warm, stable water columns that experience low flushing rates (Scheffer 1998; Reynolds, 2006), which in temperate lakes often equates to summer conditions (Blenckner *et al*., 2007).

It was under these conditions that the PROTECH model simulated the relative dominance of two Cyanobacteria, *Aphanizomenon* and *Anabaena*, which matched the observed data for 2003. What is interesting to consider about this result is that the model makes no differentiation in the general growth equations used in PROTECH for Cyanobacteria (or any other taxa); all growth is determined by the defined morphological variables (Table 1). As has been observed in real phytoplankton populations (Reynolds, 1989; Kalff, 2002), large volume phytoplankton grow relatively slower, although, significantly, this relative difference diminishes with increasing temperature. This is also the case with the PROTECH growth equations, so that when this factor is coupled with the ability to ignore nitrogen limitation and grazing (Table 1), plus the very important abilities to regulate water column position (Table 2), these factors all help considerably to enhance the performance of Cyanobacteria in PROTECH simulations. Nevertheless, this does not mean that all Cyanobacteria always perform well and it is important to note that not all of the Cyanobacteria included in this study produced large blooms. *Aphanothece* was given a large volume (representing the whole colony unit) and has no nitrogen fixing ability, features with prevented its dominance in this study. Despite this, it can be seen how the above factors would favour some PROTECH Cyanobacteria phytoplankton in the simulated conditions of a warm (thus enhancing growth rates), stable (allowing movement characteristics to be expressed) water column that is not highly flushed (so that loss rates do not exceed growth rates). Therefore, given the PROTECH model's process-based ability to respond to these factors in what can be deemed a realistic way, the response of the phytoplankton community in this modelling study indicated some significant effects caused by changing water temperature and flushing rate.

Before considering the effects on the Cyanobacteria, it is worth briefly discussing the response of the other important phytoplankton in this study, in particular the diatom *Asterionella*. This diatom's vernal bloom was the most significant in terms of its biomass during this period, yet showed little response to the changes in temperature and flow (Fig. 3b). The reason behind such a small reaction was that the main aspect limiting growth was not related to either of these factors. Phytoplankton growth in model during this earlier part of the year was limited mainly by light, both through low insolation levels and deeper mixing. In such conditions, the defined PROTECH morphology of *Asterionella* gives it the best growth performance out of the eight phytoplankton simulated and allowed it to bloom and dominate in the

spring. Thus, a change in water temperature or flow could do little to increase the predominantly light-limited biomass produced, nor select for a different phytoplankton to dominate. However, as the year progressed, insolation levels increased and, coupled with the onset of stratification, this situation changed markedly to the increasing advantage of two Cyanobacteria.

On the whole, the annual, summer and autumn results showed the general trend of increasing Cyanobacteria abundance and proportional dominance of the phytoplankton community with increasing temperature and decreasing flow. These predictions are in keeping with the perceived view on factors favourable to Cyanobacteria (Reynolds, 2006; Paerl & Huisman, 2008). Interestingly, in two relevant previous studies predicting temperature effects on Cyanobacteria abundance, the PROTECH model produced contrasting responses. In the Bassenthwaite Lake study (Elliott *et al*., 2006), a marked increase in Cyanobacteria occurred with an increase in temperature, in concurrence with the findings presented here. However, in a study on Loch Leven (Elliott & May, 2008), increasing temperature had little effect on Cyanobacteria composition relative to that caused by changing the phosphorous and nitrogen nutrient supply. These latter aspects exerted the greater control on the lake phytoplankton populations in that study.

While the overall Cyanobacteria pattern appeared uniform in response, there was a great deal of variation from the Cyanobacteria that contributed to it. *Aphanizomenon* and *Anabaena* sometimes codominated and other times one prevailed over the other. While replicating the overall Cyanobacteria trends, their individual mean chlorophyll response surfaces created by the varying scenarios did produce occasional spikes in response to certain combinations. The driver behind such spikes was nutrient supply, which was why they occurred more frequently with the low flow scenarios. Under such conditions in the summer, nutrient recharge of phosphorus and nitrogen from the inflow was very low, considering the growth potential of the system at such a time of year, thus internal phosphorus supply became a more important source. Furthermore, while this internal release went some way towards supplying the phytoplankton's phosphorus demands, nitrogen levels were not as easily replenished, affirming the adaptive advantage of the nitrogen-fixing phytoplankton (i.e. *Aphanizomenon* and *Anabaena*). This factor, in addition to them both having identical movement characteristics in PROTECH, left the two phytoplankton in close competition in the simulations. Thus, the dominance of one over the other to form a large bloom was left to other interactive factors such as light limitation through self-shading, a factor that proven to be important, if difficult to predict, in previous PROTECH studies (Elliott *et al*., 2001).

Finally, the WHO guideline thresholds provided a measure of the total number of days where water quality could be threatened by Cyanobacteria growth. For the lower threshold, an increase in number of days occurred with low flows, aping the patterns seen in the %Cb and Max %Cb, however, this was not the case with increasing temperature and higher flows (Fig. 6a). This meant that, despite %Cb and Max %Cb generally increasing with temperature regardless of flow (e.g. Fig. 2), the number of days above this threshold declined, indicating a fall in overall biomass production under these conditions. This occurred because the blooms were less prolonged and collapsed due to nutrient limitation caused by the general increase in community growth rate due to increased temperature and the increased pressure from flushing losses. Despite this, the Cyanobacteria blooms were still dominant, if of reduced duration, under these conditions. This was clear from the higher threshold data, which showed an increased number of days above this threshold with higher temperatures.

In summary, the study has clearly shown that low flows and high temperatures favour the dominance and bloom formation of Cyanobacteria. Across the range of factors tested, both stressors seem to equally promote Cyanobacteria dominance. Furthermore, given that the summer and autumn period proved to be the most sensitive to these factors, the results also demonstrate that droughts in these seasons will be more important in the future than in the winter and spring. This is important result because current predictions for the northwest England are for decreasing river flow in the summer (Fowler & Kilsby, 2007) and, in addition, by using statistical trend analysis of the past climate it was predicted specifically for Esthwaite Water that summer surface temperatures could increase by over 2 °C by the 2050s (George *et al*., 2007). However, it should be noted that internal release of phosphorus in this eutrophic lake was an important influence by providing nutrients for the growth demand that could not have been met under the low flow conditions, e.g. with half flow rate in the summer, retention time increased to nearly 2 years greatly slowing down the recharge of in-lake nutrients via catchment input. Combined with the importance of nitrogen in triggering dominance by the nitrogen fixing phytoplankton in this study, it can be seen the nutrients are still very important in shaping the carrying capacity of the phytoplankton and their responses, within this envelope, to these climate related drivers. Thus, it is possible that making general predictions about Cyanobacteria populations in lakes and reservoirs over a wide area (e.g. a country, region or continent) will remain challenging given the large influence nonclimatic *local* factors can have upon these important phytoplankton.

However, further studies utilizing data from other lakes and years are warranted to test this view.

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