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The past and future of phytoplankton in the UK's largest lake, Lough Neagh.

J. Alex Elliott[1] Yvonne R. McElarney[2] & Michelle Allen[2]

[1]Centre for Ecology & Hydrology, Lancaster, Library Avenue, Bailrigg, Lancashire LA1 4AP, UK.

[2]Agri-Food and Biosciences Institute, 18a Newforge Lane, Belfast, Northern Ireland, BT9 5PX, UK

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Corresponding author: J. Alex Elliott, Lake Ecosystems Group, Centre for Ecology & Hydrology Lancaster, Library Avenue, Bailrigg, Lancashire LA1 4AP, UK.

E-mail: alexe@ceh.ac.uk

Abstract

Lough Neagh is the largest lake in the UK and has been extensively monitored since 1974. It has suffered from considerable eutrophication and toxic algal blooms. The lake continues to endure many of the symptoms of nutrient enrichment despite improvements in nutrient management throughout the catchment, in particular a permanently dominant crop of the cyanobacterium *Planktothrix agardhii*. This study examines the historical changes in the Lough, and uses the PROTECH lake model to predict how the phytoplankton community may adapt in response to potential future changes in air temperature and nutrient load. PROTECH was calibrated against 2008 observations, with a restriction on the maximum simulated mixed depth to reflect the shallow nature of the lake and the addition of sediment released phosphorus throughout the mixed water column between 1 May to 1 October (with an equivalent in–lake concentration of 2.0 mg m^{-3}). The historical analysis showed that phytoplankton biomass (total chlorophyll *a*) experienced a steady decline since the mid-1990s. During the same period the key nutrients for phytoplankton growth in the lake have shown contrasting trends, with increases in phosphorus concentrations and declines in nitrate concentrations. The modelled future scenarios which simulated a temperature increase of up to 3 ^{o}C showed a continuation of those trends i.e. total chlorophyll a and nitrate concentrations declined in the surface water, while phosphorus concentrations increased and *P. agardhii* dominated. However, scenarios which simulated a 4 ^{o}C increase in air temperature showed a switch in dominance to the cyanobacteria, *Dolichospermum* spp. (formerly *Anabaena* spp.). This change was caused by a temperature related increase in growth driving nutrient consumption to a point where nitrate was limiting, allowing the nitrogen-fixing *Dolichospermum* spp. to gain sufficient advantage. These results suggest that in the long term, one nuisance cyanobacteria bloom may only be replaced by another unless the in-lake phosphorus concentration can be greatly reduced.

1. Introduction

In the latter half of the twentieth century, anthropogenic nutrient enrichment of freshwater lakes has been widespread and often damaging to ecosystems. The largest lake in the United Kingdom (UK), Lough Neagh has been no exception to this trend and forms the focus of this study. This polymictic, naturally mesotrophic lake has become much enriched as a result of anthropogenic eutrophication, most of which occurred in the last century (Wood and Smith, 1993). Despite the recent changes in nutrient loading the lake is still currently classed as hypereutrophic with annual mean chlorophyll *a* and total phosphorus concentrations of 46 mg m^{-3} and 108 mg m^{-3} respectively in 2014.

While many algal taxa are present in the Lough, for example the diatoms *Stephanodiscus* spp. and *Aulacoseira* spp. which have their peak biomass in spring, the phytoplankton is dominated by the cyanobacteria *Planktothrix agardhii* and *Pseudanabaena* spp. which form a perpetual large crop. These cyanobacteria have the potential to produce toxins which pose a risk to both human and animal health (Briand et al., 2003; Codd et al., 2005). Cyanobacteria may also pose problems in water treatment works with some toxins difficult to remove, especially during bloom periods (Hitzfeld et al., 2000). Furthermore, in a future with a warmer climate, cyanobacteria are predicted to become more prevalent (Carey, et al., 2012; Elliott, 2012). As Lough Neagh is the most important drinking water reservoir in Northern Ireland, supplying daily drinking water to approximately 1 million people, it is useful to understand and predict the behaviour of these cyanobacteria.

The Water Framework Directive (WFD) (EU, 2000) is the major driver of water quality legislation for European States. It is based on a holistic approach to water management and describes target biological elements, one of which is phytoplankton, which must be protected and /or improved through a required Programme of Measures. According to the Directive, Lough Neagh is considered a Heavily Modified Water Body due to water level control, however, it still must achieve ecological improvement through a management plan. In order to achieve a sustained reduction in cyanobacteria biovolume it is essential to make predictions regarding the response of lake phytoplankton to future changes in temperature and nutrient loading as temperature in the Lough is increasing and nitrogen loading from the catchment is decreasing (McElarney et al., 2015b). In order to help inform the WFD Programme of Measures, we used a computer model called PROTECH (Elliott et al., 2010). PROTECH (**P**hytoplankton **R**esp**O**nses **T**o **E**nvironmental **CH**ange) simulates the responses of up to 10 species of lake phytoplankton to seasonal changes at a daily time step. It has been applied in over 35 peer reviewed studies and is one of the most cited lake models in the world (Trolle et al., 2012).

The aims of this study were to examine the historical changes in the Lough, with particular emphasis on the phytoplankton and, through using the PROTECH model, to predict how the phytoplankton community may adapt in response to potential future environmental changes. The focus of these future scenarios was to assess the combined impact of increasing air temperature (predicted for this region of the UK to be between 1-4 ^{o}C over this century (Jenkins et al., 2009)) and reducing nutrient load, thus creating a range of potential scenarios likely to be seen in the 21st century.

2. Material and methods

2.1 Site description

Lough Neagh is located in Northern Ireland with a surface area of 383 km^2 and volume of 3.45x109 m^3. Hydraulic residence time is approximately 1.2 years (Foy et al., 2003), mean and maximum depth are 8.9 m and 34 m respectively. Six inflowing rivers drain 88% of the 4,453 km^2 catchment. As well as being a drinking water reservoir, the lake has several conservation designations under the Ramsar convention (Ramsar Bureau, 2000), and the Habitats Directive (EU, 1997). The lake supports a commercial fishery, primarily exploiting the European eel (*Anguilla anguilla*). It is also part of the UK Environmental Change Network (ECN; Sier *et al*., **this issue**). A more in-depth description of the lake and its catchment is provided in Wood and Smith (1993).

2.2 Sampling

Integrated water samples of 10m were collected by boat at a central lake location (approximately N54 35.779, W6 23.1301) either weekly (1980-1993) or fortnightly (1993 to present) using a lead-weighted polythene tube.

2.3 Laboratory analyses

Water chemistry and biological parameters were determined using standard methodologies (Wood and Smith, 1993). Water chemistry methods for the entire time period were subject to internal Quality Control and external quality proficiency testing (Aquachecks) run by the Laboratory Government Chemists. Certified reference materials were used. The laboratory is also currently UKAS accredited to ISO17025 and test methods are validated to UKAS standards. Water samples were filtered using 0.45µm pore size GFC filters and analysed for soluble reactive phosphorus (SRP), nitrate, silica and chlorophyll *a*. Chlorophyll *a* was extracted from the residue on the filter paper by being placed in tubes of 90% methanol in a water bath at 55 deg C, the pigment was measured spectrophotometrically after centrifugation (Talling and Driver, 1963). Determination of soluble reactive P concentration followed the method of Eisenreich et al. (1975). Samples were not available for 2009. Silica concentration was determined by spectrometer according to Golterman et al. (1978). Analytical methods were consistent across the period with the exception of observations of nitrate concentration which, from 1980-2011, was determined by reduction to nitrite (Chapman et al., 1967) and from 2012 was determined according to Environmental Protection Agency (1993). Nitrate is reported as nitrate N. Phytoplankton samples were obtained from a composite water sample. They were counted and their biovolume estimated using an inverted microscope (Lund et al., 1958; CEN, 2006; Brierley et al., 2007; Mischke et al., 2012). A phytoplankton sample was counted for each month.

2.4 Flow and nutrient data for rivers

Nutrient loadings to the lake were calculated using monitoring results from the inflow of the major rivers. Weekly river water samples were obtained over the time series and analysed for SRP, nitrate and silica fractions as for lake water samples. Flow rates for the rivers were available from the Northern Ireland Rivers Agency in daily mean flows ($m^3 s^{-1}$). Total phosphorus, silica and nitrate concentration entering the lake from each of the eight monitored inflowing rivers were calculated using nutrient-specific regression equations (equation 1):

$$\log_{10}(C_{ij}) = a_j + b_j \log_{10}(Q_{ij}) \quad (1)$$

where C_{ij} is the nutrient concentration (μg l^{-1}) for river j on day i, Q_{ij} is the river flow ($m^3 s^{-1}$) for river j on day i and a_j and b_j are regression parameter estimates for river j in 2008.

Daily loads (kg), L_{ij}, were derived by multiplying the daily concentrations (equation 1) by daily flow for river *j* on day *i* for 2008. The load, L_{ij}, was corrected for bias using Ferguson (1987) yielding L_{cij}, that is $L_{cij} = L_{ij} \times \exp(2.651 s_j^2)$ where s_j is the estimated standard error of equation (1) for river *j*. The daily, Ferguson corrected, total loading to the lake from all of the rivers was derived by equation 2:

$$L_{ci} = \sum_{j=1}^{r} L_{cij} \qquad (2)$$

Where *r* is the number of rivers, L_{ci} is the Ferguson corrected total loading of a nutrient to the lake and L_{cij} is the Ferguson corrected daily load for river *j*.

2.5 Statistical analysis

Mann-Kendall tests were used to detect monotonic trends in water chemistry. This nonparametric test is based entirely on ranks and is robust against non-normality and censoring. Missing values are taken into account and the method can be extended to account for seasonality (Hirsch et al., 1982 and 1991).

2.6 The PROTECH model

PROTECH simulates the responses of between 8-10 species of lake phytoplankton throughout a 1D vertical water column at daily time steps. A full description of the model's equations and concepts has been already published (Reynolds et al., 2001; Elliott et al., 2010) but the main biological component of the model can be summarised through the daily change in the chlorophyll *a* concentration ($\Delta X/\Delta t$) attributable to each phytoplankton taxon:

$$\Delta X/\Delta t = (r' - S - G - D)\, X \qquad (3)$$

where *r*' is the growth rate defined as a proportional increase over 24 h, *S* is the loss due to settling out from the water column, *G* is the loss due to *Daphnia* grazing (it is assumed phytoplankton > 50 μm diameter are not grazed) and D is the loss due to dilution caused by hydraulic exchange. The growth rate (r') is further defined by:

$r' = \min \{r'_{(\theta,I)}, r'_{P}, r'_{N}, r'_{Si}\}$ (4)

where $r'_{(\theta,I)}$ is the growth rate at a given temperature and daily photoperiod and r'_{P}, r'_{N}, r'_{Si} are the growth rates determined by phosphorus, nitrogen and silicon concentrations below these respective threshold concentrations: < 3, 80 and 500 mg m^{-3} (Reynolds, 2006). The r' values are phytoplankton-dependent (e.g. non-diatom taxa are not limited by silica concentrations below 500 mg m^{-3} and nitrogen-fixing cyanobacteria are not limited by nitrogen) and also relate to the morphology of the taxon. Temperature and light are varied at each time-step throughout the simulated water-column. The value of $\Delta X/\Delta t$ (Equation 3) is modified on a daily time-step for each algal taxon in each layer of the water column (layers are 0.1 m deep).

The PROTECH model was set up to simulate the phytoplankton observed in 2008 in Lough Neagh. This year was selected because it provided the most complete range of driving variables for the model and its assessment. This included the flow and nutrient data calculated in section 2.4 and daily meteorological drivers (air temperature, wind speed, cloud cover) from Hillsborough. The latter allowed PROTECH to calculate the lake water temperature and structure. The eight phytoplankton genera selected to be simulated were *Planktothrix* (formerly *Oscillatoria*), *Pseudanabaena*, *Aulacoseira* (formerly *Melosira*), *Aphanocapsa*, *Gymnodinium*, *Dolichospermum* (formerly *Anabaena*), *Chlorella* and *Plagioselmus* (formerly *Rhodomonas*) and reflected the most abundant observed species. Comparisons were made between the modelled and observed data and the coefficient of determination calculated.

2.6 Future scenarios

The 2008 simulation was taken as a baseline and then re-run through a combination of progressive changes to air temperature and nutrient load. Each scenario was run for 10 years using the 2008 driving data repeatedly and the last year only was used for the analysis to allow the simulation time to stabilise under the new driving conditions. The different scenarios were created by increasing the original air temperature incrementally by 1 ^{o}C (finishing with a 4 ^{o}C increase) and decreasing simultaneously the 2008 daily nutrient loads of SRP and nitrate by a factor of 0.8, 0.6, and 0.4. This produced 20 scenario combinations (i.e. five different temperature and four different nutrient changes), including the baseline, and also covered a realistic range of predicted UK air temperature increases for the 21st century (Jenkins et al., 2009).Finally, the decision to alter air temperature alone, rather than in combination with other weather related variables, was made so that any simulated effects upon the modelled phytoplankton community could be easily proscribed to just this driver i.e. temperature.

3. Results

3.1 Historic observations

Whilst the Lough's key mean variables have varied considerably between years, there have been notable trends over the last 30 years. Total chlorophyll *a*, a measure of phytoplankton biomass, has declined (Mann Kendall z score = -2.56, $p < 0.05$) over the entire period (Fig. 1a). The key nutrients for phytoplankton growth showed varying trends with SRP increasing highly significantly (Mann Kendall z score = 3.77, $p < 0.001$; Fig. 1b), silica remained unchanged (Fig1c) and nitrate concentrations declined (Mann Kendall z score = -2.22, $p < 0.05$; Fig. 1d). One of the key phytoplankton species over the study period has been the cyanobacterium *Planktothrix agardhii* (Fig. 2). The species, which forms a large perpetual crop, has been decreasing in biovolume since the mid-1990s and closely follows trends in chlorophyll *a*, to which it contributes approximately 50% in the lake at present (McElarney et al., 2015a) and has been > 75% in the past (Gibson et al., 2000).

3.2 Calibration and validation of PROTECH

The only major calibrations to the model were to restrict the maximum simulated mixed depth to no deeper than 14 m from the bottom to reflect the shallow nature of the lake and to include sediment released SRP throughout the mixed water column between 1 May to 1 October (with an equivalent in–lake concentration of 2.0 mg m^{-3}); other coefficients were left at their standard values. The resulting comparisons between observed and simulated variables for the year 2008 proved to be good for total chlorophyll *a* ($R^2 = 0.71$, $P<0.001$) and that attributed to *Planktothrix* ($R^2 = 0.70$, $P<0.001$) (Fig. 3). The goodness-of-fit for other key modelled variables were also good, e.g. surface water temperature ($R^2 = 0.95$, $P<0.001$), phosphorus ($R^2 = 0.87$, $P<0.001$) and nitrate ($R^2 = 0.88$, $P<0.001$) concentrations.

3.3 Future scenarios

The scenarios testing the sensitivity of the lake to future environmental change examined the interaction between changing air temperature and nutrient inputs. The former had, of course, an effect on lake water temperature (Table 1) but it is interesting to note that the increase in water temperature was not as great as the corresponding air temperature, e.g. a 4 ^{o}C increase in air temperature only increased the mean annual water temperature by about 3 ^{o}C.

Annual mean in-lake nutrient concentrations showed little change with increasing temperature except for the +4 ^{o}C scenarios (Fig. 4). The largest changes occurred in scenarios where the nutrient loads had been reduced, although the direction of the response trend was dependent on the nutrient i.e. mean annual nitrate concentration decreased with decreasing loads whereas SRP increased.

In terms of the simulated phytoplankton at the annual and seasonal scale, the mean total chlorophyll *a* showed little change below +4 ^{o}C except in response to declining nutrient load (i.e. SRP and nitrate) where it also showed a slight decline (Fig. 5). Again, for the +4 ^{o}C scenarios there were large changes throughout most of the year (the spring period recorded the least change), with an increase in total chlorophyll *a* that became greater with declining nutrient load (Fig. 5).

The main phytoplankton behind these predicted changes were the two cyanobacteria genera *Planktothrix* and *Dolichospermum* (Fig. 6). The annual mean *Planktothrix* chlorophyll *a* followed closely the pattern of change seen for total chlorophyll *a*, with a large decline for the +4 ^{o}C scenarios and a marked effect of reduced nutrient load lowering the annual mean chlorophyll *a* concentration (Fig. 6a). Conversely, *Dolichospermum* chlorophyll *a* only reached significant numbers at +4 ^{o}C and produced the highest values under the lowest loading scenarios (Fig. 6b). This general response in the annual means of the two phytoplankton genera was reflected in their spring, summer and autumn chlorophyll *a* means (Fig. 6), although there were notable differences. For example, the spring means showed the smallest decline in *Planktothrix* and increase in *Dolichospermum* (Fig. 6c, d). Furthermore, the greatest increase in *Dolichospermum* was in the summer period (Fig. 6f) whereas the largest declines in mean *Planktothrix* chlorophyll *a* occurred in autumn (Fig. 6g).

4. Discussion

Lake management plans traditionally focus on nutrient management in order to reduce chlorophyll concentrations and improve phytoplankton diversity. Due to the resources required to further reduce catchment export of nutrients, it is useful to understand how the future trajectory of phytoplankton change may develop in the lake. Diffuse pollution from agriculture in the Neagh catchment has been difficult to ameliorate mainly due to agricultural intensification and a high proportion of land in the catchment used for farming (Bunting et al., 2007; Foy et al., 2003). Sixty-six percent of the catchment is currently under agricultural use, the majority for grassland grazing. Nitrogen loading to the lake has decreased between 2003 and 2010 by 935 t N yr while phosphorus loading has remained more stable with a loading of 485 tonnes for both years (McElarney et al., 2015b). Over the time series, SRP concentration in the Lough has continued to rise after a brief improvement due to the point source reduction (Foy, 1995). Sources of nutrients such as diffuse sources and internal loading from lake sediments are more difficult to reduce; the former is regarded as the major cause of pollution to water bodies in Europe (Smith, 2003).

As a result of the marked changes observed in the Lough and its catchment in the last few decades it is vital to predict the behaviour of phytoplankton under reduced nutrient concentrations and increased temperature. In order to investigate the potential trends in phytoplankton as a result of changing nutrients and water temperature we tested the sensitivity of the Lough to changes in the combined drivers of air temperature and nutrient load using the PROTECH model.

All models by their very nature are simplification and PROTECH is no exception. Caution must, therefore, be taken in interpreting model predictions, particularly when simulations are based on limited driving data such as in this study i.e. one year. However, conversely, some confidence in the model can be justified if it has been applied successfully in other applications, has been shown to model observed data well and if its predictions are intuitive given what is known about lake ecology from studies of the lake or other similar lakes. We make the case that this study fits these criteria: PROTECH has been applied to many lakes (e.g. see Elliott et al., 2010) and it was able to simulate, with limited calibration, the key variables in the lake as demonstrated by the high coefficients of determination calculated for them (e.g. Fig. 3). Thus, this allows some confidence to be expressed regarding the model's predictions.

It was clear from the future scenarios investigated that two different phytoplankton community states could potentially exist and that the trigger for this change was air temperatures 4 ^{o}C warmer than observed in 2008.

However, before focussing on this point of state change, it is worth discussing the changes observed in the other scenarios where the temperature increase was below 4 ^{o}C. In these simulations, the main axis of change for in-lake nutrients and phytoplankton chlorophyll *a* was not with temperature change but with decreasing nutrient load (SRP and nitrate). When the temperature increase was less than 4 ^{o}C the decline in nutrient load to the lake caused a decrease in algal biomass production because the nutrient-based carrying capacity for the phytoplankton was reduced. Whilst the in-lake concentration of nitrate decreased in line with the decline in external load, the in-lake SRP concentration increased due to the continued internal sediment release of SRP. This simulated effect mimics the recent observed trends in these two nutrients and shows that the in-lake legacy of phosphorus pollution in the sediments could continue to be an obstacle to ecological improvement in the Lough, especially considering its hydraulic residence time is more than 1 year. Furthermore, whilst not directly simulated in this study, it is known that water temperature and nitrate concentration are key variables in determining the sediment release of phosphorus (Jensen and Andersen, 1992) and their direction of change in Lough Neagh could lead to increased internal loading of phosphorus which may offset any reductions from the catchment.

The historical dominance of the Lough Neagh phytoplankton community by *Planktothrix* has already been discussed, but it is noteworthy that this dominance prevailed through all but the +4 ^{o}C scenarios. This is concerning because it suggests that even a 60% reduction of the 2008 phosphorus and nitrate loads is not enough to break its dominance in the lake. This is a phenomenon often seen in shallow, turbid, poorly flushed and nutrient rich lakes (Reynolds, 1994), where a positive feedback is established for this low-light tolerant cyanobacteria. The PROTECH model also reflects this low-light specialization in its modelling of *Planktothrix*, hence its continued dominance in most of the scenarios. Thus, whilst it has been speculated that its rise to dominance may have been greatly enhanced by nitrogen pollution to the lake (Bunting et al., 2007), a reduction in this nutrient does not guarantee a marked improvement in the lake. Such an effect is not uncommon in the recovery of shallow, nutrient-rich lakes (i.e. the hysteresis effect, Scheffer et al. (1997)).

Of course, this simulated *Planktothrix* dominance was broken dramatically for the +4 ^{o}C scenarios where another cyanobacterium, *Dolichospermum*, emerged to dominate. Although the trigger for this change was the increase in temperature, the mechanism behind it was nutrient based. Firstly, it is important to consider that the scenario means presented are of the final year of a continual ten year run. Thus, under the +4 ^{o}C conditions, algal growth generally increased enough to cause nitrate growth limitation to persist long enough for the nitrogen-fixing *Dolichospermum* to gradually establish dominance by the end of the ten year period. This switch in dominance created another positive feedback where phosphorus was in ample supply but nitrate was not, leading to reduced growth of non-nitrogen-fixing species like *Planktothrix* particularly in the latter half of the year. As was evident from Figure 6, this effect was enhanced even more when the reduction in nutrient loads was greater, and therefore nitrate became more scarce. Nitrate limitation appears to be more frequent in the Lough in recent years (McElarney et al., 2015a) and this nutrient has had more of an effect on the phytoplankton than phosphorus (Bunting et al., 2007). Our results suggest that even with decreased nitrogen and phosphorus loading from the catchment, nutrient dynamics will still play a dominant role in deciding phytoplankton species composition in the Lough. Phosphorus from the sediments may continue to be released, potentially negating any reductions from diffuse pollution in the catchment. If the observed trend in the reduction of catchment derived nitrogen, combined with increasing temperatures continues then it is likely to favour the rise of *Dolichospermum* spp., another toxic cyanobacterial genus. Indeed, previous PROTECH studies have shown similar increases in nitrogen-fixing species with increasing temperature (Elliott & May, 2008) or reduced flow (Elliott, 2010), all caused by changes in the availability of nitrate.

Sadly for the Lough and its water managers, these results suggests that, in the long term, one nuisance cyanobacterial bloom may only be replaced by another one, a phenomenon which is predicted to be more common in the future (Carey et al., 2012). Nitrogen fixing phytoplankton such as *Dolichospermum* or *Aphanizomenon* have been prevalent in the past (e.g. pre-1980, Bunting et al. (2007)) in the Lough and their presence in the community is still observed, so such a prediction should be regarded as a real possibility. Without a way to manage and reduce the phosphorus availability and increasing temperatures in the lake, it might therefore be assumed that we are a long way from observing any notable improvement in its ecological status. This must be taken into account when setting WFD water quality objectives in future River Basin Management Plans.

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Table 1. The change in annual mean water temperature (°C) in response to changing air temperature (°C).

	Change in air temperature (°C)				
	0	1	2	3	4
Mean annual water temperature (°C)	11.37	12.05	12.79	13.55	14.34

Figure Legends

Fig. 1 Lough Neagh annual mean time series concentrations (mg m^{-3}) for a) chlorophyll *a*, b) soluble reactive phosphorus (SRP), c) silica (SiO_2) and d) nitrate (NO_3-N)

Fig. 2. Time series comparison between annual mean total chlorophyll *a* concentration (mg m^{-3}) and annual mean *Planktothrix* biovolume (μm^3 ml^{-1})

Fig. 3. Comparison between observed (solid circles) and modelled (black line) chlorophyll *a* concentration (mg m^{-3}) in Lough Neagh 2008 for a) total chlorophyll *a* and b) estimated *Planktothrix agardhii* chlorophyll *a*.

Fig. 4. Predicted in-lake annual mean concentration (mg m^{-3}) in response to changing air temperature (^{o}C) and 2008 nutrient loads: a) phosphorus and b) nitrate.

Fig. 5. Predicted mean total chlorophyll *a* (mg m^{-3}) in response to changing air temperature (^{o}C) and 2008 nutrient loads: a) annual, b) spring, c) summer and d) autumn.

Fig. 6. Predicted mean chlorophyll *a* (mg m^{-3}) in response to changing air temperature (^{o}C) and 2008 nutrient loads: a) annual *Planktothrix*, b) annual *Dolichospermum*, c) spring *Planktothrix*, d) spring *Dolichospermum*, e) summer *Planktothrix*, f) summer *Dolichospermum*, g) autumn *Planktothrix*, h) autumn *Dolichospermum*.

Fig. 1

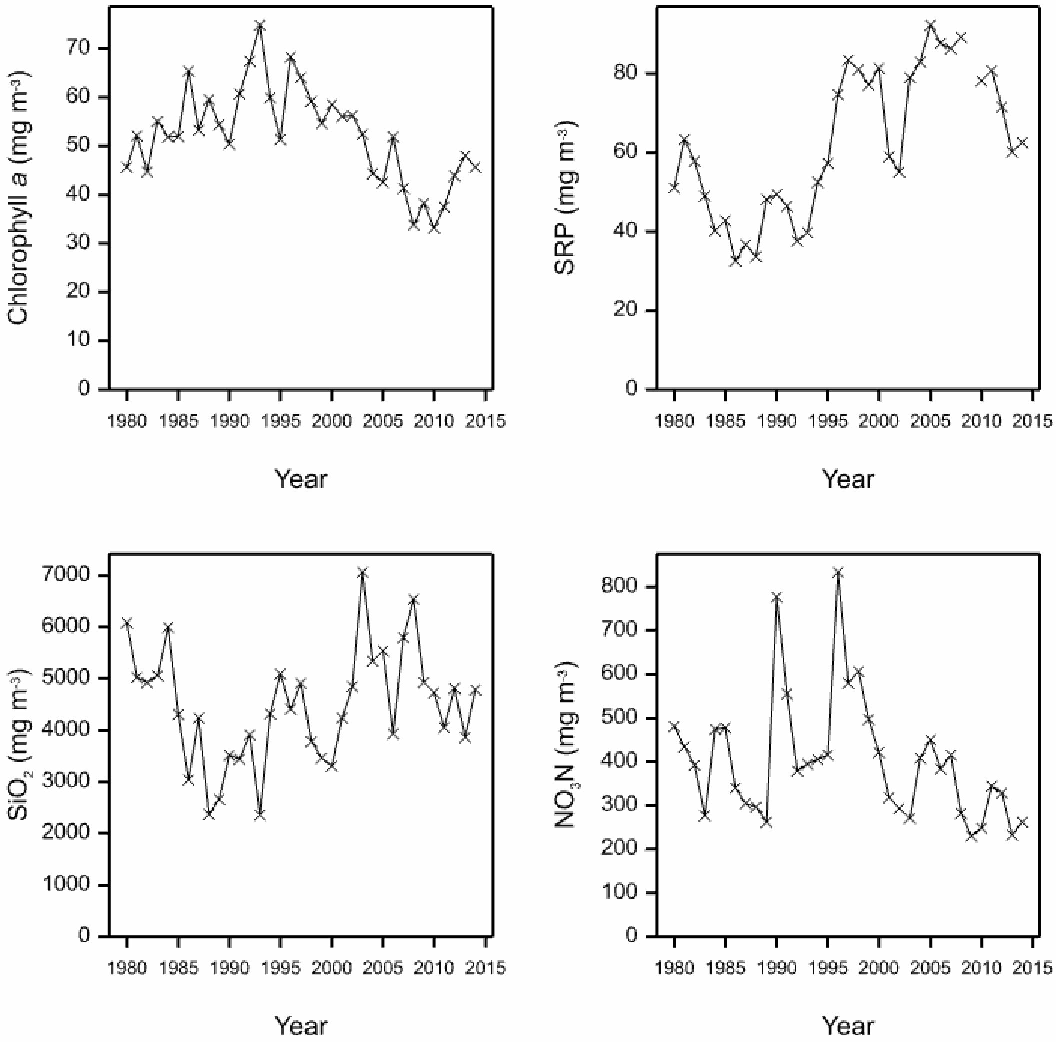
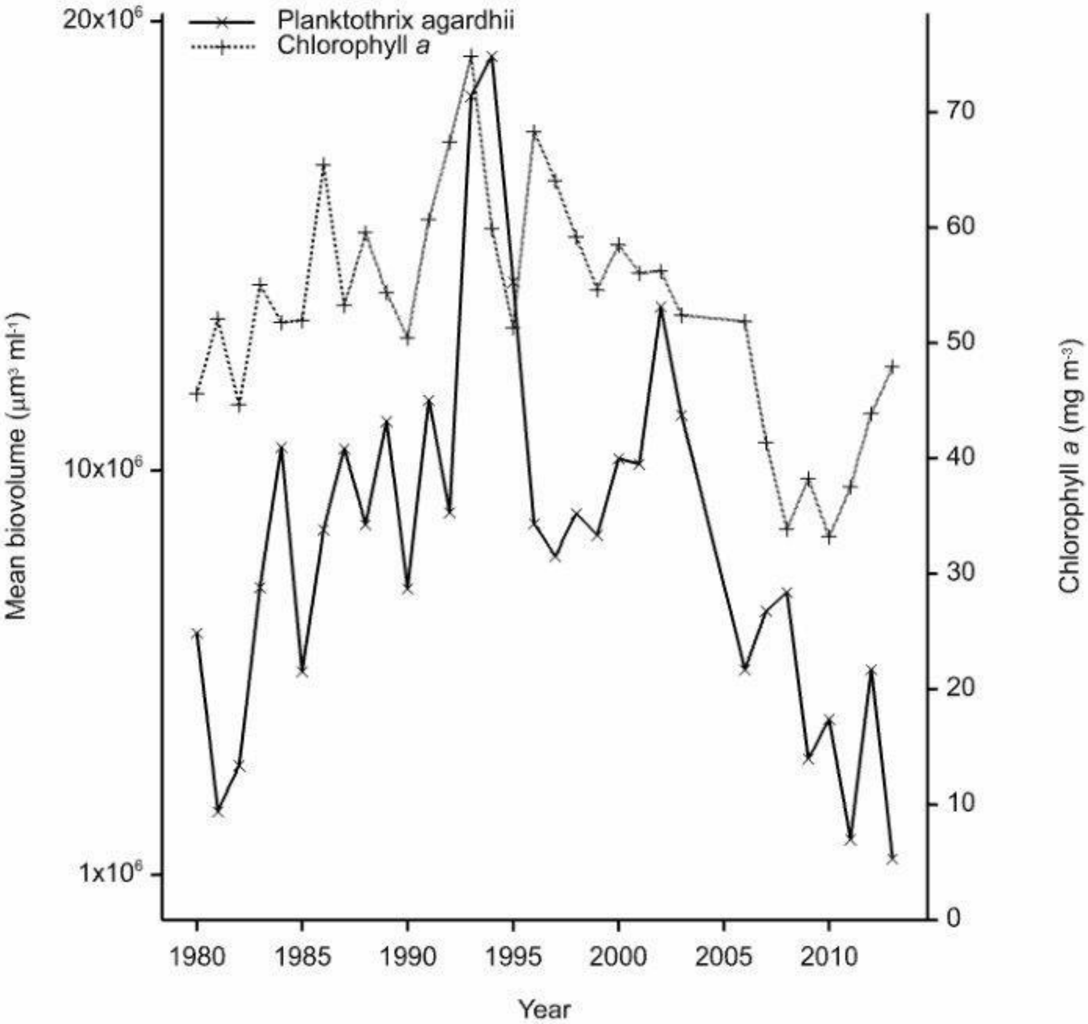
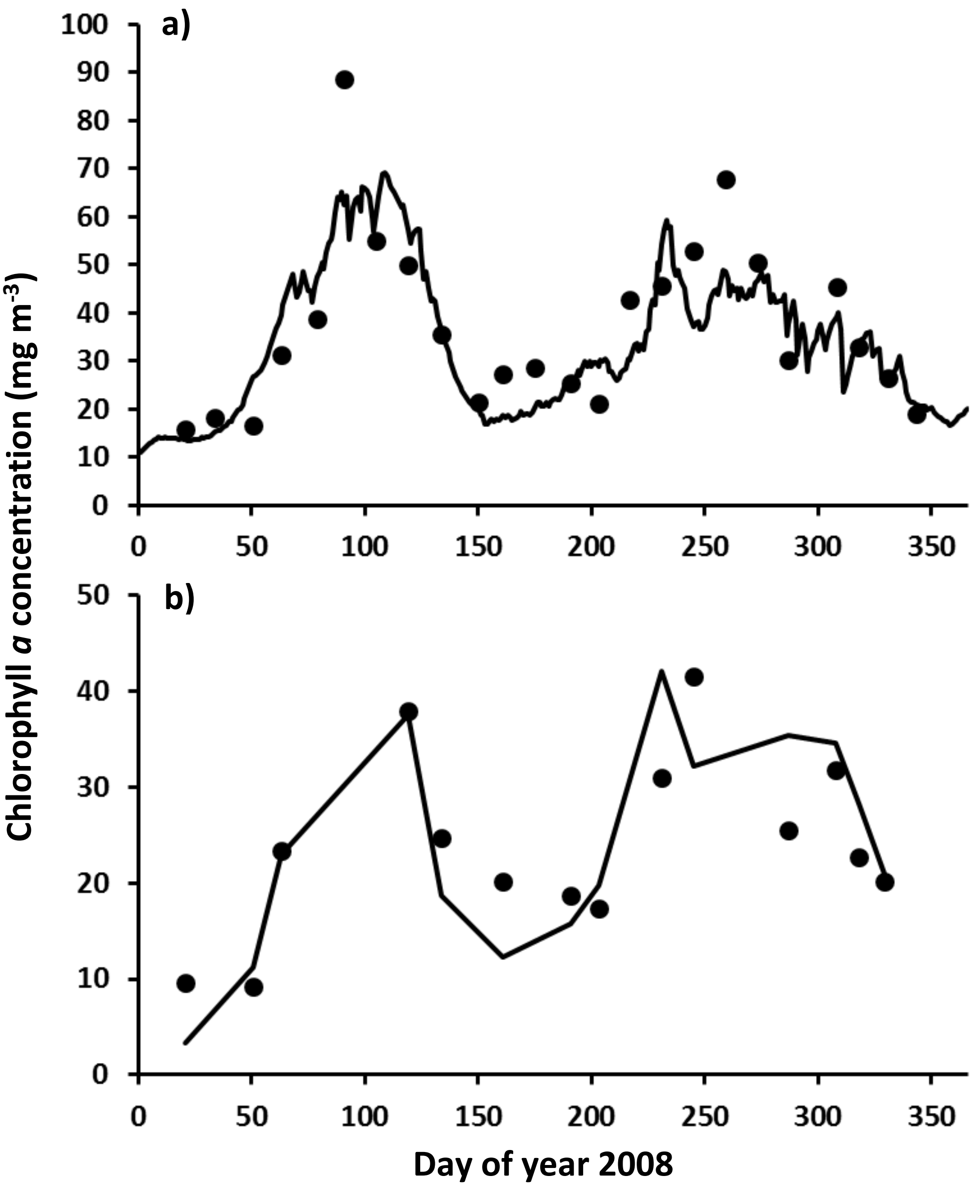

Chlorophyll a (mg m-3)
Year
SRP (mg m-3)
Year
SiO2 (mg m-3)
Year
NO3N (mg m-3)
Year

Fig. 2



Planktothrix agardhii
Chlorophyll *a*
20x10⁶
10x10⁶
1x10⁶
Mean biovolume (µm³ ml⁻¹)
70
60
50
40
30
20
10
0
Chlorophyll *a* (mg m⁻³)
1980
1985
1990
1995
2000
2005
2010
Year

Fig. 3



a)
b)
Chlorophyll a concentration (mg m-3)
Day of year 2008
100
90
80
70
60
50
40
30
20
10
0
0
50
100
150
200
250
300
350

Fig. 4

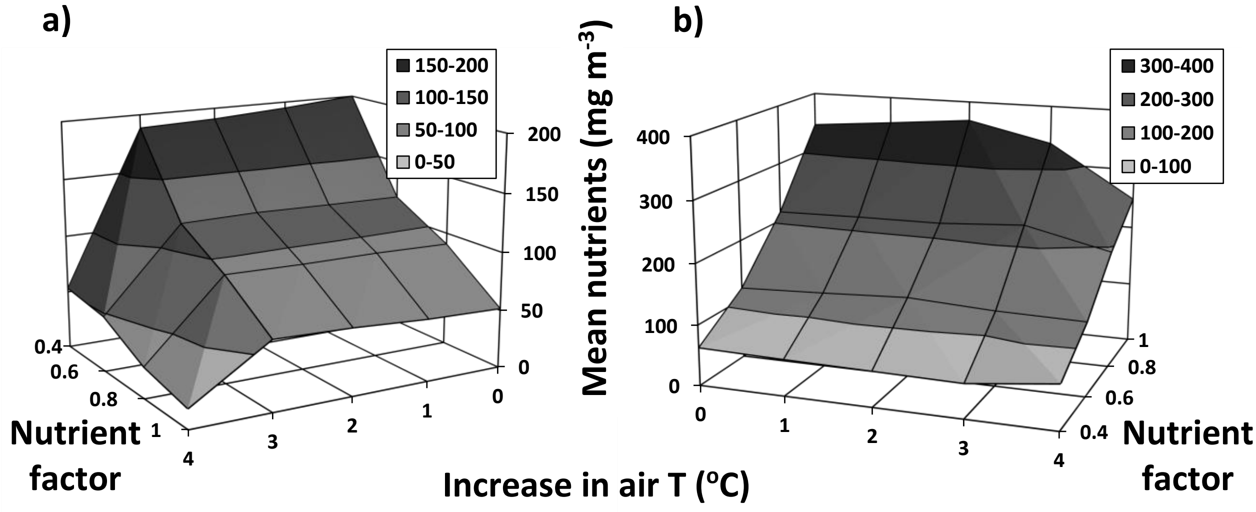
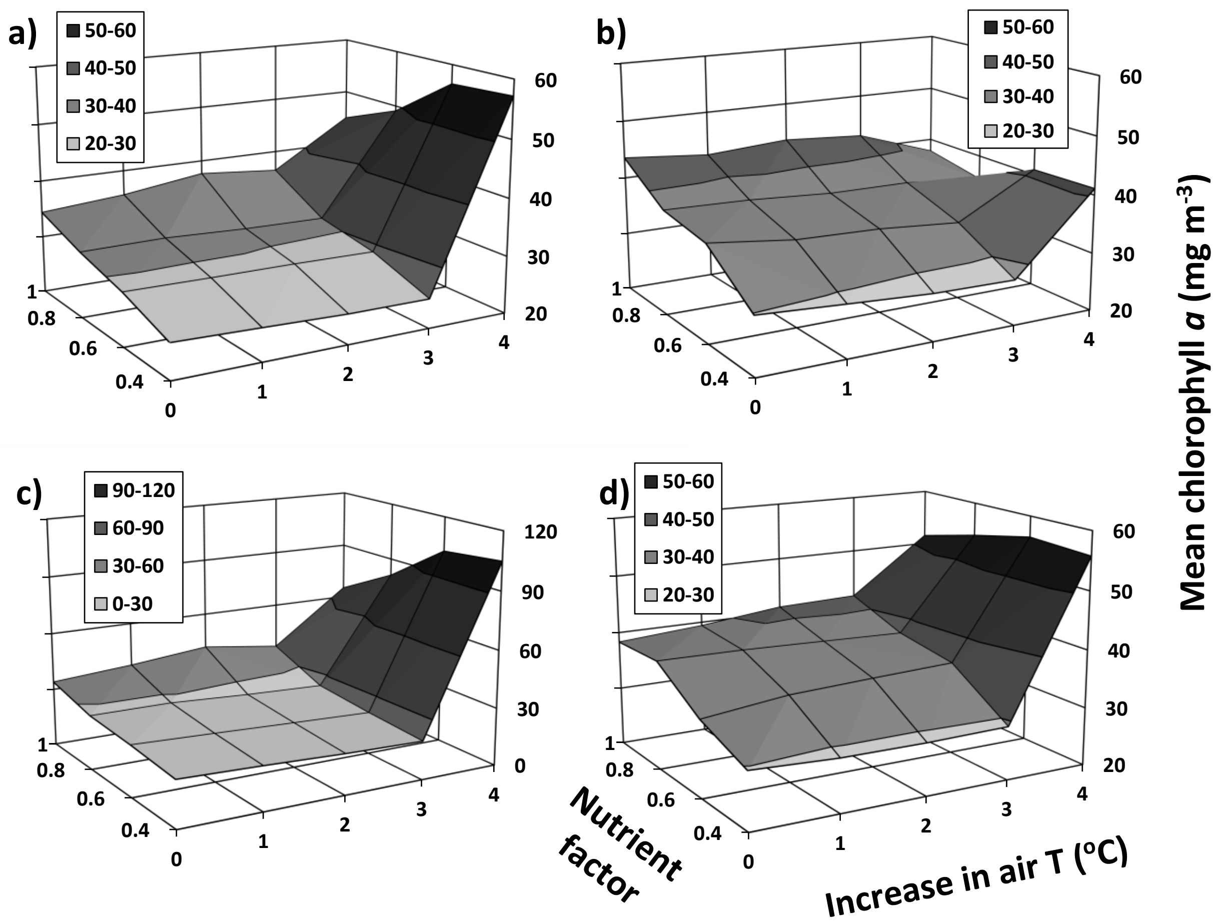
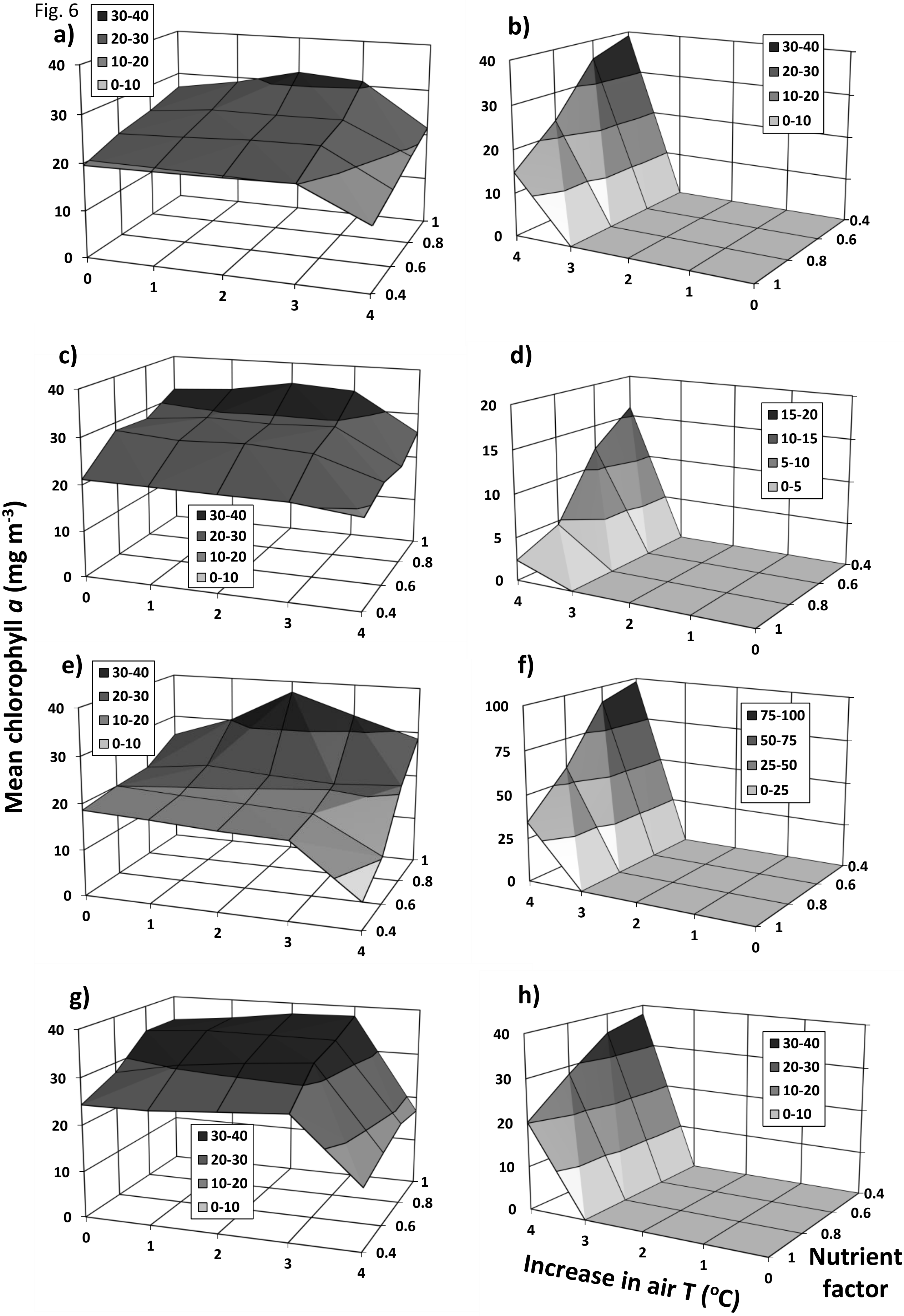

a)
150-200
100-150
50-100
0-50
200
150
100
50
0
0.4
0.6
0.8
1
4
3
2
1
0
Nutrient factor
b)
300-400
200-300
100-200
0-100
400
300
200
100
0
0
1
2
3
4
1
0.8
0.6
0.4
Nutrient factor
Mean nutrients (mg m^{-3})
Increase in air T (^{o}C)

Fig. 5



a)
50-60
40-50
30-40
20-30
b)
50-60
40-50
30-40
20-30
c)
90-120
60-90
30-60
0-30
d)
50-60
40-50
30-40
20-30
Mean chlorophyll a (mg m-3)
Nutrient factor
Increase in air T (°C)

Fig. 6



a)
30-40
20-30
10-20
0-10
b)
30-40
20-30
10-20
0-10
c)
30-40
20-30
10-20
0-10
d)
15-20
10-15
5-10
0-5
e)
30-40
20-30
10-20
0-10
f)
75-100
50-75
25-50
0-25
g)
30-40
20-30
10-20
0-10
h)
30-40
20-30
10-20
0-10
Mean chlorophyll *a* (mg m^{-3})
Increase in air T (°C)
Nutrient factor