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Title

Modelling the response of phytoplankton in a shallow lake (Loch Leven, UK) to changes in lake retention time and water temperature.

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This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiologia.

Abstract

The phytoplankton community of Loch Leven in 2005 was modelled and subjected to a combination of different flushing rates and water temperatures in order to assess the lake's sensitivity to these two climatic drivers. Whilst the simulated annual mean total chlorophyll *a* proved relatively insensitive to these changes, at the species level marked changes were recorded. Some species responded positively to increased temperature (e.g. *Aulacoseira*), some negatively (e.g. *Asterionella*), whilst others were negatively affected by increased flow (e.g. *Aphanocapsa*) and others enhanced (e.g. *Stephanodiscus*). However, this relationship with flow was season dependent with, for example, a simulated increase in summer inflows actually benefiting some species through increased nutrient supply, whereas an equivalent increase in flow in wetter seasons would have negatively affected those species (i.e. through flushing loss). Overall, the simulations showed that the range of species types simulated in the community was sufficient for one species to always benefit from the changing niches created by the multiple climatic drivers applied in this study. The level of exploitation by such a species was only constrained by the nutrient carrying capacity of the system, which led to the overall dampened response in the total chlorophyll *a* measure, both at the annual and season scale. Thus, whilst overall biomass showed relatively little reaction to the two climatic drivers tested, the phytoplankton community composition responded markedly.

Introduction

There has been increasing interest in recent years in the impacts that climate change has had, or could have, on lake ecology (e.g. DeStasio et al., 1996; Carvalho & Kirika, 2003; Winder & Schindler, 2004; Elliott et al., 2006; Elliott & May, 2008). Whilst much of this research has focused on the direct and indirect effects of increased water temperature, relatively few studies (e.g. Reynolds & Lund, 1988; Bailey-Watts, et al. 1990; Jones & Elliott, 2007) have examined the impact of changes in rainfall and the way in which it affects lake phytoplankton ecology by altering the hydrological retention time. The latter effect could be particularly important in influencing water quality because an increase in retention time can be associated with an increase in cyanobacteria, particularly in the summer months (Reynolds, 1993; Carvalho et al, 2008; Paerl & Huisman, 2008). This study investigated the impact of changes in both retention time and water temperature upon the phytoplankton in Loch Leven using a process-based computer model, PROTECH (**Phytoplankton Responses To Environmental Change**) (Reynolds et al., 2001).

Loch Leven was chosen for this study because it is a well studied water body that has already shown signs of being influenced by climate change (Carvalho & Kirika, 2003). It is also an important generator of income to the local economy, with an estimated value of \$US 2.4M ann⁻¹. In the past, however, severe blooms of cyanobacteria in the lake have sometimes reduced its economic value, with one particular event costing an estimated \$US 1.2M in lost revenue and \$US 0.25M in increased water treatment costs to downstream industry (LLAMAG, 1993). So, it is important to understand the sensitivity of the phytoplankton population in the lake to the various aspects of changing climate. The lake and its phytoplankton community

have already been successfully simulated before by PROTECH (Elliott & May, 2008) in a study that looked at the relative effects of changing water temperature and nutrient supply (both nitrogen and phosphorus) upon the lake as it was in 1995. However, the 1995 study only included one direct climate driver, i.e. temperature. In the present study, PROTECH has been used to explore the sensitivity of the phytoplankton community of Loch Leven to the combined climate drivers of changing water temperature and retention time, using a more recent (especially in terms of nutrient supply to the lake) starting state of 2005 for the baseline simulation.

Methods

Site description

Loch Leven is a large, shallow, eutrophic lake (surface area 13.3 km², mean depth 3.9 m, maximum depth 25.5 m), located in east central Scotland, UK, (56° 12' N, 3° 22' W; altitude 107 m). It has a catchment area of 145 km² and an annual retention time of 140 to 180 days (Bailey-Watts & Kirika, 1999).

Data

The driving and validation data for the simulations were taken from 2005. This year was chosen due to the availability of detailed nutrient and flow data available for most of the major inflows to the loch. These measurements included stream discharge values and associated soluble reactive phosphorus (SRP), nitrate-nitrogen and silica concentrations collected at 8-daily intervals. In-lake SRP, nitrate-nitrogen, silica and chlorophyll *a* concentrations, and water temperature had been measured every 14 days and phytoplankton species biovolume was recorded monthly. Daily meteorological data (cloud cover, air temperature, air humidity, wind speed) were available from a

meteorological station at Leuchars Airfield, 35 km north-east of the lake. These wind speed values were corrected to local conditions by applying a 20 per cent reduction, following the relationships derived by Smith (1973) from wind speeds measured at Loch Leven and at RAF Leuchars at the same time.

PROTECH model description

The PROTECH model has been developed and tested on a wide range of lakes and reservoirs around the world over the last two decades (Elliott et al., 2000; Lewis et al., 2002; Elliott & Thackeray, 2004; Elliott et al., 2005; Elliott *et al.*, 2007). The fundamental core of the biological component of PROTECH (Reynolds et al., 2001; Elliott & Thackeray, 2004) is the basic state variable equation that determines the daily change in the chlorophyll *a* concentration ($\Delta X/\Delta t$, mg m⁻³ d⁻¹) of each algal species:

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

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 (species > 50 μm are not grazed) and D is the loss due to dilution. The growth rate (r' , d⁻¹) is further defined by:

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

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 silica concentrations. The r' values are species dependent and relate to the morphology of the alga. Thus, for each species within the model, the initial 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 in the water column (see Reynolds et al., 2001, for details).

Phytoplankton simulations

Following examination of the phytoplankton count data to identify the most abundant and common species, the following phytoplankton types were selected for use in the model: *Cryptomonas*, *Anabaena*, *Gomphosphaeria*, *Aphanocapsa*, *Microcystis*, *Stephanodiscus*, *Asterionella* and *Aulacoseira*. The chlorophyll *a* biomass measurements presented in this study for these simulated species and their total chlorophyll *a* represent an integrated mean over the top 3 m of the water column, as this mimics the sampling method used to collect the observed data. These data were also used to calculate the percentage contribution of the cyanobacteria species in the simulated community. PROTECH does not include equations to simulate the release of SRP from sediment, which is an important factor in the nutrient budget of Loch Leven (Spears et al., 2007). Therefore, extra SRP was added to the water column from 1st June to 30th September. This amounted to an extra 1.7 mg m⁻³ per 0.1 m PROTECH depth layer per day. Another site-specific calibration was also applied to this simulation by modifying the mixed depth function in PROTECH. As PROTECH models the deepest point in the lake, full mixing of the water column over-emphasises the importance of this point in lakes that are predominantly shallow, like Loch Leven. So, the depth of mixing was restricted to a maximum of 14.7 m from the surface, following the approximation used in Elliott et al. (2005).

Using the 2005 simulation of Loch Leven, key factors were altered to test the effects of changing water temperature and daily discharge. This was achieved by incrementally changing the temperature in the PROTECH depth layers by 1°C to give a range of water temperatures that ranged from 1°C cooler to 4°C warmer. At the

same time, the daily discharge was multiplied by 0.5, 0.75, 1.0, 1.5 or 2.0 to give a range of discharge values. In addition, the original daily concentrations of nutrients associated with these discharges were corrected to maintain the nutrient supply at a 50:50 ratio of point to diffuse sources; it is believed that this represents the annual mean split of nutrient sources at this site (May et al., this volume). The consequence of using this ratio is that half of the nutrient load entering the lake is from point sources and independent of changes in inflow discharge whereas the other half of the load is from diffuse sources that change with discharge such that increased flow increases the nutrient load from this source. For each of these scenarios, the daily 3 m integrated chlorophyll *a* data was used to calculate an annual mean value and quarterly seasonal means for Spring (March-May), Summer (June-August) and Autumn (September-November). Winter (December-January) values were also calculated, but these showed little change and, therefore, were not considered further in this study.

Results

Comparison with observed data

In order to validate the model, its output was compared to the available phytoplankton observations (Fig. 1). Total chlorophyll *a* was often measured in three places in Loch Leven during the fortnightly sampling cycle, thus an estimate of variation in chlorophyll *a* could be calculated as well as the mean value. These mean values were compared to the PROTECH output (Fig. 1a) and found to show a statistically significant fit ($R^2 = 0.42$, $P < 0.001$), which improved further with the exclusion of the single value of 100.3 mg m^{-3} recorded on 2nd November 2005 ($R^2 = 0.67$, $P < 0.001$). However, whilst the bimodal bloom pattern was recreated well, there were some

notable differences. For example, the simulated spring bloom was about 2 weeks later and did not decline as sharply as the observed values in May.

The main simulated taxa were compared to the observed data (Fig. 2) and, because two different methods of enumeration were used (i.e. biovolume for observed data, chlorophyll *a* for PROTECH), only simple visual comparisons were made between the patterns. The model simulation captured the bimodal pattern of diatom development well throughout the year (Fig. 2a) and was broadly in agreement with the bloom of cyanobacteria in the second half of the year (Fig. 2b). However, the latter comparison did show that PROTECH's simulated changes in cyanobacteria biomass were consistently two to three weeks later in the year than those of the observed values. Nevertheless, this simulation was considered adequate for use as a baseline for scenario testing, particularly because the use of annual and seasonal means in the analysis would be less affected by the differences in timing highlighted above.

Changes in annual means of total and species chlorophyll a concentrations

Predicted annual mean total chlorophyll *a* concentrations ranged between 24 and 31 mg m⁻³ (Fig. 3a), changing relatively little with different flows and temperatures, although there was a slight tendency for the model to produce less biomass with the imposition of more extreme flow scenarios. However, such low levels of response in these annual means did not mean the community composition was unaffected.

The simulated phytoplankton that equated to *Asterionella* produced most of the total chlorophyll *a* (Fig. 3b) and responded to increasing temperature by producing slightly

less biomass over the year. The percentage of cyanobacteria in the community proved to be especially sensitive to changes in discharge (Fig. 3c), decreasing markedly with increased flushing rate. This pattern of response was closely followed by the cyanobacteria species, *Aphanocapsa* (Fig. 3d). The annual means of two other species are also worthy of mention because their responses were different from those discussed above. Firstly, the small diatom, *Stephanodiscus*, produced more biomass with increasing flow (Fig. 3e). Secondly, the filamentous diatom, *Aulacoseira*, responded positively to increasing temperature (Fig. 3f), which was the opposite response to that of its closest competitor in the simulation, *Asterionella*. Overall, it was clear that, when the biomass produced over the whole year was taken into account, the lake phytoplankton community remained diatom dominated.

Changes in spring means

Dominance by diatoms in the simulations was even more marked in the spring period (March-May), when mean total chlorophyll *a* was at its highest (30-39 mg m⁻³) and relatively unaffected by the scenarios (Fig. 4a). *Asterionella* was the dominant diatom, producing nearly all of the spring biomass (Fig. 4b), but this species showed a slight decline (*c.* 1 mg m⁻³ per level of change) in mean chlorophyll *a* concentration with increasing flow. Two other diatoms made up the rest of the total biomass, with *Aulacoseira* showing an increase in mean spring biomass at high temperatures (Fig. 4c) and flows. Similarly, *Stephanodiscus* biomass increased rapidly with larger flows, although this effect was diminished at higher temperatures (Fig. 4d).

Changes in summer means

Mean total chlorophyll *a* in the summer period (June-August), was sensitive to both

changes in temperature and flow regime, with *c.* 20 mg m⁻³ difference between the highest and lowest mean value (Fig. 5a). Most of this change was caused by increased flow reducing the mean chlorophyll *a* level.

In contrast to the pattern of change in total chlorophyll *a* concentration, *Asterionella* contributed far less to the overall biomass in this season than in spring and responded positively to increasing flow and decreasing temperature (Fig. 5b). This was because the total chlorophyll *a* comprised mainly cyanobacteria (Fig. 5c), especially *Aphanocapsa* (Fig. 5d). This species showed a marked sensitivity, decreasing in mean biomass with high and, to a lesser extent, low flows. Interestingly, it also showed a slight decline in abundance with increasing temperature. Finally, the flagellate *Cryptomonas* responded positively to decreasing flow and increased temperatures (Fig. 5e).

Changes in autumn means

The autumn (September-November) mean total chlorophyll *a* value was the second highest of the four seasons and its pattern of response was similar to that observed in the summer. The exception was that, under high water temperatures, flow ceased to have a negative effect (Fig. 6a). Again, the underlying cause for the changes in total chlorophyll *a* was due to the changes in the cyanobacteria community (Fig. 6b), which, again, showed a considerable negative response to increased flow. The most abundant diatoms in the autumn community were *Asterionella* and *Aulacoseira* but, whilst both responded little to the changes in flow, their responses to the changes in temperature contrasted markedly (Fig. 6c, d). *Asterionella* declined in biomass with increasing temperature, whilst *Aulacoseira* increased. Again, the dominant

cyanobacterium was *Aphanocapsa*, which responded negatively to extreme flows (Fig. 6e). Finally, *Cryptomonas* produced a very unusual response surface (Fig. 6f) in which it responded positively when flow and temperature were both low and also when both were high.

Discussion

Annual mean values of measured parameters are often used to determine the overall quality of a water body. In this context, measures of phytoplankton are often no more detailed than mean annual measures of total chlorophyll *a*. This study illustrates why such measures can sometimes be too simplistic. The results show that considerable changes in species composition can occur in response to changing temperature and flow scenarios, while the overall annual mean total chlorophyll *a* concentrations change very little (Fig. 3a). It was only when low temperatures (causing lower growth rates) were coupled with increased flushing losses of biomass and nutrients (caused by high flows) that total chlorophyll *a* showed a slight decline; the latter is supported by similar observations in other lakes and reservoirs (Kalff, 2002).

At the species level, a great deal of variation occurred in response to changes in temperature and flushing rate. Some species responded positively to increased temperature (e.g. *Aulacoseira*, Fig. 3f) and others negatively (e.g. *Asterionella*, Fig. 3b). Other species produced more biomass with higher flushing, such as the small, fast growing diatom *Stephanodiscus* (Fig. 3e), whilst slower growing species like *Aphanocapsa* were outcompeted under such conditions (Fig. 3d). These results showed that, as one species reacted negatively to the change in conditions, another species responded positively. This type of response pattern dampened the effect of the

changes in temperature and flow on the total chlorophyll *a* concentration in the lake. Such species changes were even more evident when the seasonal trends were examined.

The spring period was dominated by diatoms and, again, the three main species responded differently to the environmental change scenarios. High flows negatively affected *Asterionella* but positively benefited *Stephanodiscus* and, to a much lesser extent, *Aulacoseira* (Fig. 4). It seems likely that this was due, once more, to the flushing losses caused by the increased flow that the relatively small sized, fast growing, *Stephanodiscus* was particularly suited to survive (provided other factors were not limiting its growth). Such a reaction whereby smaller phytoplankton prevail under conditions of high flushing is well documented (Boucher et al., 1984; Rojo et al., 1994; Kalff, 2002) and in previous PROTECH studies, where this phytoplankton functional type (i.e. relatively small species *sensu* the C functional group after Reynolds, 1995) has often been seen to increase in prevalence under such conditions (Elliott & Jones, 2007; Bernhardt et al., 2008).

The importance of seasonal means was highlighted further when the response of *Asterionella* in the summer was considered. At that time of year, its biomass was positively enhanced by increased flows, particularly when combined with lower temperatures (Fig. 5). This opposite response to that seen in the spring was related to the decline of its two main competitors (*Cryptomonas* and *Aphanocapsa*) under these conditions, as well as receiving a net benefit of increased nutrient supply *via* the larger inflows; this latter effect has been observed before for diatoms in Loch Leven, which benefited from additional nutrients entering during high flows (Bailey-Watts, et

al. 1990). Again, we see one species benefiting over another when more of the resources essential for growth (e.g. nutrients, light) become available. However, it was also clear that low flow scenarios could be relatively unfavourable for growth, with a decline in the two most dominant phytoplankton species (*Asterionella* and *Aphanocapsa*) being evident. This occurred because the reduced flow resulted in a reduction in the supply of diffuse source nutrients to the modelled lake. By the summer period, this reduction in supply, combined with naturally lower flows, was starting to become an important factor in reducing the overall phytoplankton carrying capacity and, subsequently, increasing the competition for resources.

With natural inflow discharges increasing in the autumn, the nutrient restriction was slightly alleviated. However, it remained an influential factor at low flows for most species (Fig. 6), while high flows still generally caused a decline in biomass. Intriguingly, temperature also started to have a more obvious effect on some of the mean chlorophyll *a* values. During the autumn period, increasing temperature reduced the biomass of *Asterionella* and increased that of *Aulacoseira*. These two species are close competitors of each other, both being well adapted to low light level conditions (R-functional group *sensu* Reynolds, 1995) and, through most of the simulations, *Asterionella* was the dominant of the two. However, in this autumn period, higher temperatures increased the relative growth rate of *Aulacoseira* allowing it to produce more biomass than *Asterionella*. Finally, *Cryptomonas* produced a very diverse response in the autumn, with peaks in biomass occurring at high temperatures and flows and also under completely opposite conditions. *Cryptomonas* is a relatively large phytoplankter and, in PROTECH, is given specific motility characteristics to simulate its excellent nutrient scavenging abilities (Reynolds, 1984). Thus, it can

thrive under low nutrient conditions, but needs elevated temperatures under high flow conditions to achieve the high growth rates needed to compensate for flushing losses.

Conclusion

Temperature had little effect on the overall biomass produced by the phytoplankton in Loch Leven. This is in concurrence with the results of previous studies on the loch (Carvalho & Kirika, 2003; Elliott & May, 2008) and other experimental investigations (Moss et al., 2003; McKee et al., 2003). Furthermore, there was no evidence, either annually or seasonally, of temperature enhancing cyanobacteria abundance. Again, this was in agreement with the results of Elliott & May (2008), but is in contrast to those from a similar study where PROTECH was applied to Bassenthwaite Lake (Elliott et al., 2006).

Changes in flow and flushing rate had a greater effect on the phytoplankton community than changes in temperature, at least at the seasonal scale. When the rate of flow was changed, there appeared to be a general response of reduced biomass with extreme flows. In this instance, high flows acted by causing high flushing losses and low flows reduced the nutrient supply, particularly in the summer. However, this study also illustrates how some species possess traits that could enable them to exploit these conditions. Small, fast growing species, such as *Stephanodiscus* can recoup their flushing losses under high flow conditions. In contrast, other species, such as *Aphanocapsa*, are ideally adapted to surviving under low nutrient conditions. Thus, as one species becomes stressed by a physical change (e.g. temperature, retention time), another species becomes better able to exploit the resources available. Such allogenic succession is readily recognised across ecosystems (Begon et al., 1996).

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Figure Legends

Fig. 1 Comparison between observed (crosses) and PROTECH simulated (solid line) annual mean total chlorophyll *a* concentrations (mg m^{-3}) for Loch Leven, 2005. Error bars for observations, which are taken from multiple sites, represent 2 standard deviations (c. 95% confidence interval).

Fig. 2 Comparison between observed (crosses) total biovolumes ($\mu\text{m}^3 \text{ ml}^{-1}$) and PROTECH simulated (solid line) chlorophyll *a* concentrations (mg m^{-3}) for the major taxa in Loch Leven in 2005: (a) diatoms; (b) cyanobacteria.

Fig. 3 Impact of changing water temperature ($^{\circ}\text{C}$) and discharge on the annual mean chlorophyll *a* concentration (mg m^{-3}) in Loch Leven for: (a) total chlorophyll; (b) *Asterionella*; (c) percentage cyanobacteria; (d) *Aphanocapsa*; (e) *Stephanodiscus*; (f) *Aulacoseira*. Grey scale legends denote chlorophyll *a* concentration (mg m^{-3}) bands.

Fig. 4 Impact of changing water temperature ($^{\circ}\text{C}$) and discharge of the spring mean chlorophyll *a* concentration (mg m^{-3}) in Loch Leven for: (a) total chlorophyll *a*; (b) *Asterionella*; (c) *Aulacoseira*; (d) *Stephanodiscus*. Grey scale legends denote chlorophyll *a* concentration (mg m^{-3}) bands.

Fig. 5 Impact of changing water temperature ($^{\circ}\text{C}$) and discharge of the summer mean chlorophyll *a* concentration (mg m^{-3}) in Loch Leven for: (a) total chlorophyll *a*; (b) *Asterionella*; (c) percentage cyanobacteria; (d) *Aphanocapsa*; (e) *Cryptomonas*. Grey scale legends denote chlorophyll *a* concentration (mg m^{-3}) bands.

Fig. 6 Impact of changing water temperature ($^{\circ}\text{C}$) and discharge of the autumn mean chlorophyll *a* concentration (mg m^{-3}) in Loch Leven for: (a) total chlorophyll *a*; (b) percentage cyanobacteria; (c) *Asterionella*; (d) *Aulacoseira*; (e) *Aphanocapsa*; (f) *Cryptomonas*. Grey scale legends denote chlorophyll *a* concentration (mg m^{-3}) bands.

Fig 1

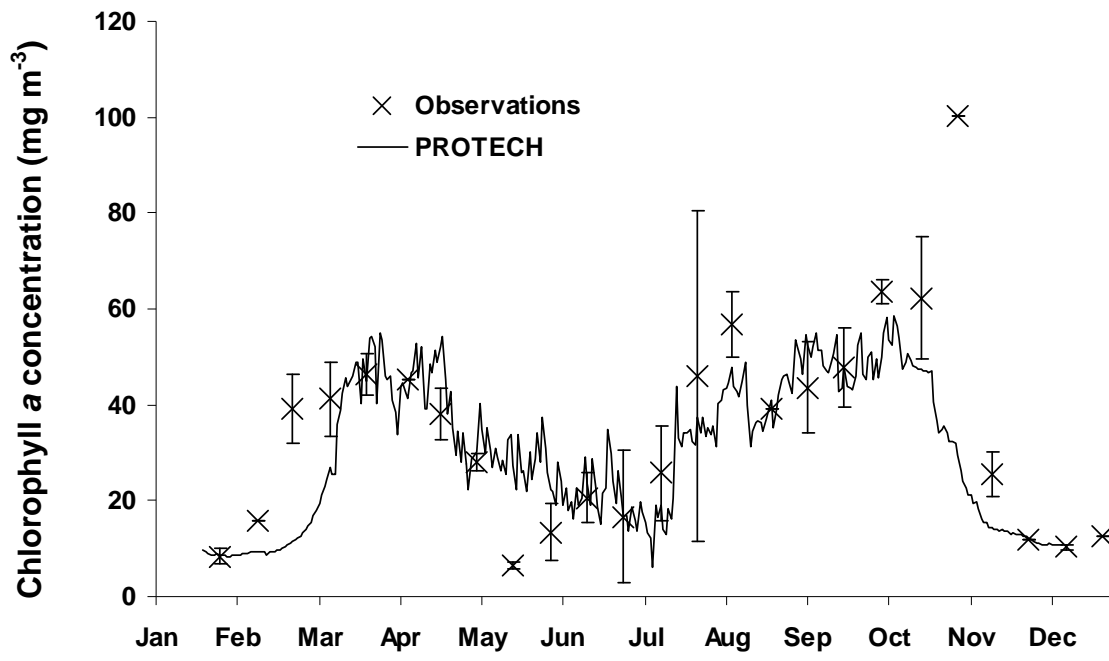


Fig 2

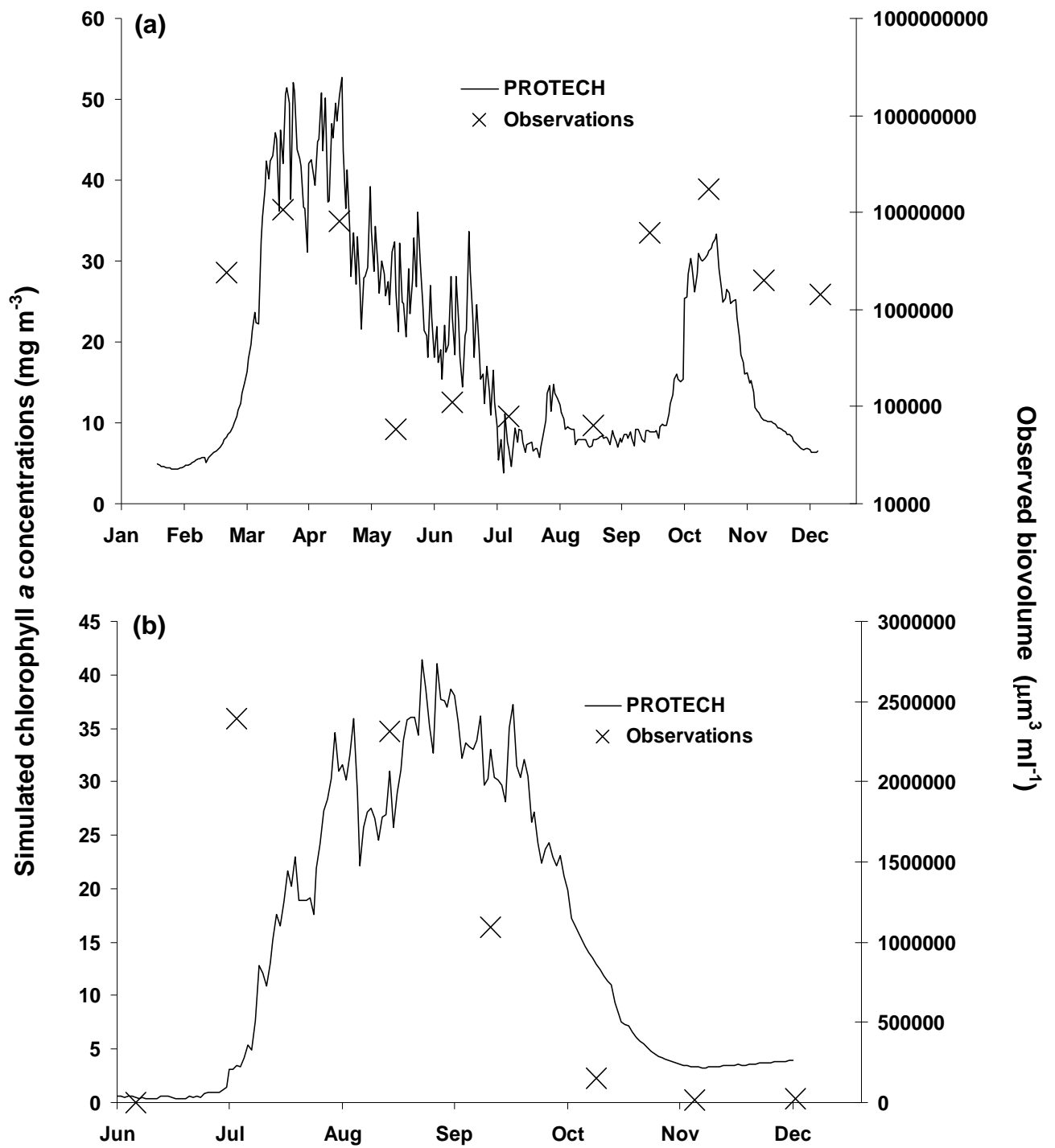


Fig. 3

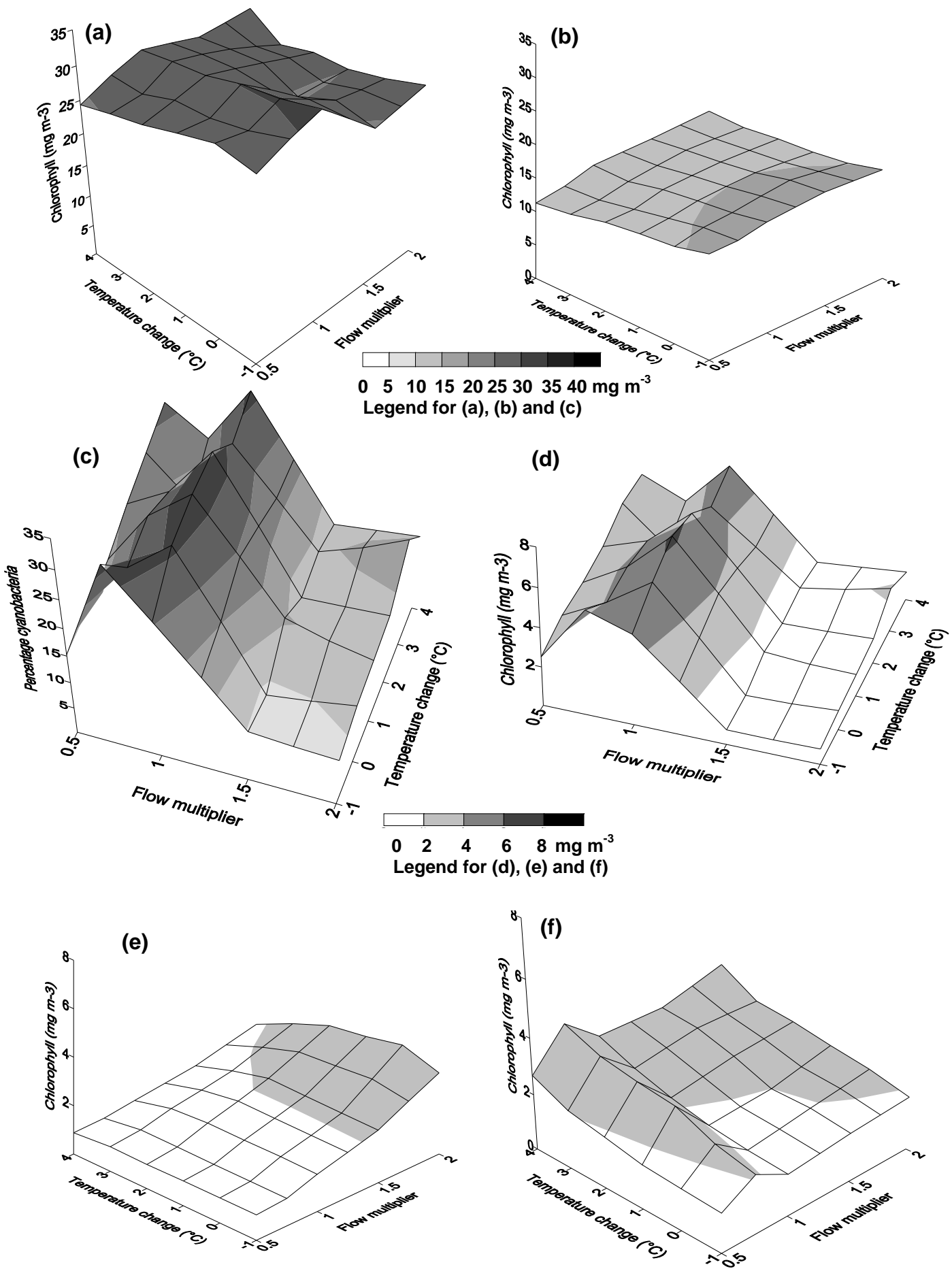


Fig. 4

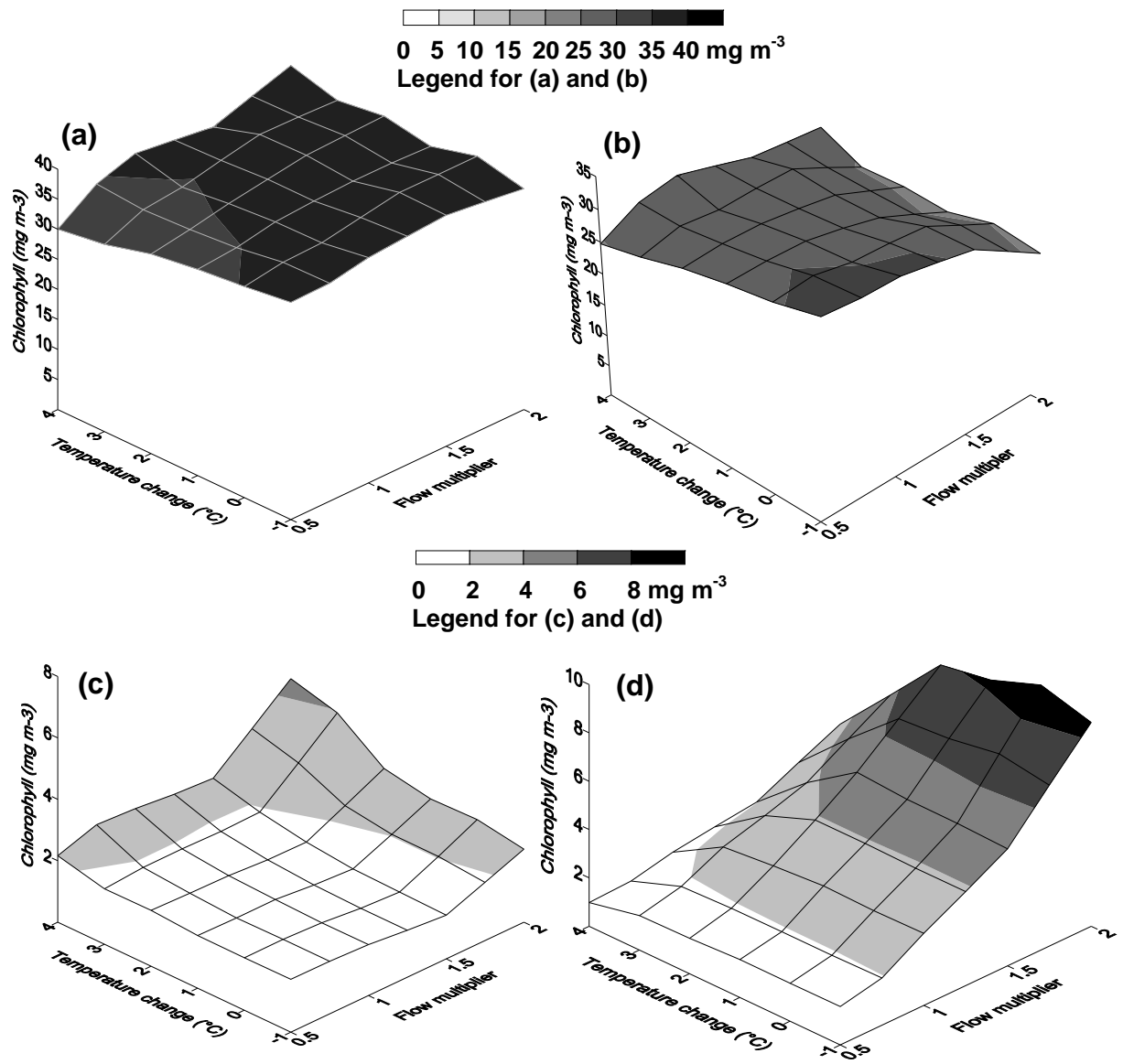


Fig. 5

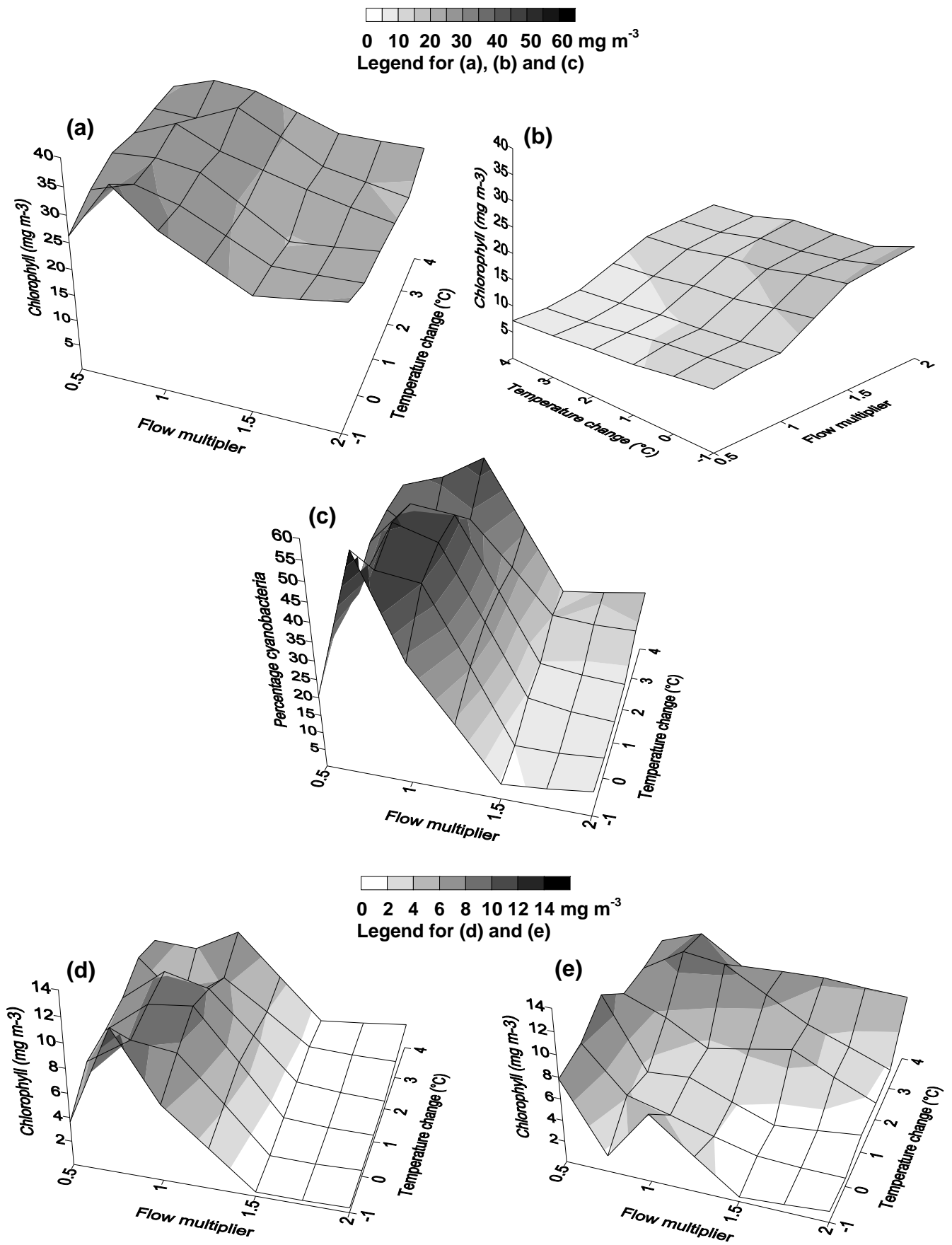


Fig. 6

