Global Change Impacts on Phytoplankton Communities in nutrient-poor Lakes

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Abstract

Phytoplankton communities are recognized as important indicators for environmental changes since they usually respond rapidly to a changing environment in aquatic systems. To evaluate how changes in the climate and atmospheric deposition might impact phytoplankton communities, we examined a complete 14-year time series of different physical, chemical and biological variables from 13 nutrient-poor Swedish reference lakes along a latitudinal gradient.

We found numerous significant changes in physical and chemical lake conditions that were highly coherent among the lakes, in particular for sulfate concentrations, surface water temperatures and intensity of thermal stratification. The phytoplankton biomass and species richness of six phytoplankton groups, measured at the same occasions as the water chemical variables, showed only few and weak significant changes over time. The only coherent significant change over Sweden, occurring in seven lakes, was observed in the species richness of chlorophytes. We claim that the response of the phytoplankton biomass and species richness to strong physical and chemical changes is comparatively weak and lake-specific.

While many studies deal with the loss of species as a response to global change, we were able to show that some species can clearly profit from global changes. Analyzing long-term data and carrying out laboratory experiments we were able to detect a direct temperature effect on the growth rates of the nuisance alga *Gonyostomum semen*, which could explain the increases in the occurrence and abundance of this species over Sweden. From the results we predict that *Gonyostomum semen* will further increase in its distribution and abundance along with increasing temperatures. The findings of this thesis give new insights into the impact of global changes on phytoplankton community structures in nutrient-poor lakes.

Keywords: biodiversity, global change, coherence, phytoplankton, nuisance alga, *Gonyostomum semen*

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The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity.

D. Tilman

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Bloch. I., Weyhenmeyer, G.A. (2010). Long-term changes in physical and chemical conditions of nutrient-poor lakes along a latitudinal gradient – is there a coherent phytoplankton community response? *Submitted to Aquatic Sciences*.

II Bloch. I., Rengefors, K., Weyhenmeyer, G.A. (2010). Rapid increase in the occurrence of the microalga *Gonyostomum semen* in response to warmer temperatures. *Submitted to Harmful Algae.*

The contribution of Ina Bloch (IB) to the papers included in this thesis was as follows:

I IB performed statistical analyses and wrote large parts of the manuscript.

II IB designed, planned and performed the experimental work and statistical analyses, wrote large parts of the manuscript and acts as corresponding author.

1 Introduction

The United Nations declared 2010 to be the International Year of Biodiversity. Human activities have resulted in an accelerated loss of species (Kerr & Currie, 1995). These losses are often irreversible and have major effects on the functioning of ecosystems and the resources we all rely on every day. Especially freshwater ecosystems act as vital resources for humans. Those ecosystems also have been recognized for disproportional contribution to the global biological richness; freshwater habitats occupy only approximately 0.8 % of the Earth's surface, yet this tiny fraction of global water supports almost 6% of all described species (Dudgeon *et al.*, 2006). But at the same time it has been realized that the extinction risk for freshwater species could be among the highest of all (Revenga *et al.*, 2005; Strayer & Dudgeon). For a sustainable future it is of vital importance for freshwater management to understand and predict changes in the different lake ecosystems. Among the global changes, changes in the climate and atmospheric deposition are of major importance everywhere, causing a variety of physical, chemical and biological changes in lake ecosystems (Weyhenmeyer, 2008; Mooij *et al.*, 2005).

The response of lake ecosystems to alterations in the climate and atmospheric deposition usually varies substantially among the ecosystems, depending on, e.g., their geographic position, their trophic status, their morphometry and their sediment and catchment characteristics (e.g. (Blenckner, 2005; Soranno *et al.*, 1999). To link recent biological changes to climate change can therefore be complicated because local, non-climatic influences such as land-use changes often have a much greater impact on the biological community. But nonetheless a systematic trend and an underlying signal from climatic changes have been documented by the

Intergovernmental Panel on climate Change (IPCC) to be the cause of recent observed changes.

Phytoplankton are fundamental components for the whole food-web as primary producers of organic matter, as oxygen producers and compartments of the microbial loop (Falkowski, 1994; Azam *et al.*, 1983) The composition of the phytoplankton community also has great influence on the structure of the grazer population (Carpenter *et al.,* 1985). Grazers feed selectively on phytoplankton, depending on the size, toxicity or availability to escape predation of the algal species (Knisely & Geller, 1986). Phytoplankton is therefore considered as an ecologically important group in most aquatic systems, and it is quite essential for future lake management to understand and study how global changes such as climatic changes are affecting the whole phytoplankton community as well as individual taxonomic and functional groups. The relation between climate warming and enhancement of phytoplankton biomass has been demonstrated by experimental approaches, showing that different functional groups will respond differently to changes in climatic conditions (Domis *et al.*, 2007; Arheimer *et al.*, 2005).

Among freshwater organisms most studies have been focused on fish and only limited information about the effects of global change on other groups exists. Especially the implications for microbial communities such as phytoplankton species assemblage are still poorly understood. Previous studies have shown that phytoplankton responds quickly to changes in weather and catchment and the composition is affected by a combination of physical, chemical and biological factors (Soranno *et al.*, 1999; Reynolds, 1998). On a longer time scale the phytoplankton community composition can also be determined by global processes such as climate warming (Adrian *et al.*, 2006). Most studies so far deal with zooplankton or refer to marine environments. To use phytoplankton as an indicator for changes in ecosystem is reasonable because the response time to environmental changes is on a suitable time scale for human observers (Reynolds, 1998).

Predicted and ongoing effects of global change on aquatic systems are increase in water temperature, changes in the duration of ice cover and the growing season (e.g. Magnuson *et al.*, 2000). In addition, changes in the magnitude and duration of run-off regime as well as alterations in water chemistry such as nutrient levels are expected (Poff *et al,* 2002; Rouse *et al.*, 1997). Aquatic biota is expected to be heavily influenced by those alterations and effects are already seen for food web structure and dynamics, primary and secondary production, and species distributions and range shifts (reviewed in: Heino *et al.*, 2009; Wrona *et al.*, 2006). All taxonomic groups are affected and for phytoplankton it has been shown that especially spring bloom dynamics are extremely sensitive to such global changes (Adrian *et al.*, 1999; Weyhenmeyer *et al.*, 1999).

Different taxonomic and functional groups are also likely to be impacted differently and have to be considered individually. In a warmer climate certain groups like cyanobacteria can gain advantage over the phytoplankton community, (Domis *et al.*, 2007; Elliott *et al.*, 2006), but also other groups like dinoflagellates or chryptophytes show greater abundances (Findlay *et al.*, 2001) due to different life strategies and ability to adapt to certain changes. A rare group in lakes are the Raphidophyceae with its most common freshwater representative *Gonyostomum semen* (Ehrenberg) Diesing, a large flagellated microalgal species (30 -100 µm). This algal species has been known to adversely affect lakes used for recreation, as it discharges mucilaginous strands upon contact, thereby covering bathers with a slimy layer, often causing itching and other allergic reactions (Cronberg *et al.*, 1988). Consequently, the Swedish Environmental Protection Agency has termed it as a noxious species. During recent decades it has become a nuisance alga in many lakes, where it forms intensive blooms (Cronberg et al. 1988) and where it can dominate the phytoplankton community by as much as 98% for extended periods (Willén 2003). The factors that promote this increase of *Gonyostomum semen* are still not fully understood.

2 Objectives

The overall objective of this thesis was to asses the impact of global change such as climate and atmospheric deposition on phytoplankton communities in nutrient-poor Swedish lakes in order to gain quantitative measures on ongoing and future global change related biodiversity changes.

The major questions addressed were:

1. How strong is the global change impact on phytoplankton communities in nutrient-poor Swedish lakes?
2. Are global change effects on phytoplankton communities coherent among lake ecosystems?
3. Can global change, in particular, temperature increases explain the increasing distribution and abundance of *Gonyostomum semen* in Swedish lakes?

The thesis consists of two papers that give answers to the questions; Paper I investigates the possible coherent response of the phytoplankton community to changes in environmental variables whereas Paper II focuses on one particular species, *Gonyostomum semen*, and factors that lead to the increase in its distribution and abundance.

3 Material and Methods

3.1 SLU database

The basis for the research is Sweden's unique long-term data series gained within SLU's monitoring and assessment task. The Swedish national monitoring of inland surface waters is financed by the Swedish Environmental Protection Agency (SEPA). The aim of the monitoring program is to provide data for an assessment of long-term changes such as changes related to global change but also regional and local anthropogenic stressors. To test the hypotheses in this thesis it was important to use complete homogenous time series on both water chemistry and biological variables. For this study we were able to investigate environmental impacts on the phytoplankton community structure and biomass in 13 widely distributed reference lakes that are not affected by land-use changes in the catchment. The Swedish national lake inventory program includes more than 13 lakes but in other lakes sampling has been infrequent, making the data inappropriate for our study.

3.2 Study lakes (Paper I and II)

We examined monthly data during the main growing season from May to October on physical, chemical and biological conditions. We used complete time series on both water chemistry and phytoplankton biomass as well as phytoplankton species richness for a total of 13 lakes distributed over Sweden (Fig. 1). For paper I the analyses was restricted to the 14 year time period from 1992 to 2005 since it was a methodological change in the monitoring program in 1992, making the species data less good to compare. For paper II a time period of 20 consecutive years from 1988 to 2007 was possible to examine since we focused only on one particular species. The northernmost lake is located in the Arctic region; the southernmost one is situated in the boreo-nemoral zone. The lakes are relatively small (mean lake area 0.81 km^2 ± 0.77), shallow (mean depth 5.4 m ± 2.7) and nutrient poor. The lakes serve as reference lakes, i.e., lakes that apart from atmospheric deposition and climate change are not or only a little influenced by anthropogenic activities in the catchment area. A detailed description of analyses and lake characteristics is available on http://www.slu.se/aquatic-sciences.

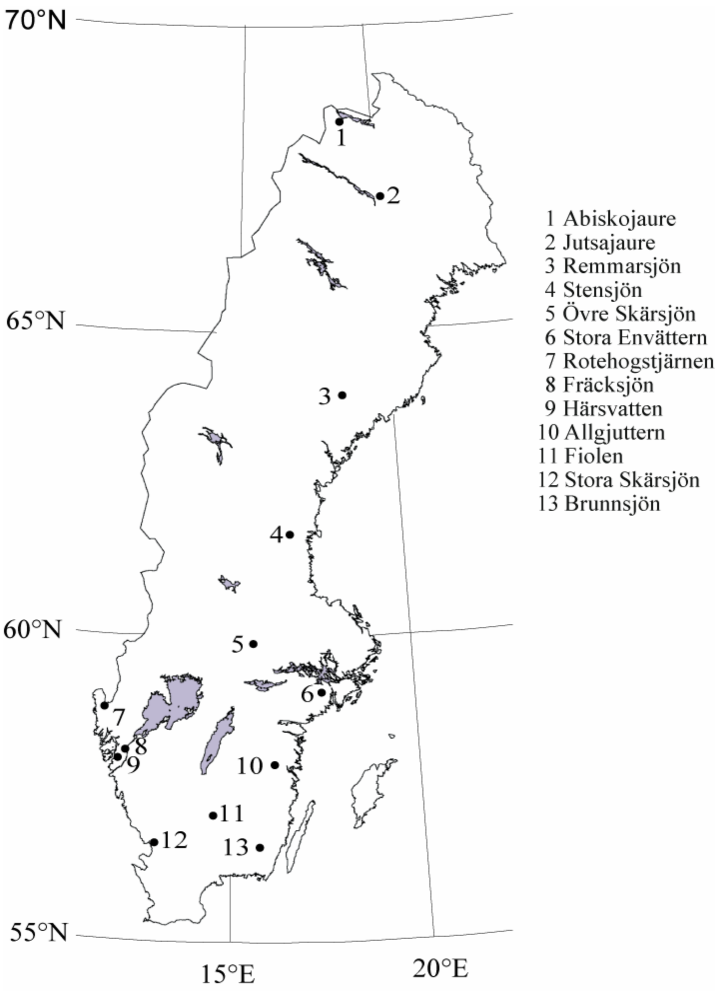

Figure 1. Map of Sweden showing the locations of the 13 study lakes.

3.3 Methods used for the coherence study (Paper I)

In this study we considered phytoplankton species richness as the number of all taxa that were found in the lake water during one sampling occasion. We analyzed the total number of species as well as the number of species in each of the six main phytoplankton groups occurring in the lakes: chlorophytes, diatoms, chrysophytes, cryptophytes, dinoflagellates and cyanobacteria. These phytoplankton groups were also used when we evaluated changes in the phytoplankton biovolume, referred to as biomass.

Trends over time were analyzed by the nonparametric Mann-Kendall test. To test the statistical significance of trends in the time series we used Kendall's tau, which is an approved tool to examine non-normal distributed data. Coherence in temporal variations of a variable between lakes was tested by pairwise correlation, giving Pearson product-moment correlations for each pair of Y variables, using all available values.

To examine the relationships between changes in physical and chemical conditions and phytoplankton biomass and species richness we used partial least square models (PLS) which can be used for predicting one or several dependent variables on the basis of several independent variables (Martens and Naes 1989; Esbensen et al. 1994). For the prediction of the phytoplankton biomass and species richness of six different groups we used all available 18 physical and chemical variables as input variables.
A detailed description of the methods can be found in the original paper (Paper I).

3.4 Methods used for the *Gonyostomum* study (Paper II)

This paper is focused on the species *Gonyostomum semen* (Ehrenberg) Diesing, a large flagellate (30 -100 µm), that belongs to the class Raphidophyceae. A combination of data base analysis and laboratory experiments were used to study the effect of climate change, in particular the effect of temperature on *Gonyostomum semen*. We used the seasonal Mann-Kendall test to analyze the statistical significance of trends in the time series, which is an approved tool to examine non-normal distributed data. A non-parametric Wilcoxon-test was applied for testing significant differences between groups. Abrupt changes in long-term time series were determined by using the Excel add-in ‘Sequential Regime Shift Detection version 3.2’ (SRSD) The multivariate analysis consisted of PLS.

Two *Gonyostomum* strains (GSB02 and GSTV1) were established from single cell isolates from the humic lakes Bokesjön in southern Sweden and Tvigölingen in central Sweden, respectively. Temperature effects on growth rates were determined using culture tubes (30 ml of medium) in an aluminum temperature gradient bar (Fig. 2), which contained holes for the insertion of culture tubes arranged in rows of four between the two ends of the bar (Rengefors & Anderson, 1998; Blankley & Lewin, 1976).

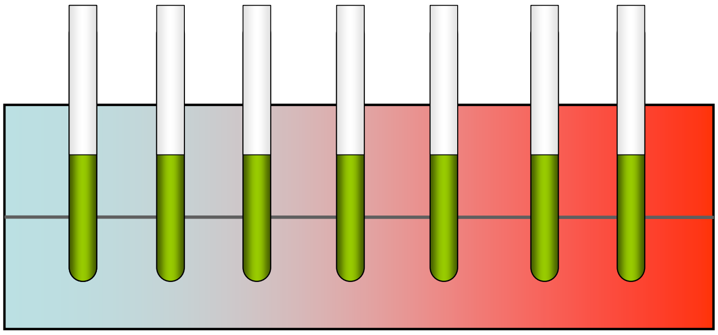

Figure 2. Schematic drawing of the aluminum temperature gradient bar. Heating one end and cooling the other results in a temperature range of 3 to 28°C.

The growth rate was monitored every 5th day with *In vivo* fluorescence measurements. The specific growth rates were compared between strains and among temperatures using repeated measures ANOVA. For a more detailed description, I refer to the original paper (Paper II).

4 Results and discussion

4.1 Response of phytoplankton communities to global change (Paper I)

Despite strong coherent physical and water chemical changes among our 13 nutrient-poor references lakes during the 14 year period we were not able to detect strong coherent changes in the phytoplankton biomass and species richness over the same time period (Fig. 3).

A lack of coherence in the response of biological variables to global changes among lakes might not be completely unexpected since it has been shown in other studies that coherence in temporal variations of phytoplankton among lakes can be hampered by the fact that there are other anthropogenically induced changes. Moreover the strong impact of local and lake-specific internal factors on the phytoplankton composition and growth such as grazing pressure, nutrient availability and underwater light availability (Kratz *et al.*, 2003, Baines et al., 2000; Magnuson *et al.*, 1990) lessen a coherent response.

However, when carrying out this study we expected at least strong lake-specific phytoplankton community responses to the strong physical and water chemical changes. According to this study it seems that phytoplankton community changes are weaker than physical and water chemical changes, no matter whether phytoplankton biomass or species richness is considered.

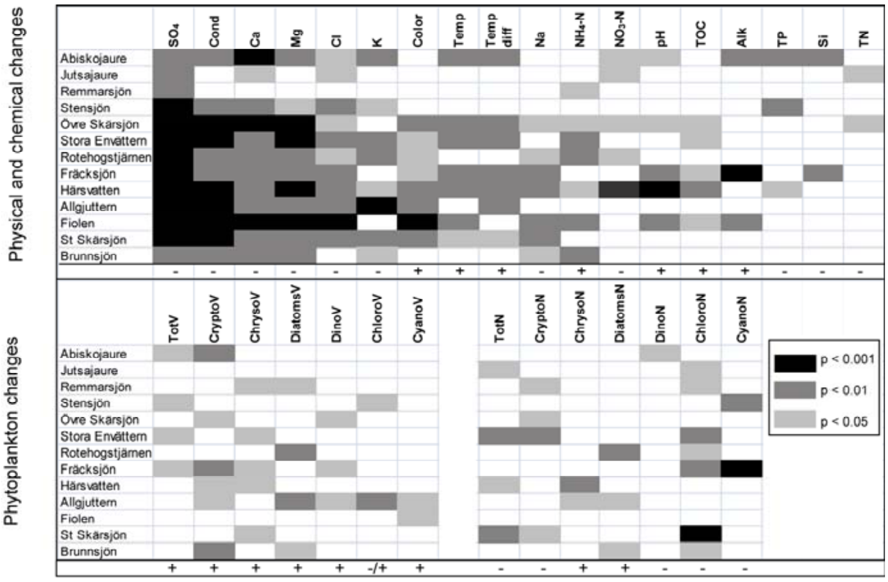

Figure 3. Temporal changes in physical and chemical lake variables and in the phytoplankton biomass and species richness in 13 nutrient-poor lakes from 1992 to 2005. The lakes are sorted from north to south. The significance levels of the changes have been determined by the Mann-Kendall test and are marked by different colors (black for $p < 0.001$, dark grey for $p < 0.01$ and light grey for $p < 0.05$). For abbreviations of physical and chemical variables see methods. Phytoplankton has been abbreviated as follows: Tot = total phytoplankton, Crypto = cryptophytes, Chryso = Chrysophytes, Dino = dinoflagellates, chloro = chlorophytes and cyano = cyanobacteria. V is the abbreviation for biovolume and N for number of species. The signs + and – indicate the overall direction of the significant trends for each variable. Very few significant trends deviated from this overall direction, in particular significant trends observed in the lake in the far North.

Several explanations are possible for a rather weak phytoplankton response. Threshold levels of resources have been shown to exist in the natural environment and the diversity of the phytoplankton community is partly governed by the available levels of the resources (Interlandi & Kilham, 2001). These threshold values might not have been reached in the nutrient-poor reference lakes so that phytoplankton responses remain weak. One other factor our data set could not account for were biological interactions, like grazing pressure that may have a greater local effect on the reaction of the algal community than global change impacts. Another explanation might be that there is a time delay between physical and water chemical changes and changes in the phytoplankton biomass and species richness. Our time series are yet too short to allow evaluation of any time delays but from long-term case studies we know, for example, that phytoplankton adaptation to other pressures like reduced lake phosphorus concentrations requires a couple of years (Willén, 2001).

Although we were not able to find a general pattern of a coherent response in the phytoplankton biomass and species richness to strong coherent physical and water chemical changes across Sweden the group of chlorophytes demonstrated a significant decline in its species richness in 7 out of 13 lakes. Chlorophytes showed the strongest and most coherent association to thermal stratification and surface water temperatures when modeled with PLS. The close association of chlorophytes to water temperatures might explain why only the chlorophyte species richness showed a coherent response over Sweden. Among 18 physical and water chemical variables, changes in water temperature were most coherent over Sweden, probably resulting in variables that are closely linked to water temperatures such as the chlorophyte species richness, also showing coherent changes. It has earlier been shown that synchronous responses of water chemical variables to global changes were restricted to variables closely linked to surface water temperature (Weyhenmeyer, 2004).

A temperature effect was also expected on cyanobacteria according to the results of other studies (e.g. Elliott *et al.*, 2006; Arheimer *et al.*, 2005; Weyhenmeyer, 2001). Indeed temperature was among the important variables of some of the PLS models for the prediction of cyanobacteria in the individual lakes but temperature was not important for the cyanobacterial development in all lakes. Instead nutrient concentrations came out as important variables. We suggest that the nutrient supply in the investigated oligotrophic lakes is not yet high enough to trigger cyanobacterial blooms, a reason why nutrient concentrations are often more important than temperature in the PLS models. In addition cyanobacteria are known to be sensitive to humic substances (Prokhotskaya & Steinberg, 2007) which might explain the lacking increase in our increasingly brownish lake waters.

Chlorophyte species were not only influenced by thermal stratification and surface water temperatures but also by water color. Increasing water color, caused by an increased input of humic substances, has been shown to influence chlorophytes, although large difference between species occur (Karasyova *et al.*, 2007). On that account we propose that a coherent decrease in the species richness of chlorophytes over Sweden might also be a result of a coherent increase in water color over Sweden.

4.2 Increase in the occurrence of Gonyostomum semen as a response to warmer temperatures (Paper II)

This study shows that *Gonyostomum semen* has significantly increased in its occurrence and abundance in Swedish lakes since 1988. At the beginning of the time series *Gonyostomum semen* was detected only in Lake Rotehogstjärnen, but over the period 1988 to 2007 it appeared in eight of the thirteen lakes (Fig. 4). Before 1997 it was found, besides Lake Rotehogstjärnen, only in three more lakes but only at one sampling occasion each and in very low concentrations.

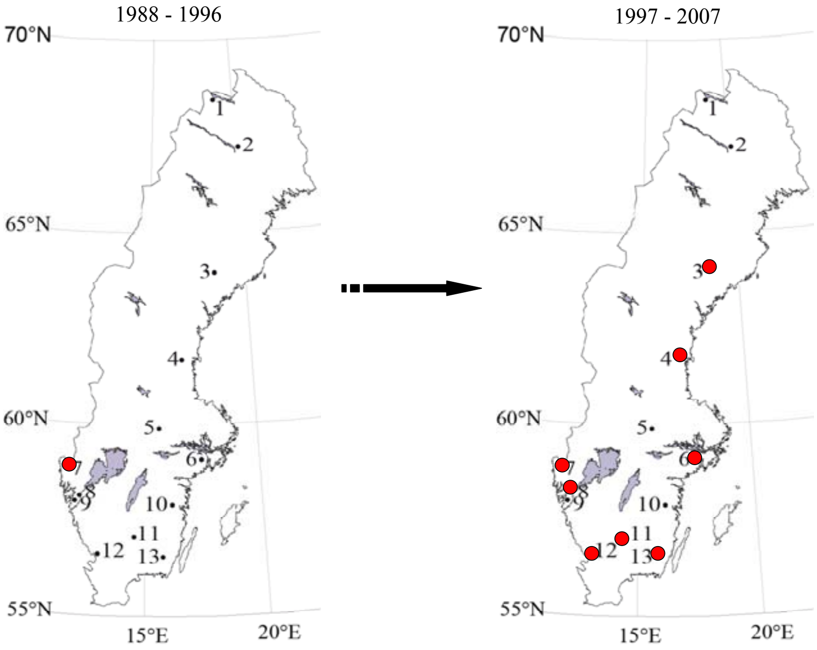

Figure 4. Occurrence of *Gonyostomum semen* in 13 lakes between 1988 – 2007. Red circles symbolize lakes where *Gonyostomum semen* was found.

Variables that best explained the observed increase were increases in surface water temperature and the intensity of thermal stratification. Temperature is an important determinant of seasonal changes in phytoplankton abundance, especially for those that have overwintering resting stages (Anderson & Rengefors, 2006). *Gonyostomum semen* is a typical example of a species that switches between a planktonic vegetative phase and an overwintering resting stage (Figueroa & Rengefors, 2006). The resting cyst is considered as an adaptation to survive during unfavorable environmental conditions (Fryxell 1983), including suboptimal abiotic growth conditions (Anderson *et al.*, 1983), as well as predators and parasites (Toth *et al.*, 2004; Rengefors & Anderson, 1998; Hansson, 1996).

Our temperature growth experiments clearly indicate that optimum temperatures for the growth of *Gonyostomum semen* lie between 9 and 12°C (Fig. 5).

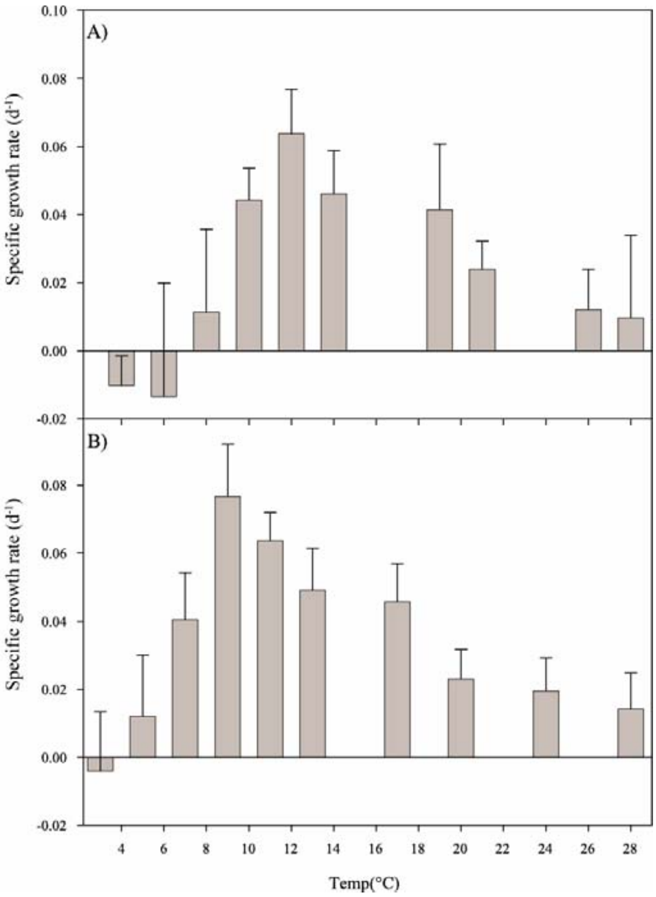

Figure 5. Specific growth rates of *Gonyostomum semen* for the strains GSB02 from southern Sweden A) and GSTV1 from central Sweden B). Shown are mean values and standard

deviations of four replicates at five sampling days that were grown at each temperature for 25 days.

Growth was still ongoing at temperatures above 12°C, indicating that *Gonyostomum* grows well at higher water temperatures. We were able to explain the occurrence of *Gonyostomum* in the study lakes to 45 % by a simple proxy, namely the period of surface water temperatures exceeding 10°C (Fig. 6). Since surface water temperatures during summer frequently exceed 10°C, most pronounced changes in the *Gonyostomum* biomass in a warmer climate are expected to occur during spring and autumn.

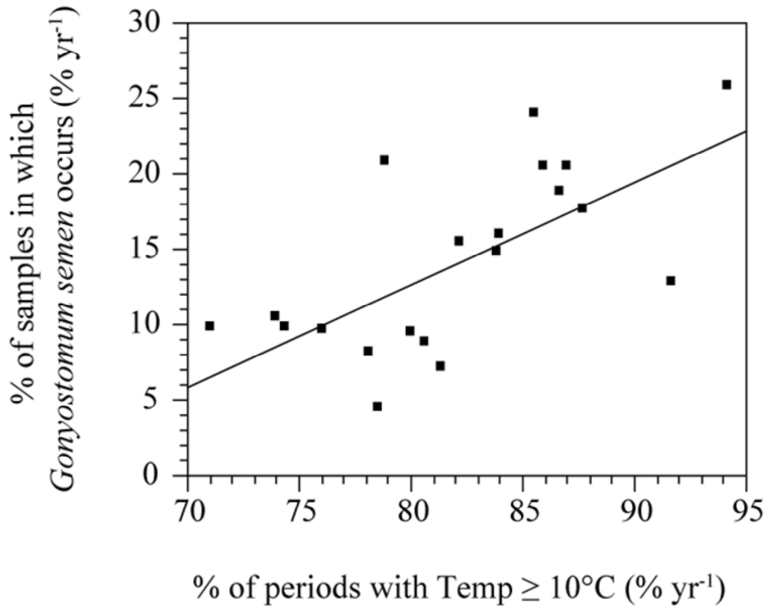

Figure 6. Relationship between the percentage of samples in which *Gonyostomum semen* occurred and in which surface water temperatures (Temp) were ≥10°C in relation to the total number of samples taken in 13 Swedish lakes on a monthly interval in the growing season from May to October during 1988-2007. Each square represents one year. The regression equation runs: y = 0.68x – 41.84 (R^2 = 0.45, p < 0.001, n = 20)

This expectation was fulfilled by our results showing most prominent changes in the *Gonyostomum semen* biomass in October. The changes were, however, not strictly linear but rather abrupt. In 2002 *Gonyostomum semen* occurred for the first time in two of our eight *Gonyostomum* lakes which coincided with an abrupt increase in surface water temperatures.

We found not only increasing surface water temperatures relevant for increases in the *Gonyostomum semen* biomass, but also increasing thermal stratification. Strong thermal stratification reduces water column mixing and results in depletion of nutrients in the epilimnion where autotrophic organisms have their habitat. *Gonyostomum semen* will be favored by such conditions since it has the capacity to migrate vertically, resulting in a maximization of nutrient uptake in the hypolimnion and photosynthesis in the epilimnion (Salonen & Rosenberg, 2000). However, this is not unique to *Gonyostomum semen* as vertical migration is also undertaken by many other species including both cryptophytes (Knapp *et al.*, 2003) and dinoflagellates (Heaney & Talling, 1980), but their occurrence is less annoying to humans in freshwaters and less often observed since their blooms are not equally pronounced as the ones of *Gonyostomum semen*. In addition, *Gonyostomum semen* is often suggested to be an invasive species that can potentially alter food web interactions (Hansson, 2000).

Our two *Gonyostomum semen* strains that we used for the laboratory experiment were taken from two different geographical regions with different climatic regimes. Our results suggest that *Gonyostomum* might have the capability to adapt its growth rate to the climatic region since the strain from the colder geographical region, GSTV1, showed its growth optimum at lower temperatures than the strain from the warmer geographical region (Fig. 5). This finding suggests that the growth optimum of *Gonyostomum semen* might shift towards warmer temperatures in a warmer climate, providing a possible mechanism to explain the development of *Gonyostomum semen* in relation to temperature. The temperature response might have negative socio-economic and ecological effects since periods when *Gonyostomum semen* occurs in the water column will prolong along with a prolongation of periods when surface water temperatures stay above 10°C. If *Gonyostomum semen* begins to dominate the phytoplankton biomass as it usually does in the lakes where it occurs, the growth of other phytoplankton species that provide a good food source for primary consumers might be inhibited. Thus decreases in biodiversity are expected. Here, we have evidence that one species is favored by temperature increases while others might not be. It remains to study what effects an increase in the distribution and abundance of Gonyostomum semen has on ecosystem structure and functioning.

5 Conclusion and future perspectives

Biological communities in aquatic systems seem to act much more unpredictable to global changes than water physical or chemical variables but it is undeniable that phytoplankton communities are affected by global change such as changes in the climate and atmospheric deposition. These effects are, however, rather lake-specific probably because algal groups respond differently to complex interactions of direct and indirect global change impacts. In addition, biological variables respond very often first when a threshold value has been exceeded. By studying the effects of global changes on phytoplankton communities, it became obvious that each lake has its unique features and every phytoplankton community is influenced by a variety of different factors. Consequently, coherent biological responses among lake ecosystems to global change are rarely detectable. This makes overall predictions of global change impacts on biodiversity extremely difficult. Focus in future should be on the detection of threshold values at which there is a danger that species disappear. There is a strong need for the development of early warning systems that indicate when species might permanently be lost from an ecosystem.

Global change, however, does not necessarily result in a loss of species. Among the phytoplankton species there are losers and winners. In this study it has clearly been shown that some species can profit from global changes. *Gonyostomum semen* is such an example. For this species we were able to confirm a direct temperature effect on its growth rates. From our results we predict that *Gonyostomum semen* will further increase in its distribution and abundance along with increasing temperatures. So far, *Gonyostomum semen* is found as far north as 64°N where its mass development might still be restricted by low temperatures, but considering climate change scenarios it is expected that more and more lakes will experience noxious *Gonyostomum* blooms in the future. Further studies are needed to reveal the effect of climate and phytoplankton community changes on whole lake ecosystem structure and function.

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