



Article (refereed) - postprint

Elliott, J. Alex. 2012 Predicting the impact of changing nutrient load and temperature on the phytoplankton of England's largest lake, Windermere. *Freshwater Biology*, 57 (2). 400-413. 10.1111/j.1365-2427.2011.02717.x

**Predicting the impact of changing nutrient load and temperature on the phytoplankton of England's largest lake, Windermere.**

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Keywords: phytoplankton, climate change, blue-green algae, PROTECH, phenology, eutrophication

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Running head: Phytoplankton response to changing nutrients and temperature

**SUMMARY**

1. Climate change and eutrophication will be two of the largest threats to lake ecosystems this century. Therefore, the effect of changing water temperature (+0 to +4$^{o}$C) and nutrient load (0.5-2.0 proportional change) on the phytoplankton of Windermere was assessed using the phytoplankton community model, PROTECH.
2. The following metrics were used for the analysis: annual, spring, summer and autumn mean chlorophyll *a* concentrations for total phytoplankton, diatoms and Cyanobacteria. Also, the timing of the spring diatom bloom was assessed and the number of days when the World Health Organisation (WHO)-derived risk threshold of 10 mg m$^{-3}$ Cyanobacteria chlorophyll *a* was exceeded.
3. The diatoms in Windermere produced their largest amount of chlorophyll *a* in the spring. Whilst the quantity of diatom biomass produced was relatively unaffected by the simulated changes in temperature and nutrient load, the timing of the bloom peak was 2-3 days earlier per 1 $^{o}$C.
4. The modelled Cyanobacteria dominated in the summer and autumn, and generally responded positively to both increasing nutrients and temperature illustrating a synergistic relationship between these two drivers. However, in the autumn this relationship was sometimes disrupted due to variations in the length of stratification.
5. Temperature as a factor alone seemed to act in two ways: it affected phenology (e.g. bloom peak timing) mainly in the early part of the growing season and enhanced the dominance of Cyanobacteria in the late growing season. Furthermore, these effects were greatly reduced under the lower nutrient scenarios, suggesting that local management of nutrient inputs to the lake potentially offers a solution to the effects caused by the increase in temperature.

## Introduction

Windermere is England's largest lake and probably its most well known (Pickering, 2001). It has acted as a cultural focal point for hundreds of years and still provides a key draw for tourism in the region. The lake consists of two separate basins, the North Basin and the South Basin separated by a relatively shallow region in the centre of the lake populated by several islands (Pickering, 2001). This region restricts movement of water from the North Basin to the South Basin sufficiently to allow marked differences between the two basins in, for example, their water chemistry, fish populations and water quality (Pickering, 2001).

Like many lakes in Europe, Windermere has experienced over many decades the impact of human populations within its catchment with the most negative influence upon the lake being eutrophication. This process began to worsen from around 1850 (with the connection of Windermere Town to the UK railway system) to the 1970s and 1980s when the lake suffered from severe eutrophication (McGowan *et al.*, 2012). Interestingly, the two basins responded differently to this pressure with the North Basin less affected, reflecting its catchment's nutrient-poor land and smaller seasonal (tourist) population compared to the South Basin (Reynolds & Irish, 2000). The main nutrient causing the eutrophication of the lake, both historically and currently, has been phosphorus rather than nitrogen. In 1992, a phosphate stripping (tertiary) treatment upgrade was introduced to the Ambleside wastewater treatment works (WwTw) that discharges into the North Basin and to the Tower Wood wastewater treatment works, which is the main works for Windermere Town and discharges into the South Basin (Reynolds & Irish, 2000). This change immediately reduced the concentration of phosphorus and phytoplankton chlorophyll *a*, especially in the more heavily impacted South Basin, although there has subsequently been a slight deterioration in water quality.

However, in recent decades new pressures caused by climate change have begun to influence the lake and there is increasing evidence that Windermere has been affected (e.g. spring diatom phenology, Thackeray, Jones & Maberly, 2008). It is clear from numerous studies that climate change has affected many lakes (e.g. Winder & Schindler, 2004; Thackeray *et al*., 2008; Adrian *et al*., 2009; Tadonléké, 2010). For lake plankton, this effect is often expressed by changes in phenology and/or abundance of certain phytoplankton types (e.g. Winder & Schindler, 2004; Huber, Adrian & Gerten, 2008; Jöhnk *et al*., 2008; Thackeray *et al.*, 2008). With such changes already observed, there is natural concern about how lake ecosystems in the future could be affected given the predicted changes in climate. However, making predictions about such future impacts that are more than just qualitative guesswork is challenging and usually requires some form of numerical computer model.

PROTECH (**P**hytoplankton **R**esp**O**nses **T**o **E**nvironmental **CH**ange; Reynolds, Irish & Elliott, 2001; Elliott, Irish & Reynolds, 2010) is just such a model, providing process-based numerical simulations of lake phytoplankton communities. It has been applied in numerous studies to nearly a dozen lake systems of varying nutrient status and size (see review in Elliott *et al*., 2010). Some of these studies have considered the future impact of just climate change (Elliott *et al*., 2005; Elliott, 2010) or in combination with changing nutrient loads (Elliott, Jones & Thackeray, 2006; Elliott & May, 2008). However, PROTECH has not been tested on a lake as large as Windermere before, providing a new challenge for the model and a test of whether the results found in these earlier studies will be reflected in a much larger and, of course, deeper lake.

Therefore, this study seeks to test the sensitivity of the phytoplankton community of Windermere to changing nutrient (phosphorus) loads and water temperature using the PROTECH model. Of particular interest are the changes in the spring bloom diatom timing and the changing abundance of Cyanobacteria in the second half of the year. This latter

factor is assessed both as a percentage abundance of the community and as the number of days where their biomass (i.e. chlorophyll *a*) exceeds World Health Organisation (WHO) guideline thresholds (Chorus & Bartram, 1999).

## Methods

*Site description*

Windermere is situated in North-West England (54° 20' N, 2° 58' W) and consists of two basins connected at a shallow region roughly halfway along its main axis. In studying the lake, these two basins are usually considered separately because they have different characteristics: the North Basin is larger (surface area 8.04 $km^2$, maximum depth 64 m, mean depth 25.1 m, 7 km long, catchment area 187 $km^2$) than the South Basin (surface area 6.72 $km^2$, maximum depth 42 m, mean depth 16.8 m, 9.8 km long, catchment area (excluding North Basin area) 63 $km^2$)(Ramsbottom, 1976). In recent decades, the North Basin has been classed as mesotrophic (Pickering, 2001), having similar concentrations of nitrate to the South Basin but nearly a fifth of the soluble reactive phosphorus (SRP)(Reynolds & Irish, 2000). In contrast, the South Basin was considered eutrophic but, since the improvements made in the 1990s to the sewage treatment works, it is now classed as mesotrophic following roughly a 50% reduction in SRP concentrations (Reynolds & Irish, 2000). The lake as a whole has an annual hydrological residence time of 263 days (Reynolds & Irish, 2000).

*Data*

All driving and validation data were taken from 1998, providing a comprehensive collection of the most important variables. Fortnightly nutrient (SRP, nitrate and silica) concentrations and daily discharges were available for the main rivers and sewage treatment works discharging into the lake and were used to provide daily input values by linear interpolation. The daily measurements of Windermere's outflow discharge (River Leven) were used to create the inflow discharges for the other rivers with no observed discharge data by making the simple assumption that each river's contribution to the total outflow discharge was

proportional to that river's catchment area within the whole lake catchment and that the lake level did not change. For the two sewage treatment works, associated dissolved inorganic nitrogen (DIN) was estimated by multiplying the SRP loads of each treatment work by 13.87 for Ambleside works (North Basin) and 14.95 for Tower Woods works (South Basin)(Maberly, 2009). No Silica load was added from the treatment works. The hydrological exchange from the North Basin to the South was calculated to be 0.8 of the River Leven discharge from the South Basin, based on the portion of the catchment that drained into the North Basin alone.

Daily meteorological data were drawn from two sources: wind speed and air temperature were measured at a shore meteorological station mid-way along the lake, whilst cloud cover (oktas) estimates were from a meteorological station situated on the north shore, near Ambleside.

For model validation, fortnightly in-lake chlorophyll *a* concentrations and phytoplankton count data (integrated over the top 7 m) were available. To make the latter data comparable with the individual chlorophyll *a* values produced for each of the taxa simulated in the model, the count measurements were converted. This was done by estimating, for each sample date, what proportion of the total cell count was made up of diatoms and Cyanobacteria and multiplying the total chlorophyll *a* observed for that day by the respective proportion. Whilst this is a somewhat crude method, it does provide a rough estimate of the relative importance of these two dominant taxa on any given sample day for comparison with PROTECH's output.

*PROTECH model description*

Reynolds *et al.* (2001) and Elliott *et al*. (2010) gave a detailed description of all the model's

equations and concepts but the biological component can be summarised by the following simple equation. It determines the daily change in the chlorophyll *a* concentration ($\Delta X/\Delta t$, mg $m^{-3}$ $d^{-1}$) attributable to each phytoplankton taxon:

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

where $r'$ is the growth rate defined as a proportional increase over 24 hours, $S$ is the loss due to settling out of the water column, $G$ is the loss due to *Daphnia* grazing (phytoplankton > 50 μm are not grazed; Burns, 1969) and $D$ is the loss due to dilution. The growth rate ($r'$, $d^{-1}$) is further defined by:

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

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, 80 and 500 mg $m^{-3}$, respectively (Reynolds, 2006). The $r'$ values are phytoplankton-dependent (e.g. non-diatoms 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 because they depend on temperature, available light and nutrients. Therefore, for each alga within the model, the starting value of $X$ mg chlorophyll *a* $m^{-3}$ $d^{-1}$ (Eq. 1) is modified on a daily time-step to predict change in the chlorophyll *a* concentration for each alga in each layer in the water column. The "base growth rate" is the cell-replication rate ($d^{-1}$) in continuous culture at 20 $^{o}$C, when all requirements for growth are saturating. According to Reynolds (1989), the values are well-predicted by:

$$r'_{20} = 1.142(s/v)^{0.325} \qquad (3)$$

where $s$ is the surface area (in $\mu m^2$) and $v$ is the volume ($\mu m^3$) of the appropriate phytoplankton unit i.e. a single cell or colony, where appropriate, including any mucilage.

This base growth rate ($d^{-1}$) is adjusted with respect to water temperature ($\theta$, °C), normalised on an Arrhenius scale. Using data from Dauta (1982), Reynolds (1989) found that the rate of growth at a particular temperature ($r_\theta$) is:

$$\log r'_\theta = \log r'_{20} + b[1000/(273+20) - 1000/(273 + \theta)] \quad (4)$$

where:

$$b = 3.378 - 2.505 \log(s/v) \quad (5)$$

A simple photoperiod adjustment is then applied, recognising the alternation of day to night to produce a growth rate in by light and temperature ($r_{(\theta, I)}$):

$$r'_{(\theta, I)} = r'_\theta (t_p/24) \quad (6)$$

where $t_p$ (measured in h) is the number of daylight hours from sunrise to sunset.

If mixing of a water column occurs beyond the photic layer then this further shortens the aggregate photoperiod. This effect on growth rate is given by the following equation:

$$r'_{(\theta, I)} = r'_\theta (Sp/24) \quad (7)$$

where Sp (measured in h) is the daily sum of photoperiods, calculated as:

$$Sp = t_p (h_p/h_m) \quad (8)$$

where $h_p$ is the light-compensated depth and $h_m$ the mixed-layer depth. As it is assumed that the growth rate is always net of respirational losses, the shorter is $t_p$, the greater is the error through dark respiration. To allow for this, both estimates of daily $r$' are corrected by the following equation:

$$r'_{cor(\theta, I)} = 1.055 r'_{(\theta, I)} - 0.055\, r'_{\theta} \quad (9)$$

For each species in turn, $h_p$ (m) is calculated because light compensation is defined by the adaptive photosynthetic characteristics of the phytoplankton and not an arbitrary light level. According to Reynolds (1989),

$$h_p = \ln(I_0'/0.5I_k)\varepsilon^{-1} \quad (10)$$

where $I_0'$ is the mean photosynthetically active irradiance penetrating the water surface, and $\varepsilon$ is the coefficient of its vertical attenuation ($m^{-1}$). $I_k$ (mol photon $m^{-2}$ $s^{-1}$) is defined from the slope of the light-limited growth rate, $a_r$:

$$I_k = r'_{\theta}/a_r \quad (11)$$

$a_r$ is the third of the species-specific terms predicted by regression (Reynolds, 1989):

$$a_r = 0.257\ (ms/v)^{0.236} \quad (12)$$

where $m$ (μm) is the longest axis of the phytoplankton unit.

Thus, when $h_m > h_p$, the full algorithm runs:

$$r'_{cor(\theta, I)} = [r'_{\theta} t_p /24h_m].[\ln\{2I_0'.0.257(ms/v)^{0.236}/(r'_{\theta}.\varepsilon)\}] \quad (13)$$

Otherwise, when $h_m < h_p$,

$$r'_{cor(\theta, I)} = r'_{\theta}(t_p /24) \quad (14)$$

Naturally, any growth leads to nutrient consumption, therefore the nutrient concentrations in the water column are modified to reflect uptake as well as through the daily supply and loss via inflow/outflow exchange. Thus, the simple assumption is made 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 (only if not a nitrogen-fixer): 1.2 g phosphorus : 1 g chlorophyll *a* (Stumm & Morgan, 1981).

An additional, and very important (Elliott *et al*., 2010), phytoplankton-specific movement function is also applied daily 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 (movement up the water column, dependent upon light intensity/nutrient availability).

An initial profile for the water column (containing temperature, nutrient concentrations, and inoculum sizes for the selected phytoplankton) is defined using the closest observed data for day 1 (i.e. 1st January in this investigation). Daily wind speed, cloud cover, river inflow (including nutrient concentrations) and outflow data are input to the model and daily insolation is adjusted to reflect the time of the year, latitude and cloud cover. For each 24 hour time-step, the physical structure of the water column is defined over vertical, 0.1 m slices that relate to the bathymetry of the lake. 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. To test the resistance to mixing of an existing density structure, the Wedderburn-number is calculated, which incorporates a term for the accumulated density difference between the water at the surface and at any chosen depth. With each daily iteration, the model works down the water column incorporating each slice until the accumulated density difference resists the incorporation, thus defining that day's upper mixed layer.

*Phytoplankton simulations*

PROTECH was applied to each of the two basins of Windermere separately. The eight phytoplankton types selected were the eight most dominant species recorded in the phytoplankton count data for both basins in 1998. These were *Asterionella*, *Aulacoseira*, *Monoraphidium*, *Cryptomonas, Paulschulzia*, *Aphanizomenon*, *Anabaena* and *Planktothrix* (Tables 1 and 2), and the same eight were used for both basins. Furthermore, these selected phytoplankton reflect the types of species typically found in Windermere over the last 65 years (Reynolds & Irish, 2000), allowing the model, potentially, to simulate any changes in relative community abundance caused by the test scenarios.

The model simulations for the two basins were compared both visually and using regression analysis to the observed 1998 total chlorophyll *a* data and the calculated proportions of diatom and Cyanobacteria chlorophyll derived from the phytoplankton count data, which in this year, and historically, are the dominant taxonomic groups in Windermere (Reynolds & Irish, 2000). These simulations were then used as a baseline for further testing by repeating the simulations but altering the air temperature and nutrient load to the lake. This was done by raising the air temperature by 0 $^{o}$C to 4 $^{o}$C in 1 $^{o}$C increments and by multiplying the SRP inflow concentrations by a factor of 0.5 to 2 in 0.5 increments. The latter loads are realistic and have been experienced by Windermere over the last 100 years e.g. the 2 factor scenario is similar to the levels seen in the 1980s before the upgrades to the two treatment works (Reynolds & Irish, 2000). This produced 20 simulations per basin that covered a realistic range of predicted temperature increases for the northwest of England in the 21$^{st}$ century (Elliott *et al*., 2005; Fower & Kilsby, 2007) and nutrient loads to the lake.

The data produced by each of these simulations were summarised by calculating annual, spring (March-May), summer (June-August) and autumn (September-November)

means for surface water temperature (top 7 m), stratification (mixed depth ≤ 7 m), SRP in-lake concentration and diatom, Cyanobacteria and total chlorophyll *a*. Furthermore, the timings of the diatom spring blooms were calculated using their respective central tendency (*T*) statistics (Edwards & Richardson 2004). This gives an indication calculated thus:

$$T = \frac{\sum_{i=1}^{182} Dx_d}{\sum_{i=1}^{182} x_d} \quad (15)$$

where $x_d$ is the mean daily chlorophyll *a* for a given species or taxa on the day of the year, *D* (1 Jan = 1.…1 July = 182 etc.). To calculate the spring bloom, only data from the first half of the year were used. Finally, in order to assess the water quality of the lake in relation to Cyanobacterial abundance, the WHO guidelines for Cyanobacteria blooms (Chorus & Bartram, 1999) were used to calculate the number of days when the Cyanobacteria chlorophyll *a* was greater than > 10 mg $m^{-3}$, i.e. water quality had deteriorated.

## Results

*Comparison with observed data*

The simulated total chlorophyll *a* followed the pattern of bloom development in both basins well (Fig. 1a, b) and produced reasonable fits to the observed values (North Basin $R^2 = 0.64$, $P < 0.01$; South Basin $R^2 = 0.68$, $P < 0.01$). Comparison with the diatom chlorophyll *a* estimated from the phytoplankton counts also closely matched the annual pattern, particularly the spring bloom, and matched the timing of the spring peak for both basins (Fig. 1c, d). The overall fit was poorer for the North Basin diatoms ($R^2 = 0.58$, $P < 0.01$) than the South Basin diatoms ($R^2 = 0.88$, $P < 0.01$), but this was mainly due to the mismatch in the timing of the second bloom later in the year (for the first half the year $R^2 = 0.95$, $P < 0.01$). Finally, the simulated Cyanobacteria chlorophyll *a* compared well to the observed patterns (Fig. 1e, f) although the match was better for the North Basin ($R^2 = 0.82$, $P < 0.01$) than the South Basin ($R^2 = 0.55$, $P < 0.01$).

*Changes in lake temperature and structure*

Each increased temperature scenario increased the surface water temperature (Table 3) and the South Basin was always warmer than the North. However, the mean increase in the water temperature was always less than 1 $^{o}$C per 1 $^{o}$C rise in air temperature. Furthermore, for both basins the mean increase in water temperature was similar regardless of season.

In addition to temperature change, the measure of stratification used in this study showed that more periods of shallow mixing ($\leq$ 7 m) occurred in the North Basin than the South (Table 3) and that increasing air temperature generally enhanced this shallow mixing,

although there seems to be a step change above +2 $^{o}$C increase, particularly in the South Basin. Seasonally, the difference seen between the two basins was maintained, with the North Basin having more days of shallower mixing than the South. However, this difference was particularly large for the autumn means, where the number of days in the South was roughly a quarter of those measured in the North Basin, regardless of temperature scenario.

*Changes in annual means*

The annual mean total chlorophyll *a* of both basins responded in similar fashion to the change in nutrient (SRP) loads and temperature (Fig. 2a, b), with the former factor having more than twice the effect; each 50% increase in nutrient load induced an increase in annual mean total chlorophyll *a* of 1-2 mg m$^{-3}$. However, this change was not due to the diatom component of the simulations, which showed little response to either factor (Fig. 2c, d), but rather to Cyanobacteria (Fig. 2e, f). This taxonomic group increased its mean chlorophyll *a* with increasing nutrient load but there was also evidence of a slight increase caused by rising temperature which was more pronounced under the more nutrient-rich scenarios.

*Changes in in-lake SRP concentrations*

In-lake SRP concentrations varied throughout the year, reflecting supply and utilisation of the nutrient (Fig. 3). Unsurprisingly, for all the seasons measured, SRP increased with each scenario of SRP load increase. There were marked distinctions, however, between the two basins because, while the summer period concentrations were similar (and low, SRP < 3 mg m$^{-3}$, Fig. 3c, d), the spring and autumn mean concentrations were quite different. In the spring, the North Basin had less SRP than the South, although both basins showed a decline

with increasing temperature (Fig. 3a, b). Similarly, the autumn mean SRP concentration in the North Basin was lower than in the South Basin (Fig. 3e, f) and < 3 mg $m^{-3}$ for nearly all the scenarios.

*Changes in spring means*

The response of the phytoplankton in the spring was different from that seen in the annual means in that both factors affected the chlorophyll *a* produced equally and created a relatively small effect. Each 50% nutrient load and 1 $^{o}$C increase generally produced a similar increase in mean spring total chlorophyll *a* (roughly 0.4 - 0.8 mg $m^{-3}$; Fig. 4a, b). This change was primarily driven by the spring diatom bloom, with the diatoms modelled producing a response surface similar to that of the spring mean total chlorophyll *a* (Fig. 4c, d).

*Changes in summer means*

The summer period was primarily dominated by Cyanobacteria, and nutrient load changes produced the largest alterations to mean chlorophyll *a* (Fig. 5), although the South Basin produced more chlorophyll. However, in both basins the increase in mean chlorophyll *a* with increasing nutrient load was generally greater as temperature increased e.g. at 0 $^{o}$C, the North Basin Cyanobacteria chlorophyll *a* increased by an average of 2.80 mg $m^{-3}$ per increase in the SRP load driver, whereas at 4 $^{o}$C the mean increase was 3.55 mg $m^{-3}$.

*Changes in autumn means*

The North Basin was the more productive during this period but both basins produced more complex response surfaces with changing temperature and nutrient load (Fig. 6). In the North Basin (Fig. 6a, c), Cyanobacteria made up most of the total chlorophyll *a*, and showed the same dome-shaped response to increasing temperature, except under the 50% lower nutrient load scenarios. In the South Basin, little changed except for the +2 $^{o}$C scenarios (Fig. 6b, d) where there was a slight dip in mean chlorophyll *a* concentration.

*Changes in the timing of spring diatom bloom*

With increasing temperature, the timing of the bloom peaks responded in the same way for both basins with the peak becoming, on average, 2-3 days earlier per 1 $^{o}$C increase (Fig. 7) although this rate of change decreased with each increase in temperature. However, a divergent response occurred in the two basins with changing nutrient load. In the North Basin, increasing nutrients caused the diatom peak to be delayed by, on average, 1-2 days per 50% change. Conversely, in the South Basin the same step increase in load caused the peak to become earlier by 1-2 days.

*Days exceeding the WHO Cyanobacteria threshold*

There was a marked contrast in the number of days that Cyanobacteria chlorophyll *a* exceeded the WHO 10 mg m$^{-3}$ threshold in the two basins (Fig. 8); in the North it was 35 days whilst in the South it was zero. Despite this, both basins responded relatively similarly to the changing drivers in the simulations. Both basins demonstrated an increase in number of days over the WHO threshold when nutrient load and temperature were also increased, although the former variable had the greater effect (c. 20-50 days more per 50% nutrient load

increase compared to c. 2-10 days per 1 $^{o}$C). It is also worth commenting that the South Basin Cyanobacteria populations in these simulations appear to be particularly sensitive to nutrient load increase, with a 50% increase in the original load (across all of the temperature scenarios) raising the number of days above the threshold from 0-8 days to 62-96 days (Fig. 8b).

## Discussion

Windermere has provided a key service in the English Lake District by acting as a focal point for culture and tourism since railway access opened in 1847 (Pickering, 2001). Given this role, and its status as England's largest natural lake, there is a considerable amount of trepidation from users and managers of the lake about how threats to Windermere, such as climate change and eutrophication, may impact upon the ecosystem. This study has attempted to address some of these concerns by producing quantitative predictions about the phytoplankton populations in the lake.

The PROTECH model proved capable of producing a realistic simulation of the phytoplankton types found in separate basins of Windermere (Fig. 1) and thus it was used to test the sensitivity of the simulated Windermere phytoplankton to changing air temperature and nutrient load. The former had a large impact on the thermal structure of the lake (Table 3) with the shallower South Basin becoming warmer but experiencing less periods of shallow mixing than the North Basin. The latter measure (mixed depth $\leq$ 7 m) was used as a proxy for stratification in this study rather than other measures of stratification because it focuses on periods that are specifically of interest for understanding the lake's phytoplankton dynamics i.e. periods of relatively shallow mixing can greatly influence the seasonal succession of phytoplankton (particularly Cyanobacteria) by affecting light and nutrient availability (Reynolds, 2006). Indeed, physical metrics used in this study reflected the size and depth differences between the two basins with, for example, the deeper, larger volume North Basin resisting warming and stratification breakdown better than the South Basin, particularly in the autumn (September to November; Table 1). Another consequence of this difference in physical response was also seen for the in-lake SRP concentrations (Fig. 3) where the prolonged autumn stratification in the North Basin caused much lower mean SRP values and

produced more phytoplankton biomass (Fig. 6) than in the South Basin where overturn led to nutrient refreshment of the surface waters through deep water upwelling but also a reduction in light availability (compare Fig. 3e and f). These physical and nutrient differences had consequences for the biological elements simulated in this study particularly for the two main phytoplankton types in this study (diatoms and Cyanobacteria) and thus each is considered in turn using all the appropriate metrics available in the study.

In the year simulated, diatom growth was mainly constrained to the early part of the year (spring) when light was limiting growth more than nutrients (Fig. 3) or temperature (Table 3). Thus, with the scenarios tested, diatom biomass (which chlorophyll *a* is a proxy for in PROTECH) varied little annually (Fig. 2c, d), although there was a slight change when only the spring period was examined (Fig. 4c, d) with increasing temperatures and nutrient load causing a small rise in mean biomass. However, such small changes in overall production did not mean that the diatoms were totally unaffected because the timing of the spring diatom bloom did change (Fig. 7). For both basins, this metric showed an advance in peak timing with increasing temperature (2-3 days earlier per 1 $^{o}$C), although the complementary effect caused by the nutrient load changes was smaller and could cause both advances and delays in the peak. Diatom blooms in Windermere have been seen to shift in this way before (Thackeray *et al*., 2008), as well in other lakes (e.g. Winder & Schindler, 2004; Huber *et al*., 2008; Meis, Thackeray & Jones, 2009), and in these studies the drivers have been primarily identified as increased temperature, nutrient enrichment and/or stratification change. Therefore, this modelling study agrees with these other investigations in identifying temperature increase as a driver of peak advancement. It is, however, worth noting that this rate of advancement decreased with each 1 $^{o}$C increase because other growth-limiting factors, such as light, often ultimately control growth in the spring (Sommer & Lengfellner, 2008).

With the exception of the spring period, however, the dominant phytoplankton types throughout the annual growing season were Cyanobacteria, although they were more predominant in the North Basin (Fig. 2). These phytoplankton demonstrated a generally positive response to both increasing nutrients and temperature during the summer period (Fig. 5), with each factor (i.e. temperature or nutrient load) generally enhancing the positive effect of the other factor. This was particularly clear when the number of days were considered where the WHO 10 mg $m^{-3}$ threshold was exceeded. Previous PROTECH studies (e.g. Elliott *et al*., 2006), as well as other investigations (e.g. Huber *et al*., 2008), have noted the importance of this interaction between higher temperatures and eutrophication. However, the effect of temperature was weaker than that caused by nutrient change, a fact particularly evident for the South Basin WHO threshold data (Fig. 8b) which for the "no change" in nutrient load scenarios (factor = 1) produced only an increase from zero days to 8 days above the threshold with even a 4 $^{o}$C increase in temperature. Therefore, this would suggest that, in terms of phytoplankton-related water quality, the nutrient load to a lake is still the most important factor, at least in the temperate climate regions.

Of course, there were some interesting exceptions to the general result of increased phytoplankton with increased temperature and nutrient load. For example, in the autumn, the importance of stratification was seen in the North Basin where the positive effect of temperature increases > 2 $^{o}$C on mean phytoplankton biomass was not seen. Whilst shallow mixing does provide benefits to phytoplankton by keeping them near the surface where light and warm water are available to support increased growth rates, prolonged periods can reduce replenishment of nutrients from deeper waters, and thus lead to reduced growth. This is what occurred here, despite Fig. 3e suggesting that the North Basin was always limited by phosphorous regardless of scenario; in this respect in-lake SRP concentrations are misleading because they only show what was left in the water *after* removal for phytoplankton growth,

which was still substantial in the North Basin even for the > 2 $^{o}$C scenarios (Fig. 6). Thus, because of long periods of shallow stratification in the +3 and +4 $^{o}$C scenarios (Table 3), the positive effects upon phytoplankton biomass production seen at other times of the year caused by the increase in water temperature were slightly reduced. However, whilst the size and depth of Windermere did sometimes play a role in its response to the modelled scenarios, the general response was similar to the other, shallower lakes previously tested by PROTECH in this way (e.g. Elliott *et al*., 2006; Elliott, 2010).

From the specific point of view of a user or manager of Windermere, these results suggest that, whilst a future warming of the lake could lead to a slight deterioration in water quality under the present nutrient load, the lake is far more sensitive to an increase in nutrient load. This is particularly evident in the South Basin which proved very sensitive to an increase in SRP load. However, the general message to the lake's managers is one of constantly trying to drive down nutrient pollution to Windermere because not only will this increase water quality but also mitigate, through local controls, the effects of global pressure of climate change-driven temperature increases.

Finally, there now seems to be a considerable body of evidence from numerous studies (Elliott *et al*., 2006; Staehr & Sand-Jensen, 2006; Huber *et al*., 2008; Elliott, 2010; Tadonléké, 2010), including this one, about the sensitivity of phytoplankton to increasing water temperature and the importance of lake nutrient status. Temperature as a factor alone seems to act in two ways: it affects phenology (e.g. bloom peak timing) mainly in the early part of the growing season and enhances the dominance of Cyanobacteria species in the late growing season. The effect on the amount of biomass produced is negligible because nutrients exert a greater control on this variable: water temperature has little ability to increase directly the carrying capacity of a lake (but see Markensten, Moore & Persson, 2010) for an example of an indirect impact on a higher latitude system). Therefore, whilst

temperature change can act by influencing temporal distribution of the annual phytoplankton as well as its composition, the expression of this influence depends greatly on the capacity of the lake ecosystem to produce phytoplankton biomass (e.g. its nutrient status). Thus, if we continue to try to improve the nutrient status of lakes around the world, we will also be able to mitigate many of the undesirable temperature-related effects caused by climate change on phytoplankton.

**Acknowledgments**

Thanks are extended to the British Atmospheric Data Centre and Mr B.C. Tebay for providing the meteorological data, and the Environmental Agency for providing the flow data. Special thanks are given to my colleagues in CEH for collecting the other data used, in particular Stephen Maberly for assembling the nutrient data. This work was partially funded by the Environment Agency. Thanks are also extended to the two reviewers for their useful comments.

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**Tables**

Table 1. The morphological and phylogenetic characteristics of the eight modelled phytoplankton. The last three columns denote simple logic statements (True/False) which, if True, activate the relevant functions in PROTECH.

| **Species** | **Surface Area ($\mu m^2$)** | **Volume ($\mu m^3$)** | **Maximum dimension ($\mu m$)** | **Diatom?** | **Grazed?** | **Nitrogen fixer?** |
|---|---|---|---|---|---|---|
| *Monoraphidium* | 13 | 101 | 8 | F | F | F |
| *Cryptomonas* | 1030 | 2710 | 21 | F | T | F |
| *Paulschulzia* | 5027 | 47710 | 45 | F | F | F |
| *Aulacoseira* | 4350 | 2970 | 240 | T | F | F |
| *Asterionella* | 6690 | 5160 | 130 | T | T | F |
| *Planktothrix* | 7350 | 13970 | 300 | F | F | F |
| *Anabaena* | 6200 | 29000 | 75 | F | F | T |
| *Aphanizomenon* | 5200 | 15400 | 125 | F | F | T |

Table 2. Summary of instructions governing vertical movements of phytoplankton in PROTECH. 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.

| Phytoplankton | Light condition (μmol photon $m^{-2}$ $s^{-1}$) | Movement (m $d^{-1}$) |
|---|---|---|
| **1. Nearly neutrally buoyant, non-motile life-forms** | | |
| *Monoraphidium* and *Paulschulzia* | all | sink 0.1 |
| **2. Non-buoyant non-motile diatoms** | | |
| *Aulacoseira* | ≤ 500 | sink 0.8 |
| | > 500 | sink 1.0 |
| *Asterionella* | ≤ 500 | sink 0.2 |
| | > 500 | sink 1.0 |
| **3. Buoyancy-regulating Cyanobacteria** | | |
| *Planktothrix* | > 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 |
| **4. Swimming flagellates** | | |
| *Cryptomonas* | > 100 | rise 0.1 |
| | ≤ 100 | rise 2.0 |

Table 3. Summary of the effect of the simulated air temperature increase on mean surface water temperatures (top 7 m of water column) and total number of days with shallow stratification (mixed depth ≤ 7 m). Values are presented for each measure from both basins of Windermere at the annual and seasonal scale.

| | Air temperature increase (°C) | | | | |
|---|---|---|---|---|---|
| Response | +0 | +1 | +2 | +3 | +4 |
| North Basin surface water temperature (°C) | | | | | |
| *Annual mean* | 11.2 | 12.1 | 12.8 | 12.9 | 13.5 |
| *Spring mean* | 8.2 | 9.2 | 9.7 | 9.8 | 10.2 |
| *Summer mean* | 16.2 | 17.2 | 18.2 | 18.9 | 19.5 |
| *Autumn mean* | 12.7 | 13.7 | 14.5 | 14.8 | 15.3 |
| South Basin surface water temperature (°C) | | | | | |
| *Annual mean* | 12.0 | 12.6 | 13.2 | 13.9 | 14.5 |
| *Spring mean* | 9.3 | 9.9 | 10.7 | 11.4 | 12.1 |
| *Summer mean* | 17.8 | 18.8 | 19.6 | 20.5 | 20.8 |
| *Autumn mean* | 13.4 | 14.1 | 14.6 | 15.5 | 16.4 |
| North Basin shallow stratification duration (day) | | | | | |
| *Annual* | 193 | 207 | 214 | 225 | 225 |
| *Spring* | 54 | 68 | 72 | 69 | 73 |
| *Summer* | 92 | 92 | 92 | 91 | 92 |
| *Autumn* | 46 | 45 | 48 | 63 | 57 |
| South Basin shallow stratification duration (day) | | | | | |
| *Annual* | 123 | 121 | 122 | 143 | 142 |
| *Spring* | 42 | 38 | 38 | 52 | 53 |
| *Summer* | 69 | 69 | 74 | 72 | 70 |
| *Autumn* | 12 | 14 | 9 | 18 | 17 |

Figure legends

Fig. 1. Comparison for both Windermere basins (North & South) between observed (solid diamonds) and PROTECH (black line) chlorophyll *a* (mg $m^{-3}$) for (a & b) total, (c & d) diatom and (e & f) Cyanobacteria chlorophyll *a*.

Fig. 2. Response in both Windermere basins (North & South) of annual mean chlorophyll *a* concentration (mg $m^{-3}$) to changing air temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load: (a & b) total chlorophyll *a*, (c & d) diatom and (e & f) Cyanobacteria. Solid circles denote the original, unaltered scenario.

Fig. 3. Response in both Windermere basins (North & South) of in-lake soluble reactive phosphorus (SRP) concentration (mg $m^{-3}$) to changing air temperature ($^{o}C$) and SRP load: (a & b) spring, (c & d) summer and (e & f) autumn. Solid circles denote the original, unaltered scenario.

Fig. 4. Response in both Windermere basins (North & South) of spring mean chlorophyll *a* concentration (mg $m^{-3}$) to changing air temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load: (a & b) total chlorophyll *a* and (c & d) diatom. Solid circles denote the original, unaltered scenario.

Fig. 5. Response in both Windermere basins (North & South) of summer mean chlorophyll *a* concentration (mg $m^{-3}$) to changing air temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load: (a & b) total chlorophyll *a*, and (c & d) Cyanobacteria. Solid circles denote the original, unaltered scenario.

Fig. 6. Response in both Windermere basins (North & South) of autumn mean chlorophyll *a* concentration (mg $m^{-3}$) to changing air temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load: (a & b) total chlorophyll *a*, and (c & d) Cyanobacteria. Solid circles denote the original, unaltered scenario.

Fig. 7. Response of diatom spring peak timing (day of year) to changing air temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load in (a) North Basin and (b) South Basin. Solid circles denote the original, unaltered scenario.

Fig. 8. Response of the number of days above the WHO Cyanobacteria concentration threshold (>10 mg $m^{-3}$chlorophyll *a*) to changing water temperature ($^{o}C$) and soluble reactive phosphorus (SRP) load in (a) North basin and (b) South Basin. Solid circles denote the original, unaltered scenario.

Fig. 1

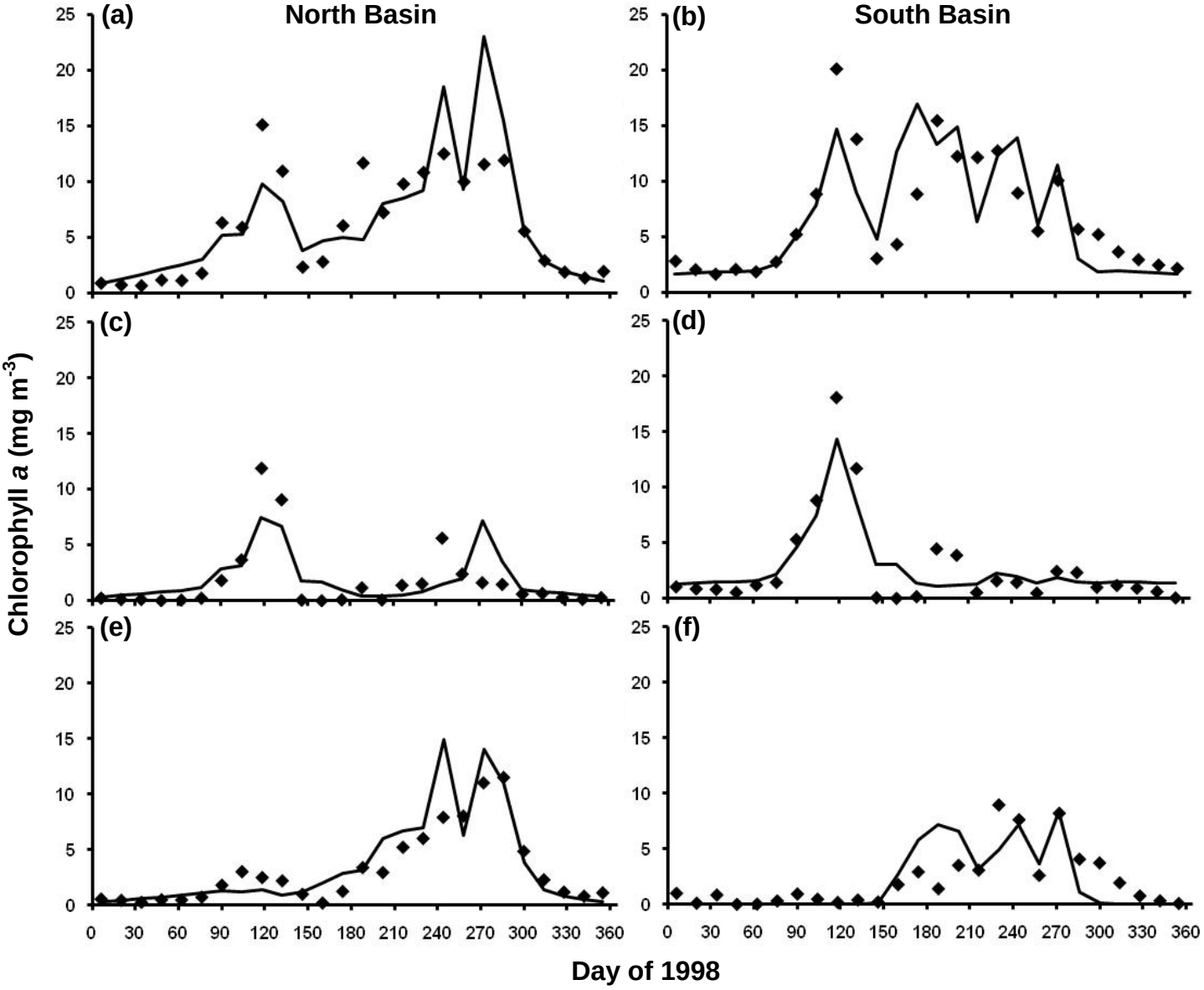

(a)
North Basin
(b)
South Basin
(c)
(d)
(e)
(f)
Chlorophyll a (mg m-3)
Day of 1998
0
5
10
15
20
25
0 30 60 90 120 150 180 210 240 270 300 330 360

Fig. 2

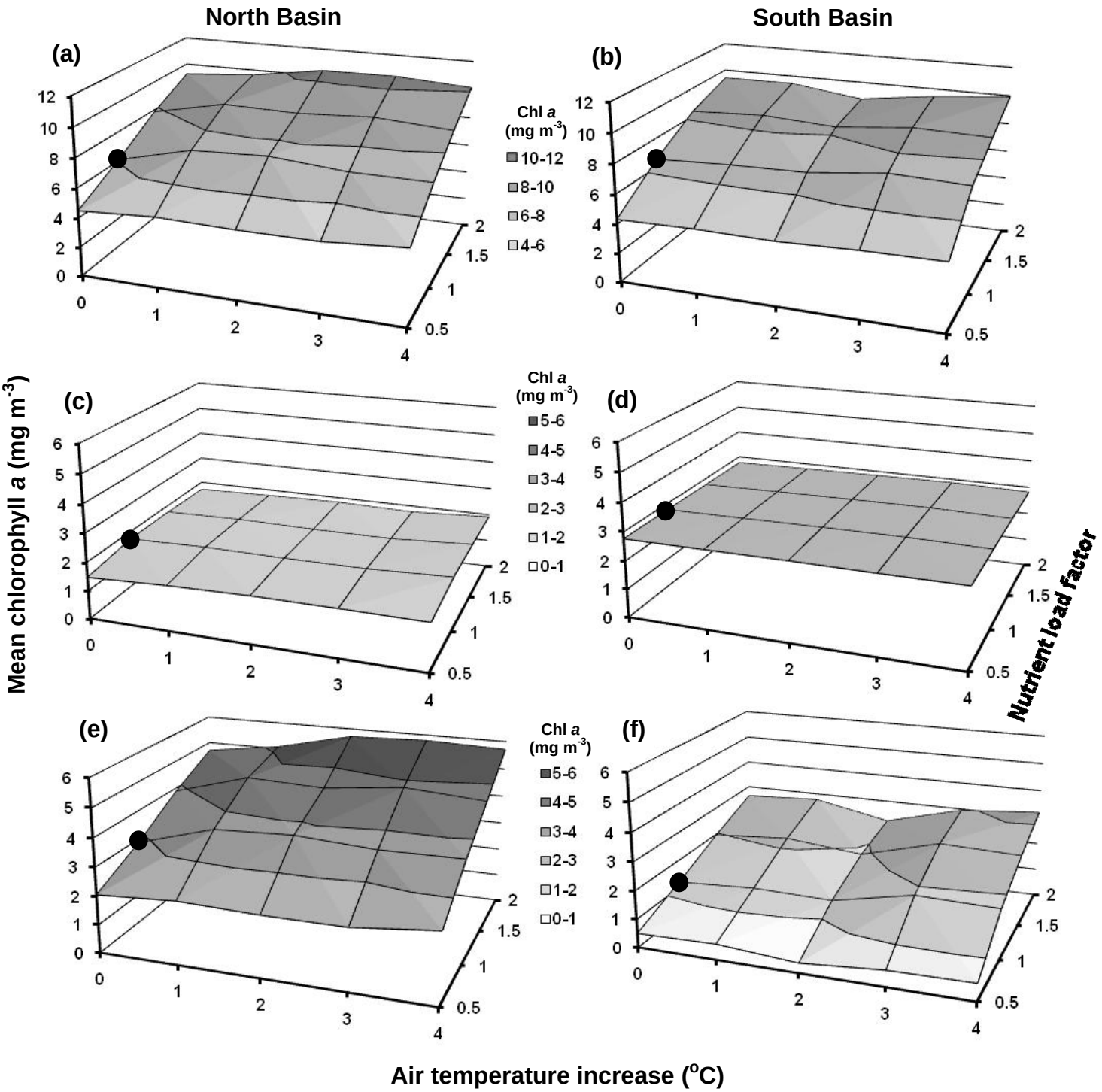

North Basin
South Basin
(a)
(b)
(c)
(d)
(e)
(f)
Chl a (mg m-3)
10-12
8-10
6-8
4-6
5-6
4-5
3-4
2-3
1-2
0-1
Mean chlorophyll a (mg m-3)
Nutrient load factor
Air temperature increase (°C)

Fig. 3

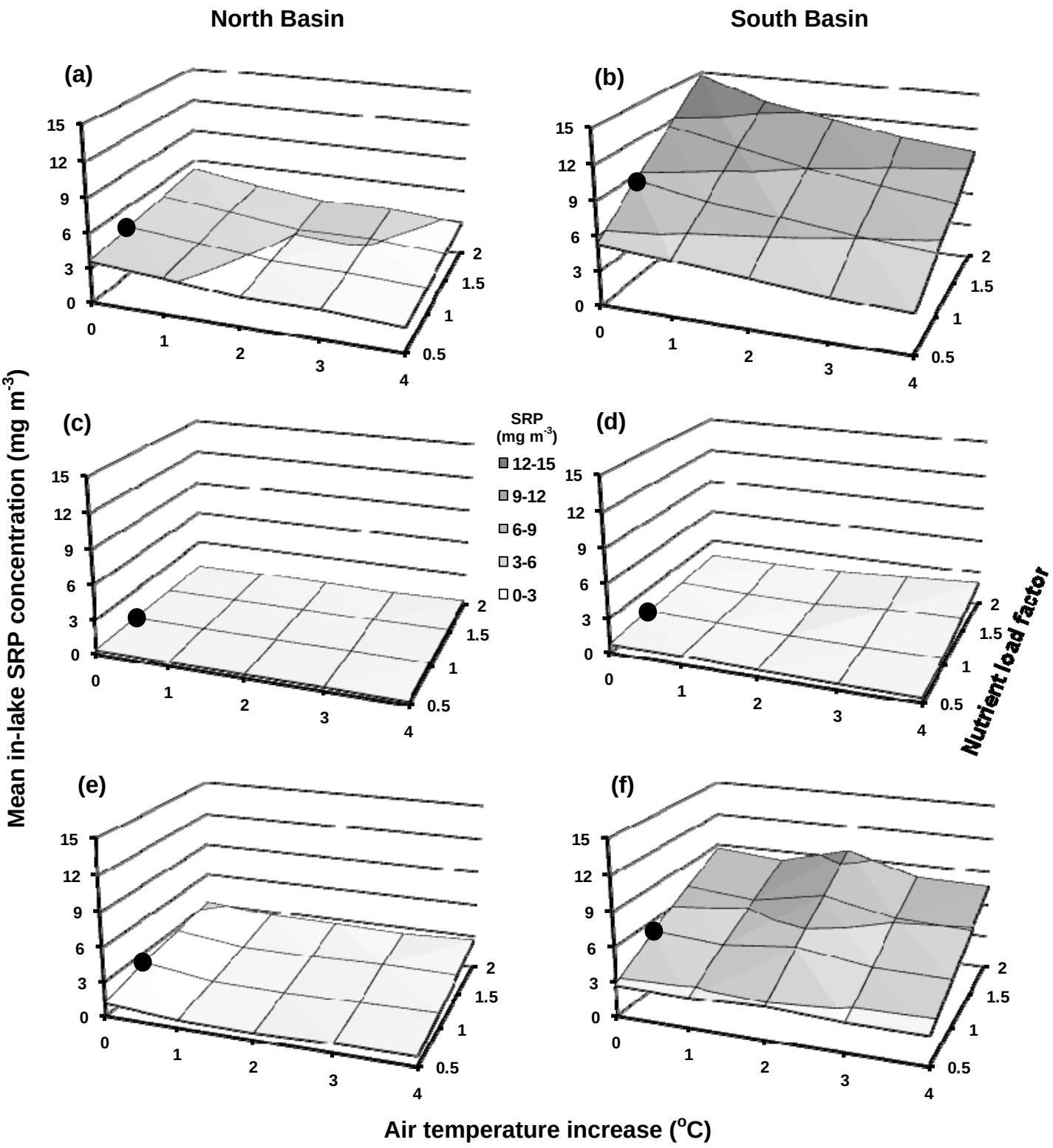

North Basin
South Basin
(a)
(b)
(c)
(d)
(e)
(f)
Mean in-lake SRP concentration (mg m-3)
SRP (mg m-3)
12-15
9-12
6-9
3-6
0-3
Nutrient load factor
Air temperature increase (oC)

Fig. 4

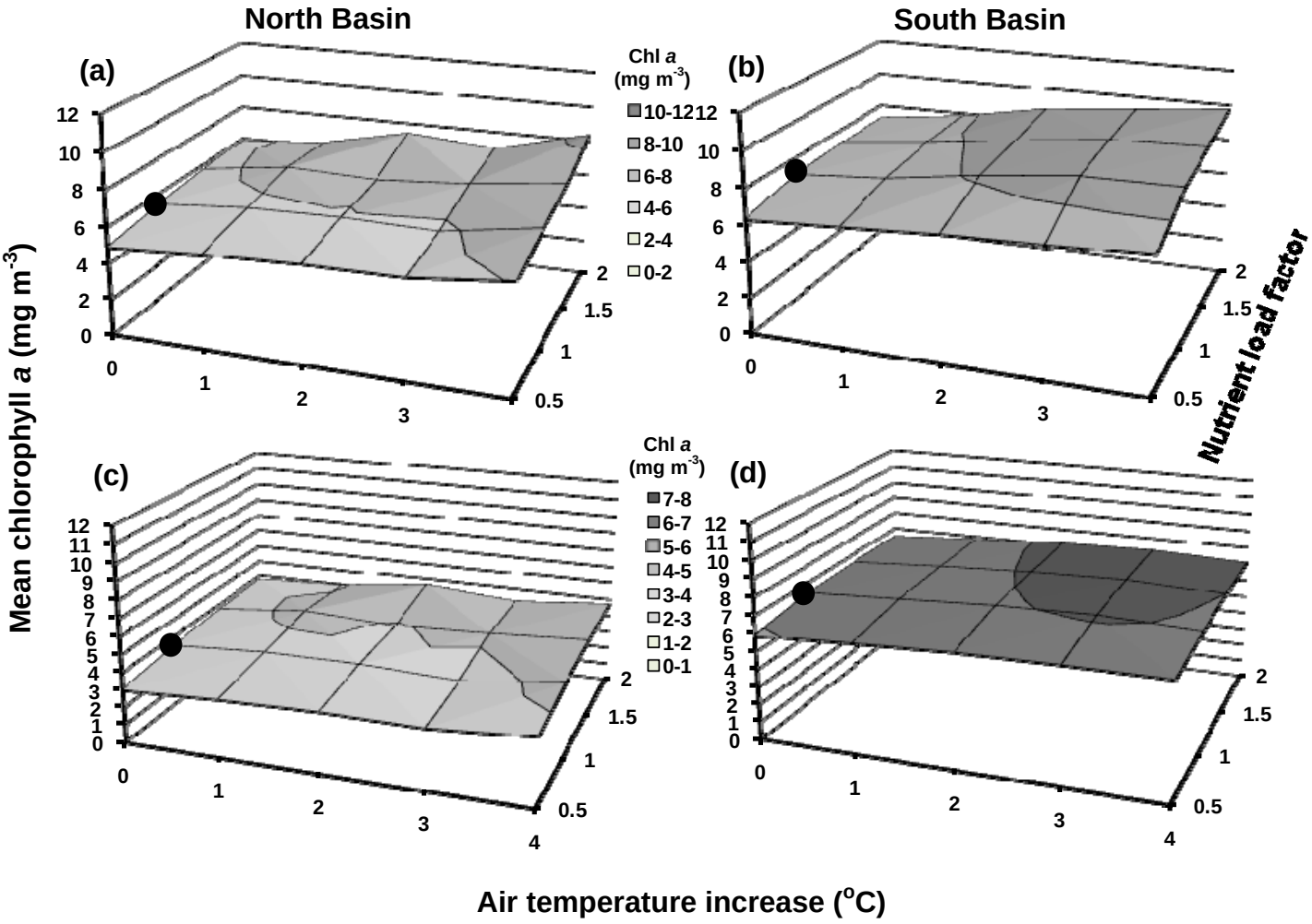

North Basin
South Basin
(a)
(b)
(c)
(d)
Chl a (mg m-3)
10-12
8-10
6-8
4-6
2-4
0-2
7-8
6-7
5-6
4-5
3-4
2-3
1-2
0-1
Mean chlorophyll a (mg m-3)
Nutrient load factor
Air temperature increase (°C)

Fig. 5

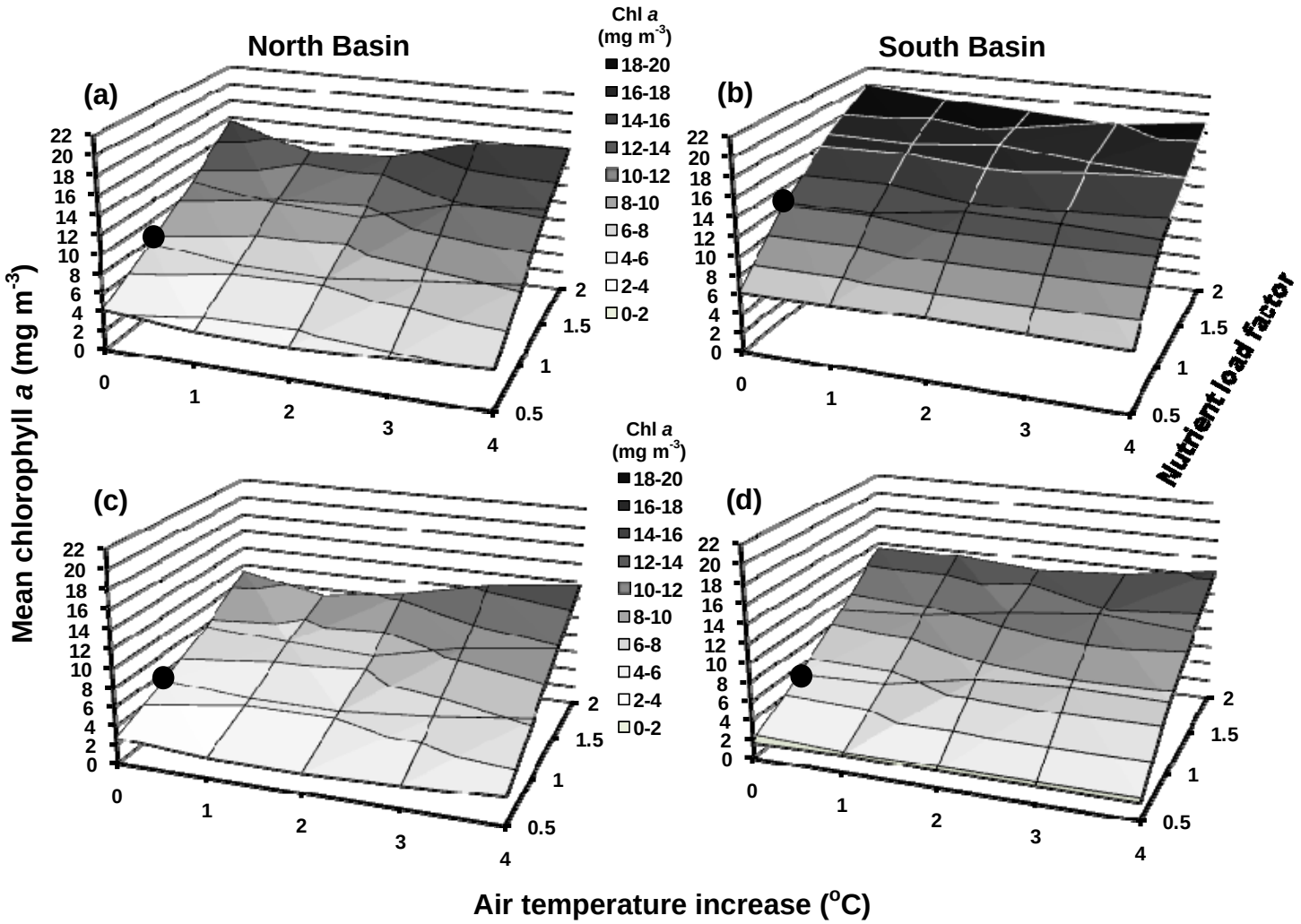

North Basin
South Basin
(a)
(b)
(c)
(d)
Chl a (mg m-3)
18-20
16-18
14-16
12-14
10-12
8-10
6-8
4-6
2-4
0-2
Mean chlorophyll a (mg m-3)
Nutrient load factor
Air temperature increase (°C)

Fig. 6

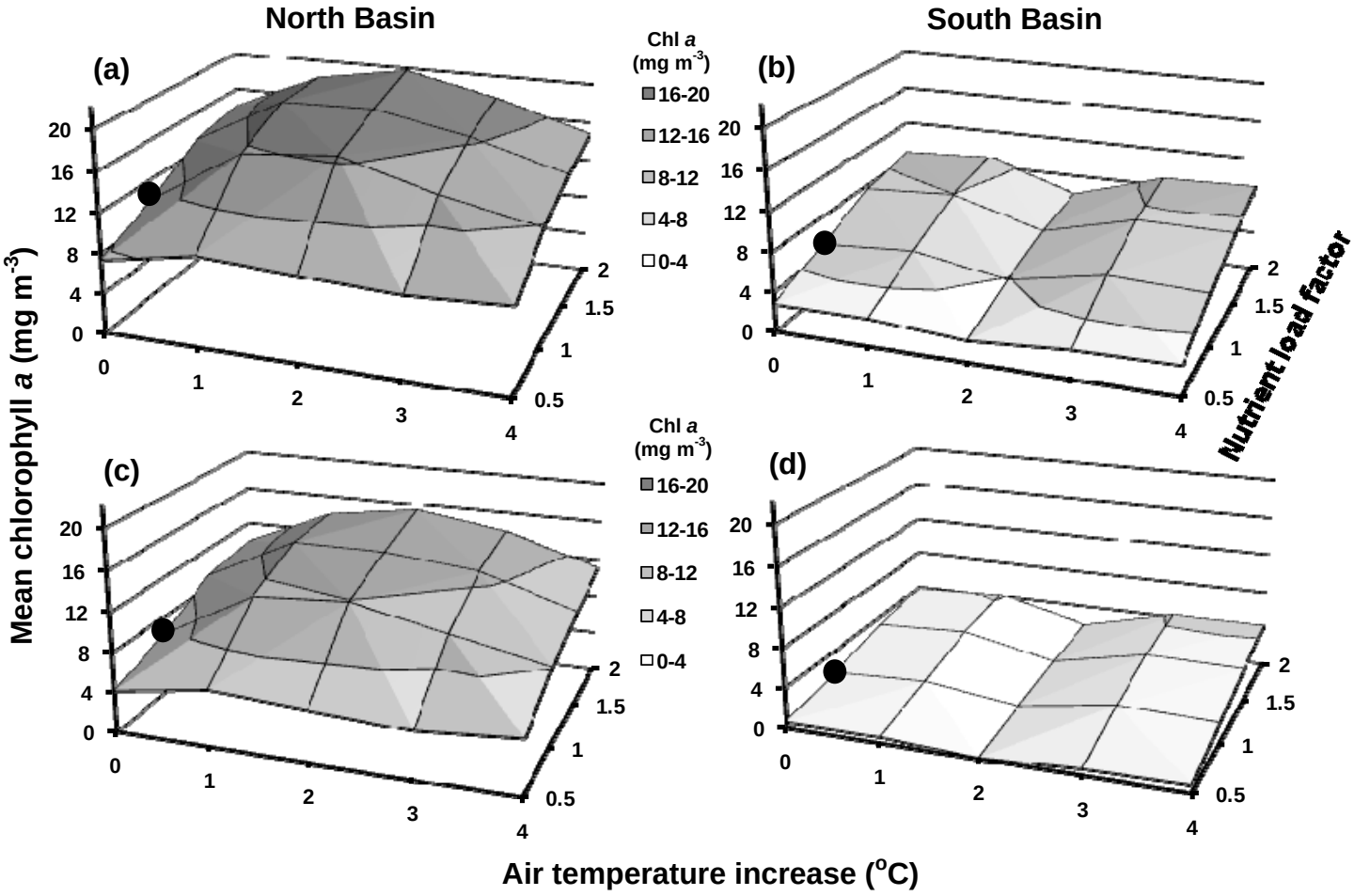

North Basin
South Basin
(a)
(b)
(c)
(d)
Chl a (mg m-3)
16-20
12-16
8-12
4-8
0-4
Mean chlorophyll a (mg m-3)
Nutrient load factor
Air temperature increase (oC)

Fig. 7

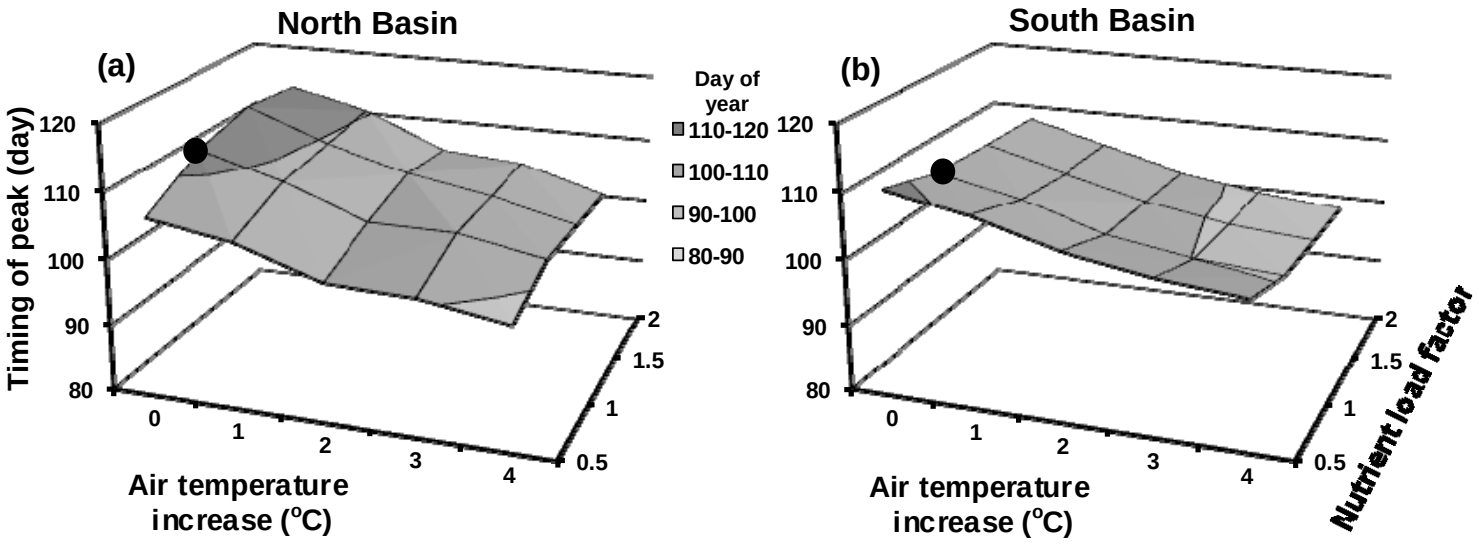
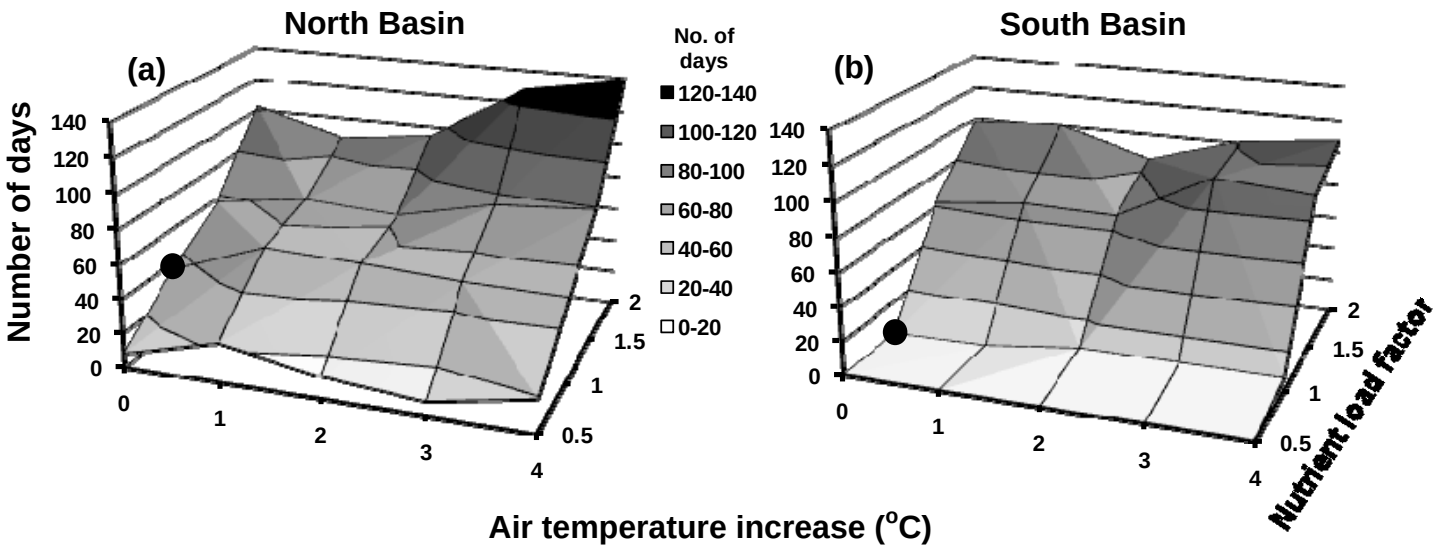

North Basin
(a)
Timing of peak (day)
120
110
100
90
80
0
1
2
3
4
Air temperature increase (°C)
0.5
1
1.5
2
Day of year
110-120
100-110
90-100
80-90
South Basin
(b)
Nutrient load factor

Fig. 8


North Basin
(a)
South Basin
(b)
No. of days
120-140
100-120
80-100
60-80
40-60
20-40
0-20
Number of days
0
20
40
60
80
100
120
140
0
1
2
3
4
Air temperature increase (°C)
0.5
1
1.5
2
Nutrient load factor