Effects of climate variability and physical forcing on the diversity of aquatic organisms

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Das höchste wozu der Mensch gelangen kann ist das

Erstaunen

J. W. von Goethe

Zusammenfassung

Der Weltklimarat (International Panel on Climate Change) berichtet, dass global 20 bis 30 % der Arten vom Aussterben bedroht sind. Nahezu alle Ökosysteme und taxonomischen Gruppen sind von der Klimaerwärmung beeinflusst. Nicht nur mittlere Temperaturen haben sich geändert und werden laut Vorhersage auch weiter steigen, auch die Variabilität klimatischer Faktoren wird sich in ihrer Häufigkeit und Intensität ändern und Extremereignisse wie Überschwemmungen und Dürren werden zunehmen.

Die am häufigsten beschriebenen ökologischen Konsequenzen sind die Verschiebungen der Lebensräume von Arten weiter nordwärts oder in höher gelegene Regionen und Verschiebungen in der Phänologie, wie frühere Blütezeiten bei diversen Pflanzen oder frühere Brut bei Vögeln und Amphibien. Beides kann weitere Effekte auf Artgemeinschaften durch unterbrochene Verbindungen zwischen Arten oder trophischen Ebenen haben. Das wird wahrscheinlich die Artzusammensetzung von Gemeinschaften und ihre Artenvielfalt verändern und möglicherweise zu regionalem oder weiträumigem Aussterben von Arten führen.

In der vorgestellten Studie wurde der Effekt klimatischer Variabilität auf die Artenvielfalt aquatischer Organismengruppen untersucht. Die Studie kombinierte Zeitreihenanalysen mit Laborexperimenten, um den Einfluss der globalen Erwärmung auf die Artzusammensetzung verschiedener Organismengruppen zu erforschen.

Zunächst wurden Langzeitdaten von Makroinvertebraten schwedischer Seen und Flüsse (gesammelt und zur Verfügung gestellt von der Schwedischen Universität für Landwirtschaftliche Wissenschaften – SLU) mit multivariaten Methoden analysiert (Part I, Chapter 1). Direkte Beziehungen zwischen der Artzusammensetzung und der Temperatur konnten nicht festgestellt werden, ebenso wie Beziehungen zwischen der Artenvielfalt und dem großskaligen Atmosphärischen System, der Nordatlantischen Oszillation, die zu einem Großteil das Klima in Europa, vor allem im Winter, bestimmt. Dennoch zeigte eine Kanonische Korrespondenzanalyse, dass 6% der Variation in der Artzusammensetzung erklärt werden konnte durch die Trendtemperatur, was viel war verglichen mit der relativ kurzen Zeitspanne von meist zehn Jahren, die untersucht wurde.

Weiterhin wurden in zwei Langzeitexperimenten über 16 und 8 Monate die Effekte von ansteigender Temperatur und ihrer ansteigenden Variabilität auf Phytoplankton-Gemeinschaften erforscht (Part II). Beide Experimente verwendeten künstliche Gemeinschaften unter gut kontrollierten Bedingungen, um fähig zu sein, die Effekte zu entwirren und mögliche Mechanismen herausfinden zu können.

Im ersten Experiment handelte es sich bei den Gemeinschaften um geschlossene Mikrokosmen (Chapter 2). In einem voll-faktoriellen Design wurde die An- bzw. Abwesenheit von Grazern in Kombination mit den beiden Temperatur-bezogenen Faktoren manipuliert. Alle Faktoren produzierten signifikante Effekte auf alle Antwortvariablen. Erwärmung reduzierte die Artenvielfalt ebenso wie Variabilität der Temperatur, aber dem konnte Grazing entgegensteuern.

Im zweiten Experiment formten die Mikrokosmen aller Behandlungen eine Metagemeinschaft die durch Verbreitung in Form

von Austausch verbunden war (Chapter 3). Das sollte die generelle Artenvielfalt erhöhen und verhindern, dass sich die Gemeinschaften so früh zu Monokulturen entwickeln, wie im ersten Experiment. In dem voll-faktoriellen Design wurden die Grazer durch Lichtintensität als dritten Faktor ausgetauscht. Die Effekte waren schwächer als im ersten Experiment, was weitgehend zurückgeführt werden konnte auf die hohen Dispersionsraten in der ersten Hälfte des Experimentes. Dennoch waren die Trends der Temperatur-bezogenen Faktoren ähnlich denen im ersten Experiment, während Licht die Gemeinschaften nur marginal beeinflusste.

Insgesamt konnten Einflüsse von Temperatur auf die Gemeinschaften während der gesamten Untersuchung entdeckt werden. In den Experimenten hatte die Erwärmung vorherrschend negative Effekte auf die Artenvielfalt aber sie wurden modifiziert durch die anderen Faktoren. In natürlichen Gemeinschaften sowie in Felddaten wurde der Einfluss der Erwärmung deutlich. Interaktionen oder nicht-lineare Antworten können die Komplexität der Reaktionen erhöhen und daher sind die Konsequenzen für zukünftige Ökosysteme schwer vorherzusagen. Die Einbeziehung weiterer Faktoren wie Nährstoffe oder die Variabilität des Lichts, mehr trophischer Ebenen und mehr Organismengruppen kann weiteres Licht bringen in die komplexen Interaktionen in auf den Klimawandel reagierenden Gemeinschaften.

Summary

The International Panel on Climate Change reported globally 20 to 30 % of species to be prone to extinction. Nearly all ecosystems

and taxonomic groups have been influenced by global warming. Not only mean temperatures have changed and are predicted to increase further, also the variability of climatic factors will change in their frequency and intensity and extreme events as floods and droughts will increase.

Most described ecological consequences are shifts in species` ranges farther north or to higher altitudes and shifts in their phenology as earlier flowering in diverse plant species or earlier breeding of birds and amphibians. Both can imply further effects on species communities by disrupting interactions between species or trophic levels. This probably will alter community composition and diversity and possibly lead to regional or large scale species loss.

In the presented study the effects of climatic variability on the diversity of aquatic organisms were investigated. The study combined time-series analyses with laboratory experiments in order to explore the impact of global warming on the community composition of different organism groups.

First, long-term data series of macroinvertebrates of Swedish lakes and rivers (collected and provided by the Swedish University of Agricultural Sciences – SLU) were analysed with multivariate methods (Part I, Chapter 1). Direct relationships of community composition and temperature could not been detected such as relationships of diversity to the large scale Atmospheric system, the North Atlantic Oscillation, which influences to a large extent the climate in Europe, especially in winter. However, a canonical correspondence analysis revealed that 6 % of the variation in community composition was explained by the trend temperature, which was much compared to the relatively short time scale of mainly ten years that was investigated.

Furthermore, in two long-term experiments over 16 and 8 months the effects of increasing temperature and its increasing variability on phytoplankton communities was explored (Part II). Both experiments used artificial communities under well controlled conditions to be able to disentangle the effects and reveal possible mechanisms.

In the first experiment the communities were closed microcosms. In a full factorial design grazer absence and presence was manipulated in combination with the two temperature-related factors (Chapter 2). All factors produced significant effects on all response variables. Warming decreased diversity as did increased temperature variability but this could be counteracted by grazing.

In the second experiment microcosms of all treatments formed a metacommunity connected by dispersal (Chapter 3). This should increase the general diversity and prevent the communities to develop to monocultures for a longer time than in the first experiment. In the full factorial design grazers were exchanged by light intensity as third factor. Effects were less pronounced than in the first experiment which could be attributed to a large amount to high dispersal rates at the first half of the experiment. However trends of temperature-related factors were similar to the ones in the first experiment while light only marginally influenced the communities.

Overall temperature influences on communities could be detected during the whole study. In the experiments warming had predominantly negative effects on diversity but they were modified by the other factors. In both, artificial communities and natural field data, the impact of warming became obvious. Interactions or non-linear responses can increase the complexity of the reactions and therefore consequences for future ecosystems are difficult to predict. Further investigation of field data combined with field and laboratory

experiments should increase the knowledge about mechanisms and patterns. Including other factors as nutrients or light variability, more trophic levels, and more organism groups could shed further light on the complex interaction in communities responding to climate change.

General Introduction

Climate change

Intensive research in the last three decades focused on the effects of recent climate change and global warming on species, communities and ecosystems and has attracted attention in society and politics. This certainly reached its hitherto climax with the award of the Nobel Peace Prize to The Intergovernmental Panel on Climate Change and Albert Arnold Gore Jr. "for their efforts to build up and disseminate greater knowledge about man-made climate change, and to lay the foundations for the measures that are needed to counteract such change" (http://www.ipcc.ch/) in 2007.

In the fourth assessment report in 2007 the International Panel on Climate Change (IPCC) described a variety of observed climate changes further supporting previous research. For instance, there is clear evidence for globally increased temperatures (IPCC 2007c). On average the linear warming trend of the last 50 years (0.13°C per decade) was twice as high as the linear trend of the last 100 years (0.74°C from 1906 to 2005). From the last twelve years (1995-2006) eleven rank among the 12 warmest years in the instrumental record of global surface temperatures (since 1850). The fact that this warming of the last half century is unusual during at least the last 1300 years is also supported by paleoclimatic information. This led to reduced ice sheets, glaciers, snow cover and with that to a rise in sea level. Additionally, on the one hand increased precipitation has been reported, on the other hand increased droughts, as also

increased heavy precipitation events and extreme heat waves. There is strong evidence that the changes were produced to a large extent by the observed increases in anthropogenic greenhouse gas concentrations. Even if the concentrations could be stabilized, the warming would continue for centuries due to the timescales of climate processes and feedbacks. Recent projections range from 0.1 to 0.2°C warming per decade and 1.1 to 6.4°C until the year 2100 (Figure 1).

Consequently, observed changes such as more frequent extreme events and shrinking ice cover will further continue. Changes in ecosystems can produce strong impacts on goods and benefits strongly influencing human society and health. Therefore, increasing knowledge about consequences of the changing climate is important to react adequately.

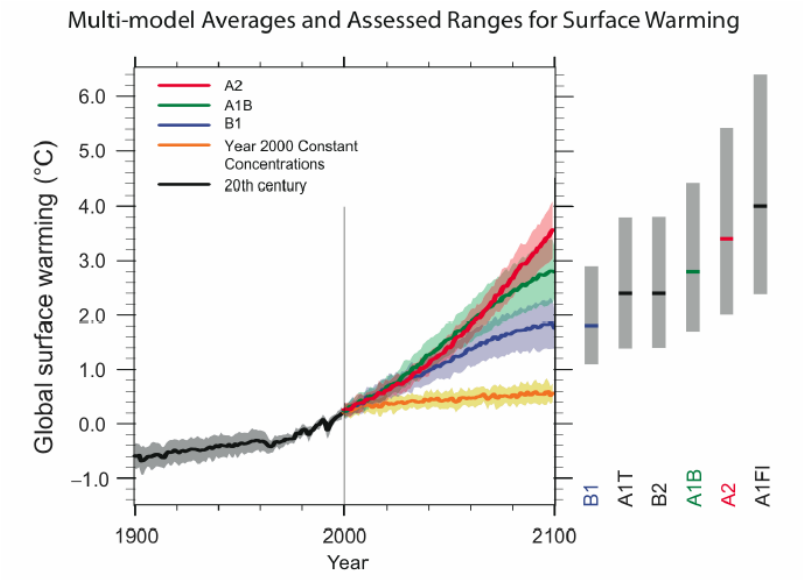


Figure 1: Warming scenarios. Solid lines are multi-model global averages of surface warming (relative to 1980-99) for the scenarios A2, A1B and B1, shown as continuations of the 20th century simulations. Shading denotes the plus/minus one standard deviation range of individual model annual averages. The orange line is for the experiment where concentrations were held constant at year 2000 values. The grey bars at right indicate the best estimate (solid line within each bar) and the *likely* range assessed for the six SRES marker scenarios. The assessment of the best estimate and *likely* ranges in the grey bars includes the AOGCMs in the left part of the figure, as well as results from a hierarchy of independent models and observational constraints.
Source: (IPCC 2007a)

Effects on ecology

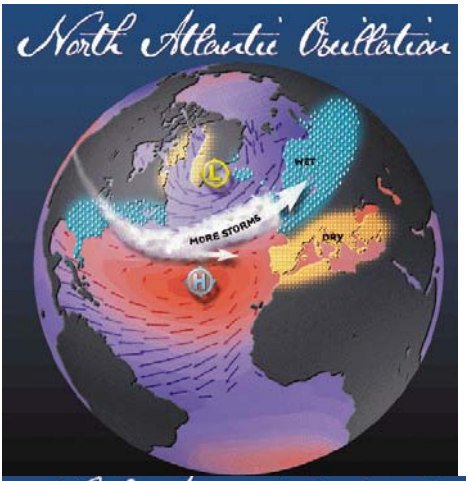
In nearly all habitats reaching from the poles to the tropics and from terrestrial to aquatic systems species from most major taxonomic groups seem to be somehow affected by climate change thereby also influencing whole ecosystems. Most effects have been found on the phenology and geographical distribution of species. A number of studies reported shifts and expansions or contractions of species ranges (Parmesan 2006). Many species ranges in terrestrial and aquatic habitats have been observed to move to higher altitudes or latitudes with changing environmental conditions such as warming. Phenology is possibly directly linked to changing temperatures leading to earlier flowering of plants, first appearance of butterflies or breeding of birds and amphibians (Parmesan 2006). If the timing of such life-history events of a predator and its prey is changing asynchronically this could cause mismatches with possibly important consequences for the whole system (de Senerpont Domis et al. 2007b; Edwards & Richardson 2004; Visser et al. 1998; Visser & Holleman 2001; Visser & Both 2005; Winder & Schindler 2004a; Winder & Schindler 2004b). Warming can also act indirectly through factors mediating the influence of temperature. For instance, earlier ice-break up in lakes led to earlier phytoplankton growth (Adrian et al. 1999; Gerten & Adrian 2000; Weyenmeyer 2001). Water temperature also influences thermal stratification and the mixing regime, further determining the light regime, sinking patterns and nutrient conditions which may shift competition between sinking and buoyant species (Huisman et al. 2004) and change community composition.

The North Atlantic Oscillation (NAO)

Climate change was linked in a number of investigations to large scale atmospheric systems as the North Atlantic Oscillation (NAO), the Pacific Decadal Oscillation (PDO), and the El Niño Southern Oscillation (ENSO) (Ottersen et al. 2001). The NAO describes the alternation in the pressure difference between the high pressure zone over the Azores and the low pressure zone over Iceland.

Depending on the recurrent pattern of atmospheric variability it largely influences weather conditions in the northern hemisphere, especially during winter (Hurrell 1996). Fluctuating between two phases – high and low – the NAO influences mean wind speed and direction, intensity und number of storms as well as heat and moisture transport from the Atlantic. When the Icelandic Low is very deep and the Azores High is very strong (high NAO) this results in an intense redistribution of atmospheric mass between the subtropical Atlantic and the Arctic with strong westerly and southwesterly winds bringing warm and wet maritime air to northern Europe resulting in warm and wet winters with higher precipitation and more storms. Southern Europe then is dominated by cold and dry winters (Figure 2a).

a)



b)

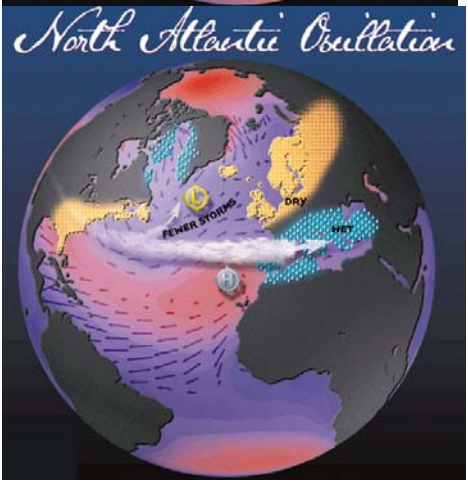


Figure 2: Graphical visualisation of a) high/positive NAO, b) low/negative NAO
(Source: http://www.ldeo.columbia.edu/res/pi/NAO/)

In contrast, when both pressure centres are weaker than normal (low NAO) the lower pressure differences implicate lower westerlies that bring warm and wet air to southern Europe while Northern Europe experiences a cold and dry winter with low rainfall (Figure 2b). For these situations dimensionless indices have been calculated, derived from surface pressure anomalies between northern and southern locations. Prominent is Hurrell`s NAO index calculated from the difference in sea level pressure between Lisbon, Portugal (winter index) or Ponta Delgada, Azores and Stykkisholmur, Reykjavik, Iceland (NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995)). Its pattern for more than one century is shown in Figure 3.

Interestingly, during the 1950s to the 1970s a predominantly negative phase occurred while in the 1980s a predominantly positive phase began (Figure 3). The indices are calculated on yearly, monthly and seasonal bases and can be used as a proxy for surface temperature, whereas the correlation of the winter index to weather conditions is pronounced to be strongest. Therefore, it has been widely used to detect correlations of a variety of physical and ecological variables with large-scale climate oscillations.

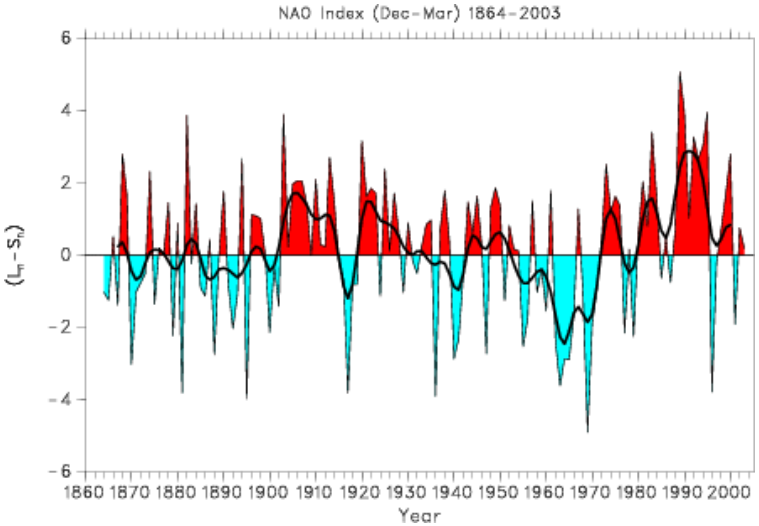


Figure 3: Winter (December through March) index of the NAO based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. The SLP anomalies at each station were normalized by division of each seasonal mean pressure by the long-term mean (1864-1983) standard deviation. Normalization is used to avoid the series being dominated by the greater variability of the northern station. Positive values of the index indicate stronger-than-average westerlies over the middle latitudes.
Source: http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html

Correlations to the NAO were described for physical, hydrological, chemical and biological variables (Blenckner & Hillebrand 2002; Mysterud et al. 2003; Drinkwater et al. 2003; Ottersen et al. 2001; Stenseth et al. 2004; Stenseth 2008; Straile et al. 2003). Many impacts were mediated by the influence of temperature such as ice phenology, earlier breeding or elongation of the growing season. The effects also occurred indirectly linked by food web interactions even resulting in ecosystem regime shifts and several organisms responded with a time delay due to life-history traits and trophic interactions (Post 2004).

Diversity

In their latest Assessment Report the IPCC stated that globally 20 to 30 % of all plant and animal species have a high risk of extinction if the temperature increase exceeds 2 to 3°C (2007b). This can be caused by several ways. First, climate change could alter the environment to conditions that are beyond species' tolerance limits, therefore destabilizing populations. Species have to adapt or to follow the often northwards or upwards shifting conditions to persist (Thomas et al. 2004; Thuiller et al. 2005; Tilman & Lehman 2001). This is often not possible because of limited dispersal abilities or geographic barriers and landscape fragmentations and can result in large scale extinctions. Additionally, high altitude or latitude species simply live at the edge of a habitat such as mountain tops or the north end of a continent and do not have the possibility to move. Second, on a more regional scale, species can be endangered if changes in spatial or temporal distribution occur. Temporally, phenology shifts could lead to mismatches of predator and prey; spatially, altered community composition, for instance by invasion of shifting species, could change ecological interactions. Altered species interactions (Bertness & Ewanchuk 2002) and changes in keystone species (Sanford 1999) possibly cause further effects in the food web with consequences for the whole community. Not only changes in species richness are highly relevant to investigate, but also changes in dominance patterns and community compositions, which can be even more important for ecosystem functioning. The relative proportions of species may be more substantial for ecosystem function than the loss of non-essential rare species or long before a key-stone species finally has gone extinct (Hillebrand et al. 2008).

In reverse, biodiversity has been found to be important for ecosystem structure, stability and function (Loreau et al. 2001; McCann 2000; McGrady-Steed & Morin 2000; Tilman 2000). Thus, high diversity can function as an insurance against a fluctuating environment (Yachi & Loreau 1999) and many different traits could built a reservoir for adaptation to changing environmental conditions. In several studies diversity was the driving stabilising factor for the variability of temporal ecosystem properties (McGrady-Steed & Morin 2000; Naeem & Li 1997). Consequently, a major task should be sustaining global and local diversity to benefit from its goods and services.

Rationale for this thesis

The approach of this thesis comprises investigations of different systems, ranging from natural and uncontrolled systems to highly controlled and artificial ones. Both approaches have their advantages and disadvantages and can not fulfil all requirements at the same time. Artificial laboratory experiments guarantee a strong control over the manipulated factors and therefore provide the possibility to reveal particular mechanisms and to disentangle effects especially of interacting factors or direct versus indirect influences. The often mentioned criticism is their difficult transferability to natural systems due to their artificiality and their restricted subset of factors which are working in the field. Additionally, results of this kind of experiments can be very restricted in terms of the factors manipulated and the artificially assembled species that often represent just a fraction of the diverse array of factors and the complex communities in nature. On the other hand, natural systems

are difficult to control and have a high variability and consequently high noise in their data. Thus, it is not trivial to clearly distinguish the impacts of several different factors. Many factors influence species, populations and communities synchronously; they interact, mask each other and responses can be highly variant. Still, it is possible to extract important conclusions from field experiments or, as another possibility, from long-term analyses of collected field data. Such long-term data can represent somehow "natural experiments" where factors as environmental variables are manipulated with natural variances and natural varieties of responses occur. Due to the observed strong climatic changes during the last decades, the 1990-2000 decade was the warmest one for a long time; a fingerprint of this warming should be detectable in long-term data series. Additionally to the analyses of long-term data the study used long-term experiments comprising about 500 generations with a high degree of control over treatments and the phytoplankton community composition.

Thesis outline

Part I: Analyses of long-term series

Chapter 1

The first chapter presents the results of analyses with multivariate methods of a long-term data series on macroinvertebrates from Swedish lakes and rivers and associated lake parameters such as temperature, pH, oxygen-content and nutrients. The intention was to detect if changing diversity and

community composition of this organism group could be related to global warming. Thus, the data were analyzed regarding on community changes connected to changing temperatures and the relationship of diversity parameters with the North Atlantic Oscillation.

Part II: Experiments

Two controlled experiments with artificial phytoplankton communities were run for 16 and 8 months, respectively. Seasons were simulated with a temperature and/or light time-course representing a lake at present and in a future scenario of the year 2100. In both experiments warming was applied by increasing the mean temperature by plus 4°C in winter and plus 2°C in summer. Additionally, increased temperature variability was manipulated with deviating temperatures of ± 2°C every second week from the temperature curve of both mean temperature regimes. The effects on total algal abundance, total algal biovolumes, community composition and diversity patterns were analysed.

Figure 4: Experimental set-up in the climate room. Four water baths were cooled by a flow through and for fine tuning heated with aquarium heaters to maintain four (different) temperatures.

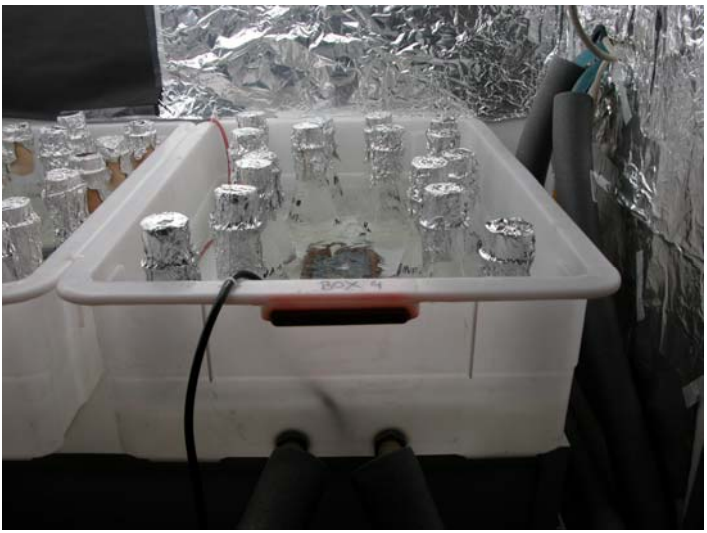


Figure 5: Water bath with experimental flasks

Chapter 2

In the first experiment a closed system was used, with an initial species number of 19 species from different algal groups. To further include the effect of a second trophic level, which can largely influence phytoplankton communities, ciliate absence and presence was manipulated in a full-factorial design with the two temperature-related factors.

Chapter 3

In contrast to the first experiment, the communities of the second one were run as a metacommunity with weekly and biweekly exchange. Another difference was that light level was used as third factor, which is also proposed to change due to global warming and can have important consequences for phytoplankton.

Figure 6: Sorted experimental flasks before sampling, each row represents one treatment

Figure 7: Sometimes differences in community composition could be detected clearly by eye due to the different colour. Here the different development of the HVC treatment in November is especially obvious.

In the next parts of the thesis the analyses of long-term data and the experimental results are presented and discussed in one chapter each, then the different aspects are synthesised in a general discussion.

Part I

Chapter I

Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates

Introduction

Interest in the regulation of diversity has increased over the last few decades as the human impact on species distribution and species richness has become more and more apparent. Biodiversity loss via habitat fragmentation (Fahrig 2003) and habitat deterioration by (for example) pollution (Smith 2001) or eutrophication (Lotze & Milewski 2004) have been viewed with concern, as has been the introduction of exotic species (Lockwood 2004). Accordingly, the observed global climate change and the proposed future acceleration of this change have also led to questions about whether this change may affect species composition and diversity (Thuiller et al. 2005; Tilman & Lehman 2001).

Two primary links between climate and biodiversity can be distinguished, which operate on different spatial scales. First, on a local scale, the expected shift in mean values and variability of climate-related abiotic forces may alter local interactions. Changes in seasonality and mean temperatures have been proposed to alter

predator–prey interactions by altering behaviour, seasonal timing and biomass production (Stenseth et al. 2002). Predator–prey interactions are strongly regulated by the timing of the population dynamics, e.g. by creating temporal match or mismatch of population occurrences through seasons (Durant et al. 2005). Competitive interactions are also affected by temporal fluctuations in abiotic forcing, as competitive advantages are changed and the exclusion of competitively inferior species is interrupted (Descamps-Julien & Gonzalez 2005; Flöder & Burns 2005).

Second, on a larger scale, climate variables such as temperature or evapotranspiration are very strong predictors of aquatic and terrestrial diversity (Hawkins et al. 2003; Hillebrand 2004). Climate envelopes set an outer limit to the ranges of many species (Svenning & Skov 2004). Accordingly, a shift in climatic variables can lead to shifts in the ranges of species across latitude (Crozier 2004; Hampe & Petit 2005; Morrison et al. 2005) and altitude (Wilson et al. 2005). Whereas such range shifts have been observed for a number of species, it is much more difficult to analyse their potential consequences for species coexistence and biodiversity due to unpredictable changes in species interactions (Davis et al. 1998; Thuiller 2004) or the adaptation of species to new climatic conditions (Jump & Penuelas 2005).

A major line of research in this framework infers species loss from predicted changes in habitat area using species–area relationships, SARs (Araújo et al. 2005a; Lewis 2006; Thomas et al. 2004; Xenopoulos et al. 2005). However, SARs vary widely between organisms, habitats and geographic regions (Drakare et al. 2006) and spatial scaling interacts with temporal patterns (Adler et al. 2005). Therefore, inferences about extinction risks made on the basis of

area–diversity relationships may be highly prone to error (Araújo et al. 2005b).

An alternative way to address potential consequences of global change on species composition and biodiversity is to look at long-term data series and to use the strong gradient in climate conditions observed over the last few decades. The 1990s were the warmest decade recorded in modern times (IPCC 2001), and several processes in aquatic communities exhibited rapid changes during this period (Belgrano et al. 2004b; Straile 2005). Therefore, we propose to analyse whether community patterns such as biodiversity also changed during these times. One requirement for such an analysis is a standardized methodology of taking and analysing samples, a high taxonomic resolution of species identification, and a duration that allows the temporal trends to be addressed. Such data were available for the macroinvertebrates within a Swedish lakes and rivers monitoring program (see Methods). We used these data to test three hypotheses on the relationship between climate change and aquatic biodiversity. These hypotheses increase in terms of the complexity of the analyses that need to be performed.

1. Temperature differences directly affect species composition, leading to a stronger dissimilarity in species composition between years of higher temperature difference. To test this hypothesis, for each sampling site we calculated the similarity in species composition between sampling years and the difference in temperature (ΔT) during the sampling period. We used a Mantel test to test for significant decreases in similarity with increasing ΔT.
2. Diversity measures correlate significantly with the North Atlantic Oscillation index. The NAOI (Hurrell 1996) has been used extensively in the analysis of climate-related effects

(Beaugrand et al. 2002; Belgrano et al. 2004a; Blenckner & Hillebrand 2002; Ottersen et al. 2001) and integrates a number of important abiotic variables such as temperature and precipitation. A potential problem with any correlative analysis is that temporal shifts in the NAOI co-vary with periods of passive restoration of aquatic habitats from other human impacts. In particular, the eutrophication and acidification of Swedish lakes and rivers has been successfully reduced by modifying the management of wastewater treatment and environmental policy, such that trends in the NAOI may reflect trends associated with decreasing phosphorus concentrations or increasing pH. Therefore, we used multiple regressions to analyse whether there was an effect of the NAO on diversity when controlling for shifts in P and pH.

3. Species composition is affected by environmental factors and shows a significant change with trend temperature. To test this hypothesis, we used multivariate approaches to analyse species-specific information on abundances and the breadth of environmental parameters addressed by the Swedish monitoring program. By accounting for these variables, we tested whether the composition of macrozoobenthos was significantly affected by trends in temperature that occurred over the last few decades.

Materials and methods

Data

Data were retained from Swedish national monitoring databases at the Swedish University of Agricultural Sciences (SLU). These databases comprise long-term data series from freshwater environments (lakes and rivers) including abundances and biomasses of different organism groups and a variety of environmental parameters. In particular, the macrozoobenthos is taxonomically highly resolved and reliable. We used 13 data sets of the intensively studied reference lakes, four data sets of sites within the largest lakes in Sweden and five data sets of rivers for analysis. The reference lakes were sampled at different depths and data sets are divided into littoral and sublittoral. All data sets spanned a time of at least ten years and were sampled once a year: the lakes in late summer/autumn (August to October) after the first mixing; the rivers in spring (May to July) after the snowmelt and the associated flood. The large lakes have the largest data sets, beginning at 1969, whereas the sampling of rivers and reference lakes began in 1987 and 1988, respectively, and 2003 was the last year included. The data sets included the environmental variables of temperature, oxygen, pH, Secchi-depth, conductivity, nutrients (different compounds of nitrogen and phosphorus) and total organic carbon.

The North Atlantic Oscillation (NAO) is a large scale ocean atmospheric oscillation system which represents fluctuations in the pressure difference between the high pressure zone over the Azores and the low pressure zone over Iceland. It influences air temperature

and precipitation over large areas of the Northern Hemisphere (Hurrell 1996). An index which reflects mild and rainy winters (positive values) and dry and cold winters (negative values) has been created. These NAO indices were derived from the homepage (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) of the National Centre for Atmospheric Research. They are based on the differences in normalized sea level pressure (SLP) between Lisbon, Portugal (winter index) or Ponta Delgada, Azores and Stykkisholmur/Reykjavik, Iceland since 1865. SLP anomalies were normalized by dividing each seasonal or monthly mean pressure by the long-term mean (1864–1983 for winter index, 1865–1984 for seasonal and monthly indices) standard deviation.

Analyses

We divided the analyses into three different steps, increasing the complexity of the analysis and the covariates taken into account.

1. We first analysed whether temperature has a direct effect on community composition. Given this, dissimilarity of species assemblages should be higher in years with larger temperature differences than in years with lower temperature differences. Therefore, we calculated two similarity indices for all combinations of years in each data set. The Jaccard index is based on presence–absence data and thus measures only qualitative differences. It is calculated as

   a/a+b+c

where a is the number of species present in both samples, b is the number of species only present in sample one, and c is the number of species only present in sample two (Koleff et al. 2003). To also account for quantitative differences, we calculated the Bray–Curtis index, which is based on abundance data, using the program Ecological Methodology, Version 5.1 (Exeter Software, Setauket, NY, USA). We also calculated the differences in the corresponding temperatures (ΔT) and tested for correlation of similarity and ΔT with a normalized Mantel test (Fortin and Gurevitch 1993).

2. We hypothesized that a climate index such as the NAOI might affect diversity when accounting for the main factors associated with temporal trends. We obtained a variety of NAO indices. The winter NAO (December to March) has the most pronounced correlation with temperature, wind and precipitation, but we also tested monthly and seasonal indices (average over three months). We used the NAO indices for the months two (M1) and one month (M2) before sampling and the sampling month (M3) itself as monthly indices. Seasonal index 1 included monthly index 1 as the last month of the season (S1), and the seasonal indices 2 and 3 included monthly indices 2 and 3, respectively (S2, S3). Because Sweden underwent passive lake restoration during the time span examined, leading to increased pH and decreased phosphorus content in lakes, we included both habitat pH and total phosphorus as additional independent variables in a multiple regression. We tested different diversity indices, each emphasizing different aspects of diversity (standardized species richness S_{std}, Shannon index H`, Pielou`s evenness index J`, Simpson's index D, and

Simpson's measure of evenness E1/D) (Magurran 2004). Species richness was standardized for sampling effort with rarefaction performed using EcoSim (Gotelli & Entsminger 2001). All indices were transformed to percentages of the maximum to obtain relative measurements. The analyses were performed with Statistica (2003).

3. We used multivariate analysis techniques to detect the influences of environmental factors on community composition in the macrozoobenthos. Because of their different sampling times and communities, the rivers were not included in these analyses.

Limnological variables

We used all of the parameters described above as environmental variables. To avoid any effects of colinearity in the environmental variables, they were subjected to a principal component analysis (PCA). The PCA resulted in four meaningful axes (eigenvalues larger than expected from a broken stick model). EnvPCA1 accounted for 37.9% of the total variation and was mainly determined by the total phosphorus content (correlation to the axis 0.91) and O_2 content (-0.64). The second most important axis, EnvPCA2, representing 16.0% of the total variation, was most influenced by the pH (-0.68) and ammonium content (0.68), while EnvPCA3 (11.9%) reflected the conductivity (0.71). The last axis, EnvPCA4 (10.1%), was a reflection of total organic carbon (0.68).

Spatial and temporal variables

Spatial and temporal effects on species abundances were accounted for by the variables of latitude and longitude and the respective year of sampling. As species composition is most likely also influenced by the depth of the sampling point and the total size of the lake, these variables were also incorporated.

Climatic variables

We used the NAO winter index as the climate variable, as described above. Water temperatures during the winter months were thought to exert the greatest influence on the species communities. Unfortunately, measurements from this season were incomplete. Therefore, water temperatures in October, taken at 5 m depth or, if the lake was not that deep, the deepest measurement, were used as a proxy for the amount of warmth the respective lake had accumulated during summer. This stored caloric energy also determines the temperature development during winter (Brönmark & Hansson 1996). Any occasional missing data from years with no temperature records were filled in as the average of the preceding and the following year (variable WaterTemp). We tested for the presence of a significant linear trend in the temperature data using the Mann-Kendall test and calculated Sen's slope estimate with the Excel application MAKESENS 1.0, provided by the Finnish Meteorological Institute.

In order to extract a trend signal from year-to-year variations in the temperature data, we applied the caterpillar method as implemented in the software Caterpillar 1.0 (Group C 1997). To this end, the time series was centred before decomposition with a lag size

of 10. Only the caterpillar average was used to reconstruct the trend. The resulting temperature trend time series was also tested for significance as described above (variable TrendTemp).

Data analysis

Canonical correspondence analysis (CCA) (Ter Braak 1986) was applied as a multivariate ordination technique to analyse the spatial and temporal variations in the species abundance data. To remove any unwarranted effects of rare species on the ordination results, species occurring in less than four samples and/or with less than 100 individuals were excluded from further analysis. This yielded a matrix of 147 species. Abundance data were square-root-transformed prior to analysis, and rare species were downweighted.

Initially, principal patterns in species distributions were ordinated via detrended correspondence analysis (detrended by segments). The gradient length exceeded 3 in standard deviation units, indicating that a unimodal model adequately represented the species` responses (Jongman et al. 1995). Statistical correlations between species abundances and environmental variation were further assessed via CCA, a nonlinear eigenvector ordination technique in which the axes are constrained to be linear combinations of the measured environmental variation. The environmental variables were ordered by forward selection according to the amount of explained variance in the species data. Treating each variable as the sole predictor variable in a first step, all environmental variables were ranked on the basis of the variance they explained separately, thus representing marginal effects. Selecting the best fitting variable in a second step as covariable, the remaining variables were again ranked according to their explanatory power for the remaining

variance. This procedure was repeated until all variation was explained, thus yielding the conditional or unique effects of each variable. At each step, the statistical significance of each variable added to the model was tested using a Monte Carlo permutation procedure with 999 unrestricted permutations. The statistical significance of the first four axes and associated constrained eigenvalues was also tested with 999 unrestricted permutations, using the sample scores as covariables for the higher order axes (Ter Braak & Verdonschot 1995).

As we were predominantly interested in the effect of the climatic variables on the species composition, we performed a series of partial CCAs by considering in turn the spatial, temporal and climatic variables as explaining factors and all remaining variables as cofactors. The partial models were also tested using a Monte Carlo permutation approach. The percentage of species variation explained by the different CCA models was calculated as the ratio of the sum of canonical eigenvalues over the total inertia in an unconstrained CA. All ordination calculations were performed with Canoco 4.5 (Ter Braak & Smilauer 2002).

Results

There was no significant relationship between similarity in macroinvertebrate community composition and measured differences in water temperatures. None of the lakes or rivers gave a significant Mantel test, neither for the Jaccard index nor for the Bray-Curtis index. However, we found a tendency towards negative slopes (57% of the correlations were negative for Jaccard indices, 65% for Bray-Curtis indices, Fig. 1).

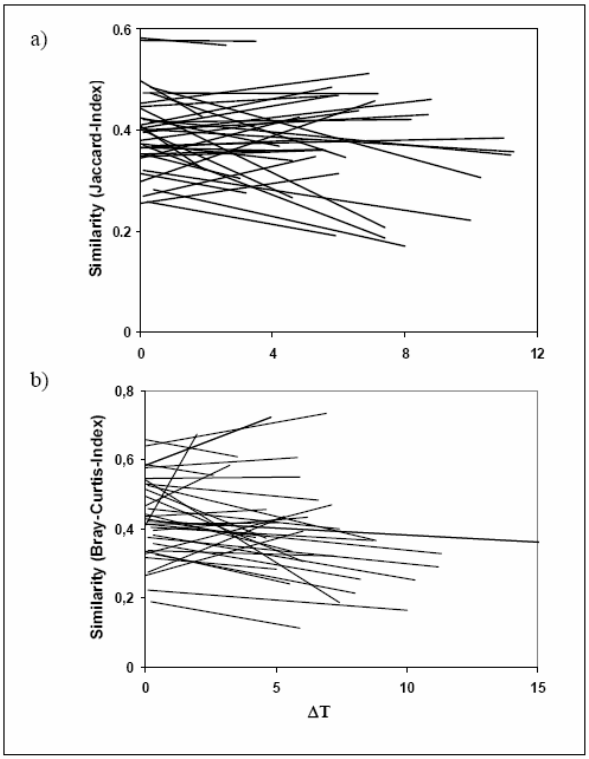


Figure 1. Trend lines of ΔT versus similarity for all sites.
a) Jaccard index, b) Bray-Curtis-Index

Apart from some exceptions (5.5% of the analyses), we found no significant relationships between the NAO and the diversity of macrozoobenthos. This was true for all NAO indices tested and for all aspects of diversity (see Appendix). Significances mainly appeared in analyses with few data points, due to short time spans and missing data leading to low degrees of freedom in multiple regressions with three independent variables. It also sometimes seemed that outliers drove the whole regression line. After a Bonferroni-like adjustment was performed, none of the NAO effects were found to be significant.

In contrast, the water temperature in the lakes showed a strongly increasing trend and species composition of macroinvertebrates was significantly affected by this temperature trend. With one exception, all measured lake temperatures in October showed a positive trend during the time period considered (Table 1). Four of these slopes were significantly different from zero, and three showed a tendency ($P<0.1$). The remarkable exception from this overall pattern was Lake Brunnsjön, where the October temperature decreased significantly by about 0.2 °C per year. This outlier was therefore removed from the following analyses, but not from the ordination analyses.

After removing random fluctuations, all trends were significantly different from zero, with an average lake temperature increase of 0.11±0.05 °C per year. The rate of temperature increase was negatively correlated with the first measured temperature; i.e. the colder the lake was initially, the stronger the temperature increases ($r=-0.58$ $P=0.024$).

Table 1. Results of the Mann-Kendall Trend Test and Sen's slope estimates for the water temperatures and trend temperatures in 5m depth in October for the reference lakes in Sweden. Significance of trends is coded as + p < 0.10, * p < 0.05, ** p < 0.01, *** p < 0.001.

Time series	First year	Last Year	n	Test Z	Significance	Slope estimate	Test Z	Significance	Slope estimate
				WaterTemp			TrendTemp		
ENV	1988	2003	16	1.76	+	0.171	4.82	***	0.156
STS	1988	2004	17	2.64	**	0.245	5.31	***	0.130
FIO	1988	2004	17	1.89	+	0.218	5.40	***	0.107
OVR	1988	2004	17	2.27	*	0.197	5.56	***	0.136
ROT	1990	2004	15	1.89	+	0.167	2.88	**	0.167
ALL	1988	2003	16	0.45		0.015	3.15	**	0.071
BRU	1988	2003	16	-2.83	**	-0.220	-5.32	***	-0.117
FRA	1988	2004	17	2.97	**	0.171	5.56	***	0.163
HAR	1987	2003	17	1.06		0.090	4.74	***	0.104
JUT	1990	2004	15	0.40		0.150	3.27	**	0.168
STE	1988	2004	17	1.31		0.114	2.35	*	0.025
ABI	1988	2003	16	0.95		0.100	3.65	***	0.115
TAR	1988	2004	17	1.28		0.050	4.49	***	0.058
MEG	1988	2004	17	1.37		0.056	4.62	***	0.028
REM	1988	2004	17	2.84	**	0.255	5.31	***	0.198
MAR	1988	2003	16	1.22		0.100	4.51	***	0.057

Table 2. Results of canonical correspondence analysis (CCA) for macrobenthos species abundance data in Swedish reference lakes from 1988 - 2003 (n = 339). Inter-set correlations between the first three significant canonical axes and environmental data are presented. Marginal effects denote the percentage of variance explained using the respective variable as sole predictor. Conditional effects take in account the covariation of other environmental variables already selected by forward selection. Significance levels are based on a Monte Carlo permutation test with 999 unrestricted permutations.

CCA	Axis1	Axis2	Axis3
Eigenvalue	0.644	0.241	0.171
Species-environment correlation	0.981	0.804	0.743
Cumulative % variance			
of species data	13.8	19	22.7
of species-environment relation	47.9	65.8	78.6

Enviromental variable	Conditional effects	*p*
NAOw	0.01	n.s.
WaterTemp	0.01	n.s.
Year	0.04	<0.001
TrendTemp	0.06	<0.001
EnvPCA3 (conductivity)	0.02	n.s.
Latitude	0.09	<0.001
EnvPCA4 (TOC)	0.11	<0.001
Longitude	0.13	<0.001
EnvPCA1 (total P, oxygen)	0.06	<0.001
EnvPCA2 (pH, ammonium)	0.16	<0.001
Surface	0.04	<0.001
SampleDepth	0.61	<0.001

Ordination analysis

The CCA of species abundance data with stepwise forward selection retained nine environmental variables (Table 2). The first three axes of the ordination were statistically significant ($P<0.01$), with eigenvalues of 0.644, 0.241 and 0.171, respectively. The variables
NAOw, WaterTemp and EnvPCA3, which also showed small marginal effects, were removed from the model. Together, the selected environmental variables accounted for 28.8% of the total inertia (Table 3). SampleDepth explained most of the environmentally determined variance in the species data (61% of the environmentally explained variance), followed by EnvPCA2 (16%), Longitude (13%) and EnvPCA4 (11%). The only climatic variable retained, Trend-Temp, explained 6% of the species variance (Table 2).

Table 3. Results of the partially constrained ordinations, showing the fraction of total variation explained by environmentally, spatially, temporally and climatically structured variation.

Variation accounted for in species data			
	Eigenvalue	%	p
Total variation	4.665	100.0	
Environmental variation	1.345	28.8	<0.001
Spatial variation	0.157	3.4	<0.001
Temporal variation	0.013	0.3	0.109
Climatic variation	0.081	1.7	<0.001
Unexplained variation		71.2	

Axis 1 described a gradient of samples from deep sites in large lakes at the positive end to samples from shallow sites in small lakes. The second axis showed the highest correlation with the longitudinal position of the sampling sites, but was also determined by pH and ammonium content (EnvPCA2), latitudinal position and trend temperature (Figure 2).

The series of partial CCA allowed the species data to be partitioned into spatial, temporal and climatic components. Spatial variation accounted for 3.4% of the total species variance, while temporal variation was not significant. Climatic variation explained 1.7% of the total inertia and 6% of the environmentally structured variation.

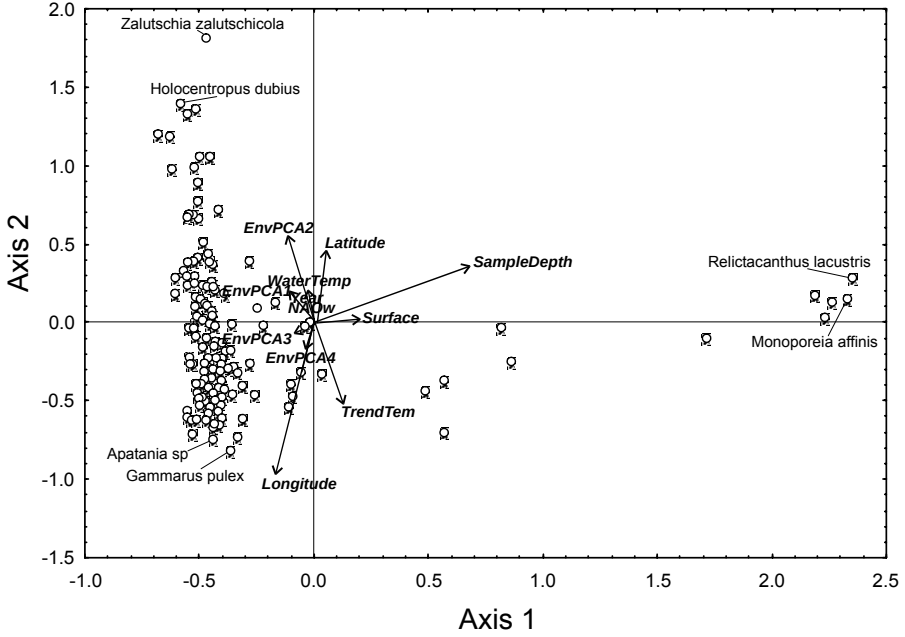


Figure 2. Species ordination results of Canonical Correspondence Analysis (CCA) for macrozoobenthos abundance data. The plot shows the species scores along the first and second axis in relation to the environmental variables. The direction and length of the arrows indicate importance and correlation to the respective axes. The names of some species occupying extreme points along the environmental gradients are indicated.

The species associated with either high or low trend temperatures are taxonomically very heterogeneous. Species correlated with high TrendTemp, and thus likely to increase both in abundance and range, were: *Saduria entomon*/Malacostraca, *Nemoura avicularis*/Plecoptera, *Coenagrion* sp./Zygoptera, Libellulidae indet./Anisoptera, *Glaenocorisa propinqua*/Heteroptera, *Sialis lutaria* gr/Megaloptera, *Paramerina* sp./Diptera, *Monodiamesa* sp./Diptera and *Heterotrissocladius marcidus*/Diptera. In contrast, species correlated with low TrendTemp and therefore in danger of shrinking in abundance and range or vanishing were: *Valvata piscinalis*/Gastropoda, *Cloeon dipterum* sp./Ephemeroptera, *Gyrinus* sp./Coleoptera, Limnephilidae indet./Trichoptera, *Zalutschia zalutschicola*/ Diptera and *Chironomus reductus*-typ/Diptera.

Discussion

Temperature is known to influence the physiological processes of species, possibly leading to changes in the timing of life history events and trophic interactions (Sweeney 1984; Vannote & Sweeney 1980; Ward 1992). This may alter diversity and community composition. Thus, temperature differences between two years should be related to the dissimilarity between the communities for these years. Especially in a lake, the water temperatures should reflect the previous thermal conditions. Nevertheless, we could not prove a connection between differences in measured temperatures and dissimilarities in assemblages of benthic invertebrates in Swedish lakes during the past decade. The temperature difference itself does not seem to be strong enough to determine the species composition of macroinvertebrates (refuting hypothesis 1).

(Scarsbrook 2002) found that lotic invertebrate communities fluctuated around a relatively stable state over a nine-year period, with higher stability exhibited at sites with relatively harsh flow conditions. As in our study, there were weak relationships between changes in environmental conditions and community composition until environmental changes were averaged over the time period, revealing greater persistence with more constant conditions. Other studies manipulating temperature also found no effect of warming on species composition (taxon richness) of stream invertebrates, although densities decreased (Hogg & Williams 1996).

It can be demonstrated that the NAO is connected with many processes in ecosystems affecting abiotic and biotic factors. These range from lake temperatures and date of ice break-up to timing events such as the phytoplankton peak, the emergence of alderflies or the spawning time of fish, and trophic interactions (Drinkwater et al. 2003; Ottersen et al. 2001; Straile et al. 2003). In particular, the winter NAO has been found to be correlated with population dynamics, shifts in community composition and distribution in terrestrial and aquatic systems. However, we detected no simple direct relationship between the NAO and the diversity of macrozoobenthos (refuting hypothesis 2). There was little evidence that such a relationship exists at all, because only 5.5% of the multiple regression analyses revealed significant results. Three potential aspects may hinder the discovery of stronger NAO signals on species composition. First, the macrozoobenthos is a very heterogeneous group of organisms which have different life cycles, sometimes with long generation times up to several years (Brittain 1982; Butler 1984; Oliver 1971). It is reasonable to suggest that climate impacts at different times on different components of macrozoobenthos. This possibly masks effects on diversity.

Nevertheless, effects of the NAO on biomass, abundance and community composition have been found in marine systems (Hagberg & Tunberg 2000; Kröncke et al. 1998) and on community persistence in freshwater (Bradley & Ormerod 2001). Briers et al. (2004) found a positive relationship between the winter NAOI and the growth of the mayfly *Baetis vernus* Curtis, but not of the stonefly *Nemurella picteti* Kapálek. Second, climatically influenced life history traits such as fecundity can possibly lead to effects occurring with time delays, which have been shown for several organisms (Post 2004). Third, the NAO may be a strong nonlinear measure of climatic conditions with differential regional impacts across the Swedish landscape. The correlation of the large-scale NAO with European climate variables is most pronounced in winter (Hurrell & van Loon 1997), but additionally depends on the region. Regional atmospheric circulations can have a greater influence on ecosystems than the large-scale NAO. This has been shown for Lake Erken (Sweden), where air and water temperature, ice phenology and phytoplankton spring bloom were related to both types of climate indices, but more strongly to regional ones (Blenckner & Chen 2003).

Temperature effects on species composition became significant when accounting for a variety of environmental and spatial variables by multivariate statistics (confirming hypothesis 3). The observed temperature trend explained 6% of the variation in community composition, which is astonishingly high given the environmental diversity of the lakes included and the comparably short time period analysed. The yearly increase in lake temperature averaged 0.1 °C, resulting in a mean warming of 1.5 °C over the 15 years of observation included here. Predicted temperature increases over the next 100 years range from 1.4 to 5.8 °C (IPCC 2001), which

suggest that future impacts increase as we observe longer periods of time and stronger temperature trends.

Taxa correlated to high trend temperatures included such diverse groups as Malacostraca, Plecoptera, Zygoptera, Anisoptera and Diptera, even though Plecoptera are known as cold-adapted species, in contrast to Odonata (Zygoptera, Anisoptera) (Pritchard et al. 1996). However, these taxa have obviously profited from the overall increase in lake temperature by increasing in abundance and/or range. The taxa for which the opposite is true are also very heterogeneous. The number of individuals and/or the places of occurrence decreased with increasing temperatures for species of Gastropoda, Ephemeroptera, Coleoptera, Trichoptera and Diptera, respectively. As temperatures increase further, these species are likely to vanish from the investigated area. This indicates that global warming has no overall effect on entire taxonomic groups, but that responses are species-specific.

Nevertheless, a large amount of variation was not explained by temperature. Other local factors such as pH, nutrients and total organic carbon as well as large-scale factors as latitude and longitude were also important. A similar pattern was found for macrofauna in Swedish streams (Sandin 2003) and lakes (Stendera 2005).

We observed significant changes in species composition of metazoans in the face of temperature shifts due to climate warming. Previously, such effects have been mainly observed in experimentally manipulated communities. Several terrestrial experiments have manipulated mean temperature or carbon dioxide and monitored their effects on the diversity of plant and insect assemblages (Hartley & Jones 2003; Klanderud & Totland 2005; Klein et al. 2004). Klein et al. (2004) showed a strong decline in plant species richness with

experimental warming, which was counteracted by grazers. Hartley and Jones (2003) found site- and assemblage-specific changes in community structure with elevated CO2. Klanderud and Totland (2005) found that community diversity dropped with experimental warming, primarily because changes in the abiotic environment modified biotic interactions. We know of only one similar aquatic experimental study, which also showed strong effects of warming on diversity (Petchey et al. 1999).

In conclusion, we observed no simple direct relationship between diversity and temperature or large-scale climate indices. However, we did find significant changes in species composition of benthic macroinvertebrates with the shifts in mean temperature observed over the last two decades. Even though they are weak and possibly affected by changes in other environmental characteristics, they are potentially highly important as they became evident over a rather short time period and upon moderate increases in mean temperature. Therefore, aquatic invertebrates are likely to show strong responses to climate warming.

Part II

Chapter 2

Effects of climate change on phytoplankton in a long-term microcosm experiment

Introduction:

Increasing average global temperatures were recorded for the last decades and predicted to further increase in the future up to plus 6.4°C (IPCC 2007c). Many studies have investigated the impact of this warming on physical, chemical and biological properties of ecosystems (Straile et al. 2003; Parmesan & Yohe 2003; Root et al. 2003; Walther et al. 2002). Apart from direct physiological effects (Hughes 2000) species have been shown to shift their ranges higher in altitude or latitude (Parmesan 2006; Root et al. 2003) to meet their ecological requirements in changing climate. But if a species is neither able to disperse due to ecological or geographical boundaries nor able to adapt to the new conditions, it is highly prone to extinction, at least regionally. Another often reported phenomenon found in many functional or taxonomic groups is the shift in phenology to mainly earlier timing of spring events as breeding or flowering but also later timing of autumn events (Parmesan 2006; Root et al. 2003; Walther et al. 2002). These changes can be associated to altered

species interactions. For instance, asynchrony between the timing of dependent life-history events between predator and prey could lead to mismatches with possibly important consequences for the whole system (de Senerpont Domis et al. 2007b; Edwards & Richardson 2004; Visser et al. 1998; Visser & Holleman 2001; Visser & Both 2005; Winder & Schindler 2004a; Winder & Schindler 2004b).

Moreover, complex interactions can result in altered ecosystem structure and function and may have consequences for biodiversity. The IPCC reported that globally 20 to 30 % of all plant and animal species have a high risk of extinction if the temperature increase exceeds 2 to 3°C (IPCC 2007b). Regionally, diversity is possibly affected in different ways. On the one hand regional extinctions could decrease species number; on the other hand species richness could increase by asymmetrical range shifts, if invading species move faster than evading species (Walther et al. 2002). Although this status can be transient, increased species richness due to a higher increase of warm-water species compared to the decrease of cold-water species has been shown for copepods (Beaugrand 2004) and for fish (Hiddink & Ter Hofstede 2008) in the North Sea. However, species number is just one aspect of diversity; another is the relative abundance of species reflecting dominance or evenness in a community. The relative proportions of species and/or functional groups may have important implications for ecosystem function, more substantial than the loss of non-essential rare species or long before a key-stone species finally has gone extinct (Hillebrand et al. 2008).

Furthermore, not only changes of the mean values of climatic variables have been predicted but also of their variance on inter-annual and daily time scale (IPCC 2007c). Changes in the variability of environmental variables can have even more important

consequences for population dynamics and interactions among species and functional groups and consequently for diversity. Several studies demonstrated the influence of the variability of environmental variables on species richness (reviewed by Shea et al. 2004). Corresponding to the intermediate disturbance hypothesis (Connell 1978) intermediate variation in frequency or magnitude of variables such as nutrients (Gaedeke & Sommer 1986; Sommer 1985), light (Flöder et al. 2002; Litchman 1998), salinity (Flöder & Burns 2004) or temperature (Descamps-Julien & Gonzalez 2005; Jiang & Morin 2007; McCabe & Cyr 2006) promoted highest diversity by preventing competitive exclusion. In contrast the combined effect of changes in the mean and in the variability of such variables is poorly understood (Benedetti-Cecchi et al. 2006).

Effects of climate warming have been intensely studied in aquatic ecosystems due to the correlation of their surface temperature to air temperature and the physical properties resulting from the thermal regime. Phytoplankton mainly consists of organisms with short generation times responding rapidly to changing environmental conditions and therefore can be considered good model organisms for experimental manipulations investigating climate change. Complex responses were found especially for freshwater phytoplankton which was affected directly and indirectly by the timing of ice-break-up (Adrian et al. 1999; Weyhenmeyer et al. 1999) and changed mixing regime (Berger et al. 2007; Tirok & Gaedke 2007; Wilhelm & Adrian 2008). Moreover, growth rates of phytoplankton are positively related to temperature. The magnitude also depends on body size (Brown et al. 2004; Gillooly et al. 2001; Litchman et al. 2007) owing to the relationship of metabolic rates such as the uptake of nutrients to the surface-to-volume ratio (Irwin et al. 2006; Litchman et al. 2007). Consequently, the temperature effect may be larger for

more rapidly growing small species than for slow growing large species, possibly leading to a community shift with dominance of smaller species as reported for diatoms (Winder et al. 2008).

Additionally, trophic interactions may modify the effects of global warming on phytoplankton. Grazers can increase prey diversity depending on their selectivity and the produced grazing pressure (McCauley & Briand 1979; Sarnelle 2005). Several studies found the direction of the effect to interact with the trophic status of the system, influencing diversity positively under eutrophic conditions, but negatively under oligotrophic conditions (Hillebrand et al. 2000; Proulx & Mazumder 1998; Worm et al. 2002). It can be speculated that grazers could also counteract the influence of warming if they are feeding on parts of the phytoplankton community, which would profit most from higher temperatures. Autotrophic and heterotrophic parts of the plankton community are probably differently affected by global warming because of differing relationships between temperature and the metabolism processes respiration and photosynthesis (Allen et al. 2005; Allen & Gillooly 2007; Gillooly et al. 2001). While both processes will increase with temperature, theory states that respiration will be enhanced relatively more than the less temperature sensitive photosynthesis. This will lead to stronger heterotrophy in the system (López-Urrutia et al. 2006; Rose & Caron 2007) which was supported in experiments conducted with a marine pelagic food web (Müren et al. 2005). Consequently, indirect temperature effects such as changing predation pressure or competition are probably more important for algae than the direct effects on photosynthesis.

For organisms with short life cycles such as most phytoplankton species experimental durations of several weeks up to one season are “long-term” compared to their generation times. However, these experiments still don’t capture the whole pattern.

Temperate lakes are strongly characterised by seasons. For Northern Europe warming is predicted to be stronger in winter than in summer (IPCC 2007c) and this situation can lead to different but not independent impacts of climate change in each season. For instance, the winter conditions could influence the qualitative and quantitative species composition which then functions as the starting assemblage for the spring development which would propagate through the seasons. Effects could also accumulate with time. Adrian et al. (Adrian et al. 1995) found that during a period of five consecutive warm years the development of phytoplankton in the first year was similar to the pattern of the year before, followed by a transitional phase with a similar species composition, but earlier succession. At last a regime shift occurred with a time lag of two years.

In the present study, a highly controlled long-term (16 months) laboratory experiment was performed to test the effect of global warming on phytoplankton diversity and to disentangle the single and combined effects of changes in means and variances of temperature. Additionally the effect of a second trophic level and the possible interactions were investigated. It was hypothesized that an increase in mean temperature would have a positive effect on algal abundance and biomass, especially in winter. Diversity should be affected negatively, shifting the community to dominance of small species and species with higher temperature preferences. Increased temperature variability and selective grazing should increase diversity and therefore were hypothesized to counteract the negative impact of warming.

Methods:

Experimental set-up

In the long-term experiment mean temperature, temperature variability and the presence or absence of grazers were manipulated in a full factorial design (Table 1) according to predictions of the International Panel on Climate Change (IPCC 2001). The experiment was conducted in a climate room, where a system of water baths allowed simulating yearly temperature curves such as in a European lake. The low (L) main temperature regime mimicked the present day pattern of a lake with a winter temperature of 4°C and a summer temperature of 20°C. In contrast, the high (H) mean temperature regime approximately mimicked the lake in the year 2100 where winter temperatures are supposed to have increased by 4°C (8°C absolute) and summer temperatures by 2°C (22°C absolute) because of the more pronounced warming in winter. Both temperature regimes were simulated in a smooth (S) and in a variable (V) pattern reflecting enhanced temperature variability by superimposing a sinus curve with $\pm$ 2°C every second week on the smooth curve without changing the mean temperatures (10.5°C and 14.5°C annual mean, respectively). The temperatures were changed once a week and produced by a simple system with a cooling unit cooling down the water and one aquarium heater in each bath which was connected to a control unit and adjusted the temperatures by heating. Light was provided from above using BioSun fluorescent lamps, which emit light with a natural spectrum and an average light intensity of 160 µmol photons m^{-2} s^{-1} in a 12h/12h light/dark rhythm. Modified WoodsHole (WC) Medium (Guillard 1975) was used with the concentrations of the major nutrients (50 µg P L^{-1}, 1000 µg N L^{-1}, 1500 µg Si L^{-1}) corresponding to

a eutrophic lake with a tendency towards phosphorus limitation. The medium was buffered and adjusted to pH 7 using hydrochloric acid and sodium hydroxide. The experiment was started in August 2005 and lasted until December 2006. Nineteen phytoplankton species covering different taxonomic groups, size-classes, mobility and growth forms of phytoplankton (Table 2) were grown on WC-medium and inoculated in similar abundances. Except for *Crytomonas sp.* (strain number 24.80 from the Experimental Phycology and Culture Collection of Algae, SAG, Göttingen) and a small cyanophyte (isolated from the culture of *Coleps sp.*), phytoplankton strains were obtained from the Culture Collection of Algae at the University of Cologne, CCAC (Table 1). Two algivorous ciliates were added as grazers; *Coleps sp*. was provided by D. Martin-Creuzburg (University of Constance Limnological Institute, Konstanz) and *Urotricha furcata* was provided by T. Weisse (Institute for Limnology of the Austrian Academy of Sciences, Mondsee). Both species were not able to graze on all algal species and thus could be assumed to produce selective grazing pressure.

Table 1: Experimental set-up with treatment abbreviations

Factor	Abbr.							
Temp (**L**ow/**H**igh)	**L**				**H**			
Var (**S**mooth/**V**ariable)	**S**		**V**		**S**		**V**	
Grazer (**A**bsent/**P**resent)	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**
Number of replicates	8	8	8	8	8	8	8	8

Table 2: Phytoplankton species used in the experiment, their taxonomic group, and their origin

Name	Group	Strain number - source
Phacus smulkowskia	Euglenophyceae	M 2282 - CCAC
Cryptomonas sp.	Chrysophyceae	24.80 - SAG
Gymnodinium sp	Dinophyta	M 2391 - CCAC
Peridinium cinctum	Dinophyta	M 1576 - CCAC
Closterium navicula	Streptophyta	M 2096 - CCAC
Staurastrum hirsutum	Streptophyta	M 2094 - CCAC
Tetmemorus laevis	Streptophyta	M 9181 - CCAC
Cosmarium biretum	Streptophyta	M 2123 - CCAC
Chlamydomonas terricola	Chlorophyta	M 1259 - CCAC
Oocystis sp.	Chlorophyta	M 1782 - CCAC
Stichococcus sp.	Chlorophyta	M 1830 - CCAC
Tetraedron sp.	Chlorophyta	M 1793 - CCAC
Ankistrodesmus sp.	Chlorophyta	M 2209 - CCAC
Microthamnion sp.	Chlorophyta	M 2196 - CCAC
Eudorina elegans	Chlorophyta	M 0547 - CCAC
Nitzschia sp.	Bacillariophyceae	M 1771 - CCAC
Fragilaria capucina	Bacillariophyceae	M 1767 - CCAC
Cylindrospermum sp.	Cyanophyta	M 1160 - CCAC
Synechocystis-like, not further det	Cyanophyta	Isolated by T.B.

Experimental cultures (150 ml) were grown in 250 ml Erlenmeyer flasks .Each treatment was replicated 8 times buffering the risk of loosing some of the species mixtures completely due to contamination during the long experimental duration. A semi-continuous culture technique was used with a daily exchange rate of 10 %. To maintain high diversity in the cultures over a long time, 70% of the culture suspension were exchanged with new medium once a week resulting in an average dilution rate of 0.17 d^{-1} ($-\ln(v_t/v_0)/t$). This produces nutrient pulses with time intervals that were found to produce highest diversities compared to lower or higher intervals (Gaedeke & Sommer 1986; Sommer 1985; Flöder & Sommer 1999; Gaedeke & Sommer 1986; Sommer 1985). Nevertheless it could be expected to get monocultures as endpoints because they were grown

in a closed system where species can go extinct but cannot come back by invasion or dispersal. However, it also can be assumed that species can return, if they have not become extinct in a microcosm but fallen under the detection limit of the counting method. To minimize wall effects such as periphytic or bacterial growth on the inner surfaces of the culture flasks, Erlenmeyer flasks were replaced with clean sterile ones every week. The culture flasks were swirled gently three times a week to keep them in suspension and thereby their places were changed randomly in between each water bath to account for slight differences in light intensity.

Sampling and measurements

Sampling took place normally every fourth week, but every sixth week in winter (December to March) and every third week in spring (April to June) to account for different dynamics depending on the season. The first sampling was done in September when the experiment already ran for one month. Samples were taken from the remaining solution after transfer. One subsample (10 to 20 ml) of each replicate was filtered through a GF/F-filter and the filtrate was stored in a freezer (-20 °C) until determining the content of soluble reactive phosphorus after Grasshoff et al. (Grasshoff et al. 1983) to control for nutrient limitation at the end of each nutrient pulse interval. Another subsample (50 ml) was fixed with Lugol`s iodine solution and stored in dark bottles for phytoplankton identification in 3 ml sedimentation (Utermöhl) chambers under an inverted microscope (Leica DMIRB). Depending on algal concentration, the samples were diluted (two to ten times) or, rarely, concentrated and counted after settling time (over night) with different magnifications (100x to 630x)

depending on algal dimensions. A minimum of 400 cells and ten fields were counted for each magnification, if not possible the whole chamber was examined. In total a minimum of 800 cells was counted for each sample.

Biovolumes for each species were calculated using the most appropriate geometrical formulas with measurements of linear dimensions of a minimum of 20 cells (Hillebrand et al. 1999). Algal diversity was determined as species richness defined as species number and the Shannon-Index H`, calculated on both abundance and biovolume proportions to account for quantitative and qualitative changes in the communities.

Statistical Analysis

Repeated-measures Analysis of Variance (rm-ANOVA) was used to detect significant effects of treatments as well as significant changes over time within treatments. Prior to analyses all data were log-transformed to stabilise the variances and a Cochran test was done to check for their homogeneity. Main temperature, temperature variability and grazer represented the factors between subjects, whereas time as well as all interactions involving time were analysed within subjects. Effects were considered significant if $p < 0.05$ and highly significant if $p < 0.001$, trends were identified if $p = 0.05 - 0.1$. Significant results from the Analysis of Variance were subjected to Tukey's honestly significant difference (HSD) to compare treatment combinations. All analyses were performed with STATISTICA (2003).

Results:

Experimental set-up

The technical system worked well in producing the temperatures with deviations up to ± 0.5°C and only some exceptions of that range. Three times the highest temperature was 1°C too low for one week and twice temperatures for all treatments were too high during one day due to technical problems. Additionally, in March 2006 the cooling unit broke and the system had to work without it for 5 days until a new unit was attached. This resulted in temperatures 2-5°C too high but only for the cold temperature treatments. Similarly the unit broke down again in September and did not work for three days resulting in higher temperatures than intended (2-4°C) for all water baths except for the one with the highest temperature. However, this didn't seem to have any effect on the results, as these short-term events did not produce visible changes in either abundances or biomass or community composition. None of the cultures was lost ad it was possible to maintain multiple-species communities for a long time in the microcosms, at least in some experimental flasks for more than one year. To our knowledge highly controlled experiments with artificial communities in small microcosms have rarely been performed for such a long period before (Benincà et al. 2008). The replication worked well, replicates developed similarly although treatments diverged in their composition. Only some communities differed in algal composition from their respective replicates (LSA: 2, HSP: 3, HVP: 4) at the end of the experiment.

Phosphorus

Soluble reactive phosphorus measured one week after addition was always below detection limit (5 µmol L^{-1}), probably completely consumed by algae. This was consistent in all treatments and throughout the whole time of the experiment. Therefore, conditions for algae changed weekly and regularly from high nutrient supply to strong phosphorus limitation.

Phytoplankton

Phytoplankton communities showed complex responses to all three factors with interactions and time dependencies. The responses to single factors were highly modified by the other factors resulting in many significant interaction terms in the ANOVA up to complex three-way interactions (Table 3). For all analysed variables clear differences in the dynamics and timing of responses could be demonstrated even if the final outcome was similar in all treatments. In the following these dynamics are described in detail.

Table 3: Results of rm-ANOVA for all measured variables. Significant results are printed in bold, trends in italic. Abbreviations: T = temperature, V = Variability, G = grazer

Dependent variable	df	Abundance		Biovolume		Species richness		Shannon-I. H´ Abund.-based		Shannon-I. H´ Biovol.-based	
Effect		F	p	F	p	F	p	F	p	F	p
Temp	1	10.22	**0.0024**	19.4	**0.0001**	0.26	0.6113	3.59	*0.0636*	0.90	0.3482
Var	1	25.54	**0.0000**	6.0	**0.0174**	37.41	**0.0000**	20.38	**0.0000**	39.53	**0.0000**
Grazer	1	4.21	**0.0453**	5.3	**0.0246**	48.66	**0.0000**	22.27	**0.0000**	84.17	**0.0000**
T x V	1	37.45	**0.0000**	3.8	0.0554	13.83	**0.0005**	4.77	**0.0335**	4.58	**0.0366**
T x G	1	87.56	**0.0000**	30.3	**0.0000**	112.83	**0.0000**	52.15	**0.0000**	14.45	**0.0004**
V x G	1	16.15	**0.0002**	1.6	0.2071	3.99	*0.0509*	0.10	0.7477	4.38	**0.0410**
T x V x G	1	8.66	**0.0049**	3.3	*0.0738*	5.41	**0.0239**	2.96	*0.0913*	1.01	0.3187
Time	16	39.06	**0.0000**	43.7	**0.0000**	570.56	**0.0000**	59.70	**0.0000**	196.21	**0.0000**
Time x T	16	17.77	**0.0000**	7.1	**0.0000**	8.41	**0.0000**	11.68	**0.0000**	8.47	**0.0000**
Time x V	16	11.47	**0.0000**	2.5	**0.0007**	8.64	**0.0000**	5.62	**0.0000**	6.25	**0.0000**
Time x G	16	3.26	**0.0000**	2.8	**0.0002**	6.67	**0.0000**	22.08	**0.0000**	13.18	**0.0000**
Time x T x V	16	11.56	**0.0000**	3.0	**0.0001**	6.55	**0.0000**	3.58	**0.0000**	5.30	**0.0000**
Time x T x G	16	14.24	**0.0000**	1.4	0.1565	13.34	**0.0000**	19.51	**0.0000**	4.20	**0.0000**
Time x V x G	16	3.83	**0.0000**	2.6	**0.0004**	0.93	0.5380	0.41	0.9814	3.37	**0.0000**
Time x T x V x G	16	3.14	**0.0000**	0.8	0.7390	2.17	**0.0000**	5.04	**0.0000**	1.66	**0.0487**

Abundance

Algal abundances decreased in late winter in all treatments with lowest numbers in February of the first year. This trend was more distinct in low mean temperature treatments and only slightly visible in warmed treatments without grazers (Figure 1), where a strong increase until December and persisting high abundances throughout the year could be observed. During spring and summer algal abundances increased reaching highest values from August to October and decreased in autumn and winter again.

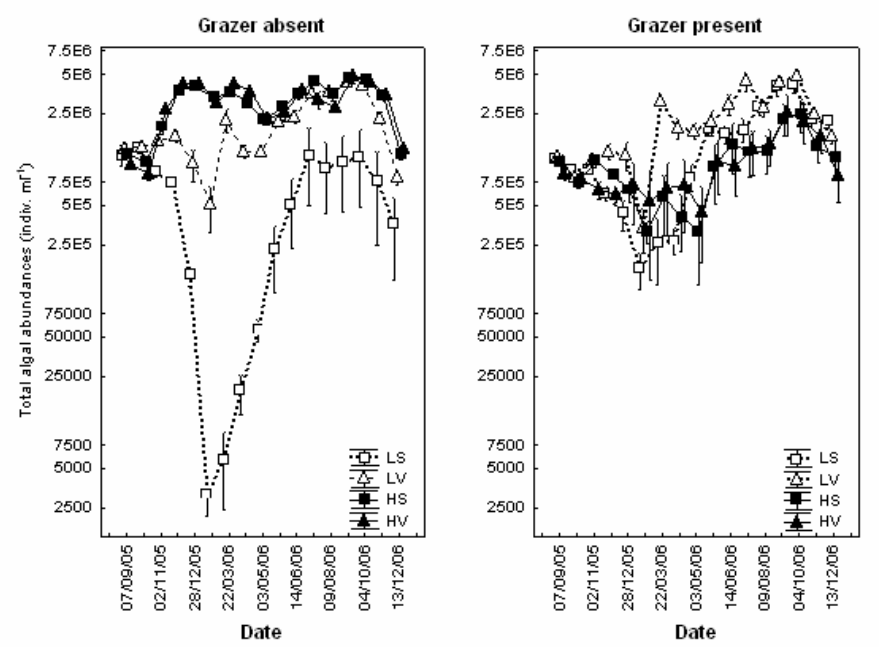


Figure 1: Development of total algal abundance through time (means and standard errors) on a logarithmic scale. For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

All factors affected total algal abundances significantly with a positive mean temperature effect ($p < 0.01$), a positive effect of enhanced temperature variability ($p < 0.001$) and a negative grazer effect ($p < 0.05$). Likewise, all two-way interactions were significant. Thus enhanced temperature variability buffered the positive effect of increasing mean temperatures and similarly high main temperatures moderated the positive effect of enhanced temperature variability ($p < 0.001$). Grazer presence switched the effect of increased mean temperature from positive to negative and in the same manner the grazer effect switched from a positive influence on algal abundances in low temperature treatments to a negative influence in high temperature treatments ($p < 0.001$). Similarly, temperature variability and grazers modified their impact mutually. Enhanced temperature variability increased total algal abundances, when grazers were absent and likewise grazers had a negative effect with variable temperatures ($p < 0.001$).

Rm-ANOVA revealed also a significant three-way interaction of the factors on total algal abundances. Higher mean temperatures increased abundances significantly, when grazers were absent and without temperature variability, whereas warming had a negative effect when grazers where present and temperatures had a higher variability. With low mean temperatures and without grazers temperature variability influenced total algal abundances positively (Figure 1 - Appendix/Chapter 2). The effects and interactions were all time dependent (Table 2).

Biovolume

Total algal biovolumes were highest during the first months and decreased only slowly until a sharp decline beginning in November or December (Figure 3). The subsequent main dynamics were similar to the development pattern of total algal abundances. Generally, biovolumes increased in spring and summer and decreased in winter which was most pronounced in cold treatments. However, in warm temperature treatments biomass increased only slightly during spring and especially in the grazed and warmed treatments biovolumes did not go up any more, whereas in the non-grazed low temperature treatment without enhanced temperature variability (LSA) biovolumes rose to high amounts compared to other cold temperature treatments and those without grazers.

Figure 2: Development of total algal biovolume through time (means and standard errors) on a logarithmic scale. For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable)

All three single factors produced significant effects on total algal biovolumes. Increasing the mean temperature increased biovolumes ($p < 0.001$) as did grazer presence ($p < 0.05$). On the contrary increasing temperature variability reduced biovolumes ($p < 0.05$). The effect of grazers was dependent on the temperature treatment and vice versa reflected by a significant temperature x grazer-interaction ($p < 0.001$). In warm treatments grazers had a positive effect and high mean temperatures had a clear positive effect when grazers were present. All of these effects were time dependent.

A modifying trend of mean temperature and variability level could be observed, even though the interaction term was not significant ($p = 0.055$). In cold treatments biomass was significantly reduced with enhanced temperature variability while warming had its strongest effect in more variable environments (Figure 2 - Appendix). Similarly, a trend for a three-way-interaction could be observed ($p = 0.074$), demonstrating that the variability level had the strongest effect in low temperature treatments without grazers and warming decreased biovolumes in non-grazed treatments while it increased the values in grazed treatments, independent of the variability level (Figure 2 – Appendix/Chapter 2).

Diversity

Species richness

Species richness was strongly reduced from the beginning of the experiment on and comparably for all treatments until December of the first year (Figure 3). Then three to four species persisted together in some treatments for a long time while others became monocultures quickly. The warm temperature treatments without grazers were the first ones (in March) where in all eight replicates the same species was left as single species. The next treatments becoming monocultures were the low mean temperature treatments with variable temperatures and without grazers (LVA) in June and the respective grazed treatment (LVP) in October. In the remaining four treatments at least some replicates still contained two or more species until the end of the experiment.

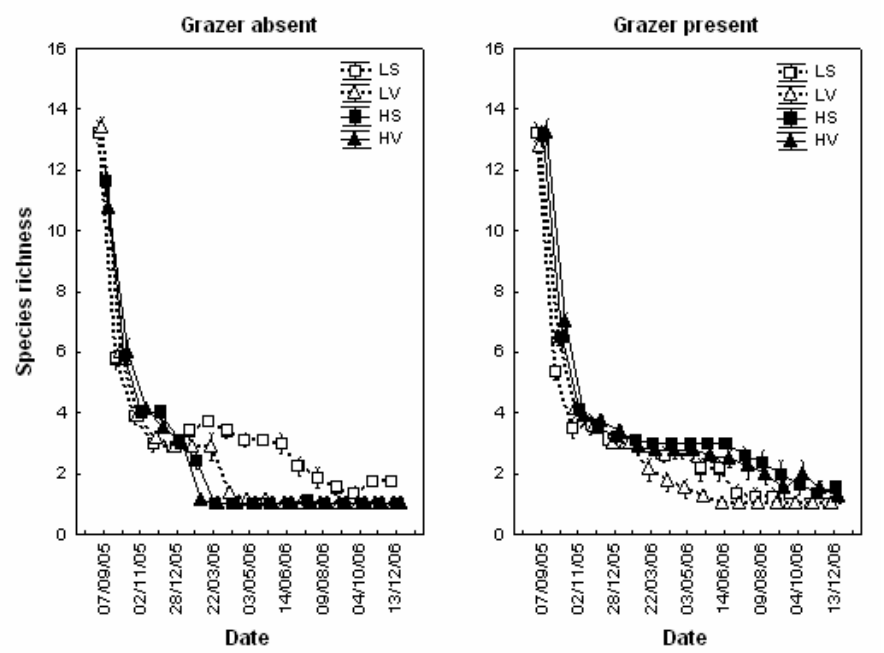


Figure 3: Development of species richness through time (means and standard errors). For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Several times a species reappeared after it had not been counted for several sampling dates, affirming the assumption that species can come back and reach high values when they were persisting in numbers below the detection limit. This was especially prominent for the low mean temperature treatments without temperature variability and grazers (LSA) from February to March where *Fragilaria* formed a bloom in most replicates. Similarly *Cylindrospermum* returned to one replicate each of the warmed temperature treatments with grazers (HSP, HVP) becoming the dominant species from late summer/autumn of the second year on thereby representing exceptions to all other samples. It could also be found in one of the other treatments, but here the returning species was mostly represented with very low numbers and did not re-establish.

Among the three single factors mean temperature had no significant effect on species richness whereas enhanced temperature variability decreased species numbers ($p < 0.001$) and grazer presence increased species richness ($p < 0.001$). The two-way interactions were significant or, in case of the temperature variability x grazer interaction, only marginally non-significant. Thus the negative effect of enhanced temperature variability was distinct in low temperature treatments ($p < 0.05$); means for high temperature treatments were comparable. Likewise, there was a positive grazing effect in warm treatments ($p < 0.001$) whereas low temperature treatments did not differ. The effect of increasing mean temperature switched from negative without grazers (Tukey HSD: $p < 0.05$) to a positive effect with grazers (Tukey HSD: $p < 0.05$). Furthermore, there was a trend for a negative effect of enhanced variability in non-

grazed treatments and a positive grazer effect for both variability levels, but this was not significant with the chosen levels ($p = 0.0509$).

A significant three-way interaction of the factors could be detected ($p < 0.05$) reflecting a complex pattern. Higher mean temperatures had a negative effect on species richness in non grazed treatments without enhanced temperature variability switching to a positive effect in grazed treatments independent of variability. Likewise, the positive grazing effect in warm treatments was independent of the variability level. In non-grazed low temperature treatments enhanced temperature variability negatively influenced species richness, i.e. missing temperature variability increased species richness (Figure 3 – Appendix/Chapter 2). All significant effects were time dependent (Table 2).

Shannon-Index H`

In contrast to species richness abundance-based Shannon-diversity increased after three to four months of stagnation in all treatments (Figure 4), before diversity decreased again in all treatments but with clearly different dynamics. These reflected the pattern found for species richness representing the extinction of species. Nevertheless, Shannon-diversity increased in warmed and grazed treatments and without temperature variability until April.

The pattern for biovolume-based Shannon-diversity was similar, but diversity was higher at the beginning of the experiment and did not increase to higher levels in any treatment afterwards (Figure 5). The dynamics of decreasing diversity were also similar, but not as clear as when calculated on the basis of abundances.

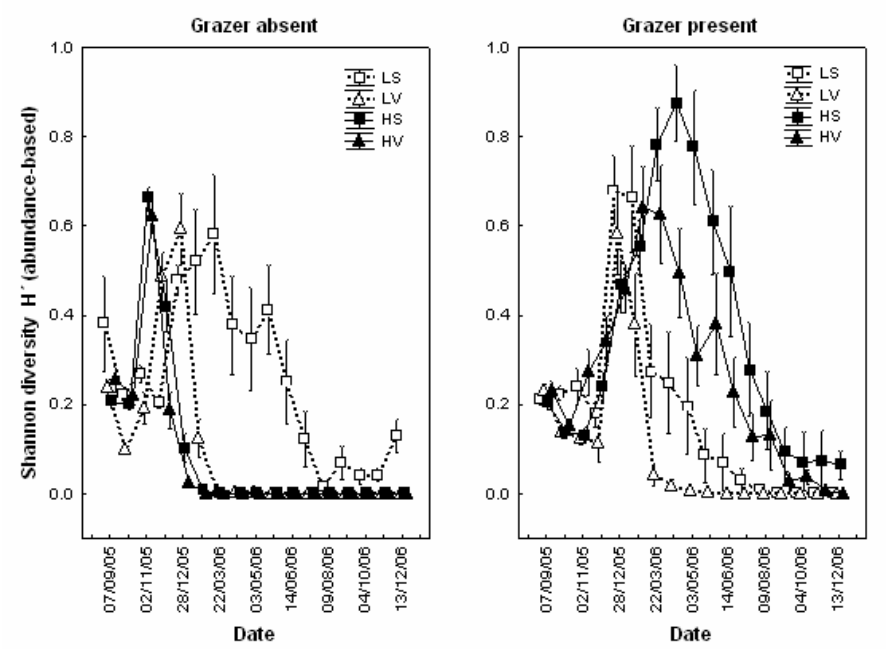


Figure 4: Development of abundance-based Shannon-diversity through time (means and standard errors). For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

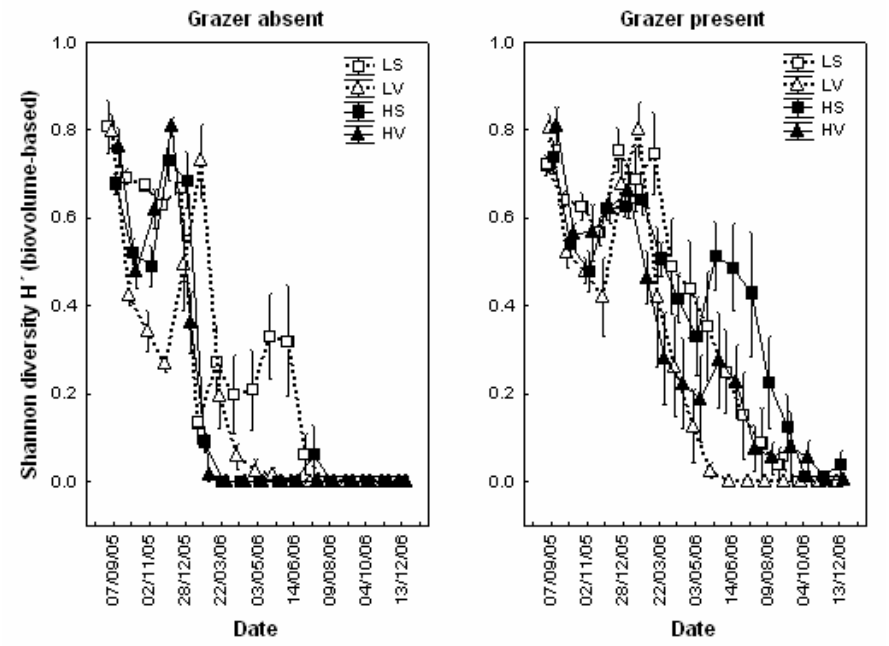


Figure 5: Development of biovolume-based Shannon-diversity through time (means and standard errors). For better overview treatments with and without grazers are shown in different graphs Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

While temperature variability had a negative effect on abundance- and biovolume-based diversity ($p < 0.001$ for both) and grazer presence a positive effect ($p < 0.001$ for both), mean temperature had no significant effect on Shannon diversity, neither abundance- nor biovolume-based. However, significant interactions with both other factors could be found (Temp x Var: $p < 0.05$ for both, Temp x Grazer: $p < 0.001$ for both, Figure 4, 5). For both Shannon-diversities variable temperatures had a negative effect when temperatures where low (Tukey HSD: $p < 0.05$ for both), for biovolume based diversity this was also significant for warm treatments (Tukey HSD: $p < 0.05$). Similarly, grazers increased diversity in warm treatments (Tukey HSD: $p < 0.05$ for both), for biovolume-based diversity this was also detectable in low temperature treatments (Tukey HSD: $p < 0.05$). Furthermore, the positive temperature effect could be detected in grazed treatments for abundance-based diversity (Tukey HSD: $p < 0.05$) while warming influenced diversity negatively in non-grazed treatments irrespective of being based on abundances or biovolumes (Tukey HSD: $p < 0.001$ for both). Whereas the interaction of grazing with the temperature variability level was not significant for abundance-based Shannon-diversity, a trend to modify each other could be detected for biovolume-based Shannon-diversity, but this was very weak. The positive grazing effect seemed to be stronger in less variable environments and enhanced temperature variability seemed to reduce diversity more strongly (Figure 4, 5 – Appendix/Chapter 2). The effects were time dependent (Table 2).

Community composition

The community composition changed comparably in all treatments during the first two to three months (Figure 6-9), when *Ankistrodesmus* appeared as the most important species during that time, strongly dominating the community with highest numbers of individuals and total biovolumes. The second most important species was *Chlamydomonas*. Also important during the first two months was *Eudorina*, but after that time this species vanished in all treatments. This was similar for *Fragilaria* which persisted in low numbers a little longer. In contrast to all other treatments, this diatom showed a spring bloom in the low temperature treatment without variability and grazers, while it was only rarely to find in the other treatments after the first winter. Considerable numbers and biovolumes were also reached by the cyanophytes *Cylindrospermum* and cf. *Synechocystis* during the first three to four months. After the first winter the community composition substantially changed. Cf. *Synechocystis* dominated nearly all treatments while *Ankistrodesmus* was becoming rare. In some treatments *Chlamydomonas* could persist, and then became the dominant species in terms of biovolumes. At the end of the experiment some replicates of grazed and warmed treatments (two out of eight in HSP and three out of eight in HVP respectively) were monocultures or highly dominated by *Chlamydomonas* or (one each) by *Cylindrospermum*. Also in the non-grazed low temperature treatment without enhanced temperature variability (LSA) six out of eight replicates were highly dominated by *Chlamydomonas* but all other replicates of all treatments developed to monocultures of cf. *Synechocystis* (Figure 6-9). Thus five to six species were important at times or in particular cases while all others died out quickly.

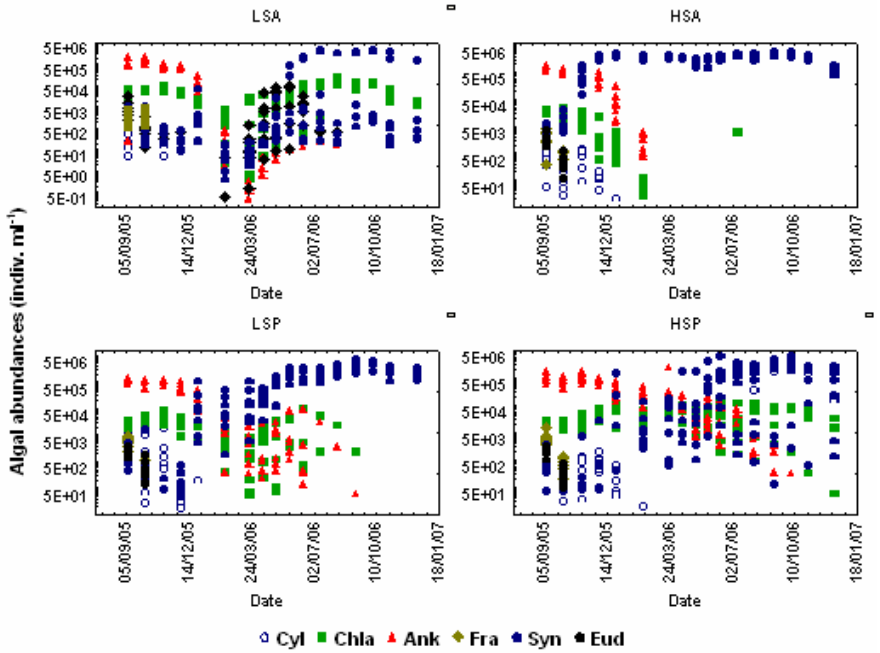


Figure 6: Community composition based on cell abundances. The most important six algal species in the eight replicates at each time point are shown in one plot. Open blue circles represent *Cylindrospermu*m sp., green quarters represent *Chlamydomonas terricola*, red triangles represent *Ankistrodesmus* sp., brown-green diamonds represent *Fragilaria capucina*, blue circles represent cf. *Synechocystis* and black circles represent *Eudorina elegans* (L = low temp., H = high temp., S = smooth, V = variable, A= grazer absent, P = grazer present)

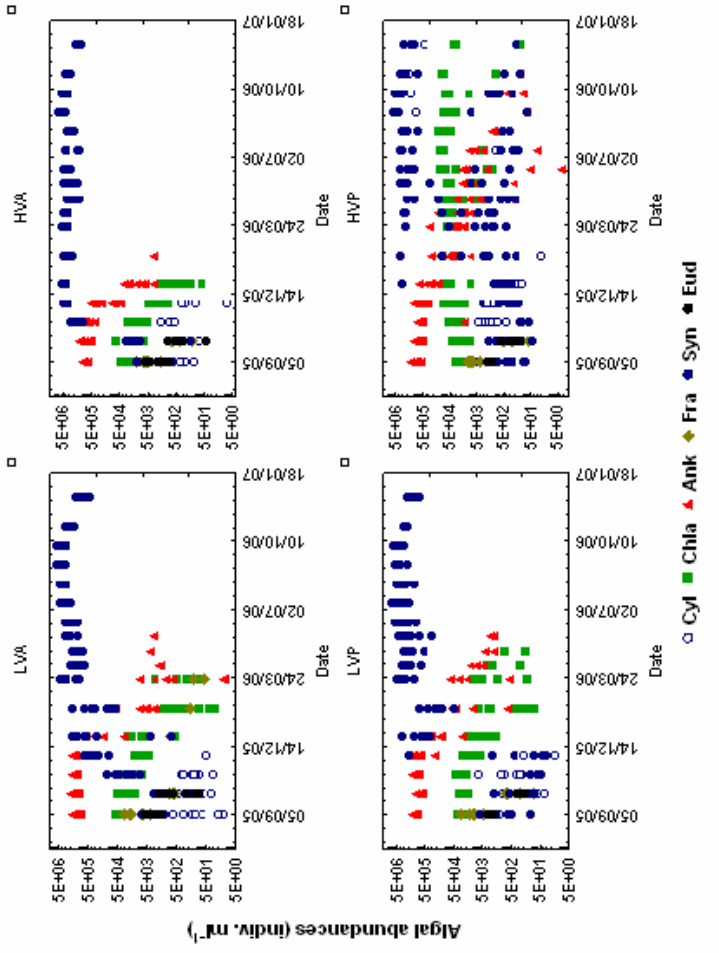


Figure 6: Continued

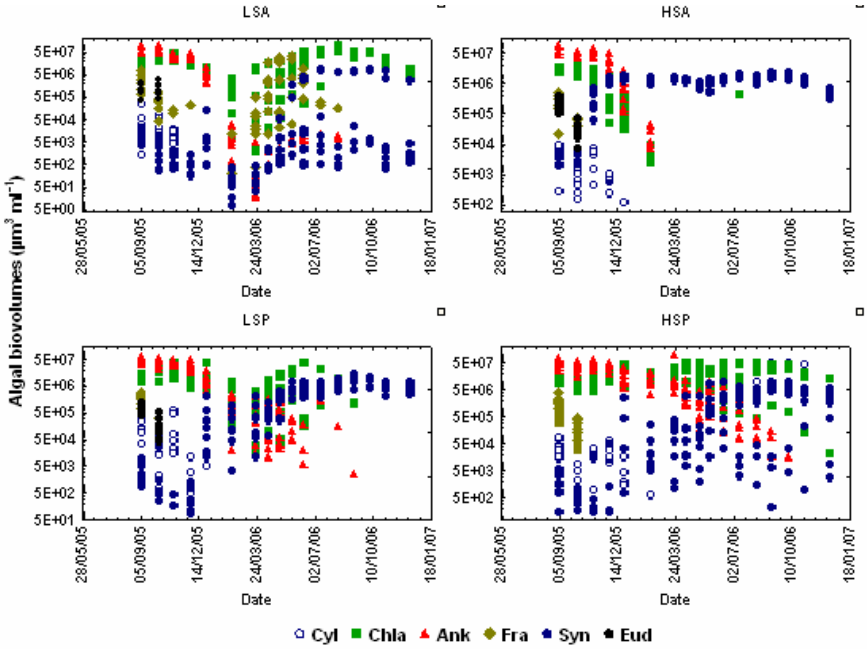


Figure 7: Community composition based on cell biovolumes. The most important six algal species in the eight replicates at each time point are shown in one plot. Open blue circles represent *Cylindrospermu*m sp., green quarters represent *Chlamydomonas terricola*, red triangles represent *Ankistrodesmus* sp., brown-green diamonds represent *Fragilaria capucina*, blue circles represent cf. *Synechocystis* and black circles represent *Eudorina elegans* (L = low temp., H = high temp., S = smooth, V = variable, A= grazer absent, P = grazer present)

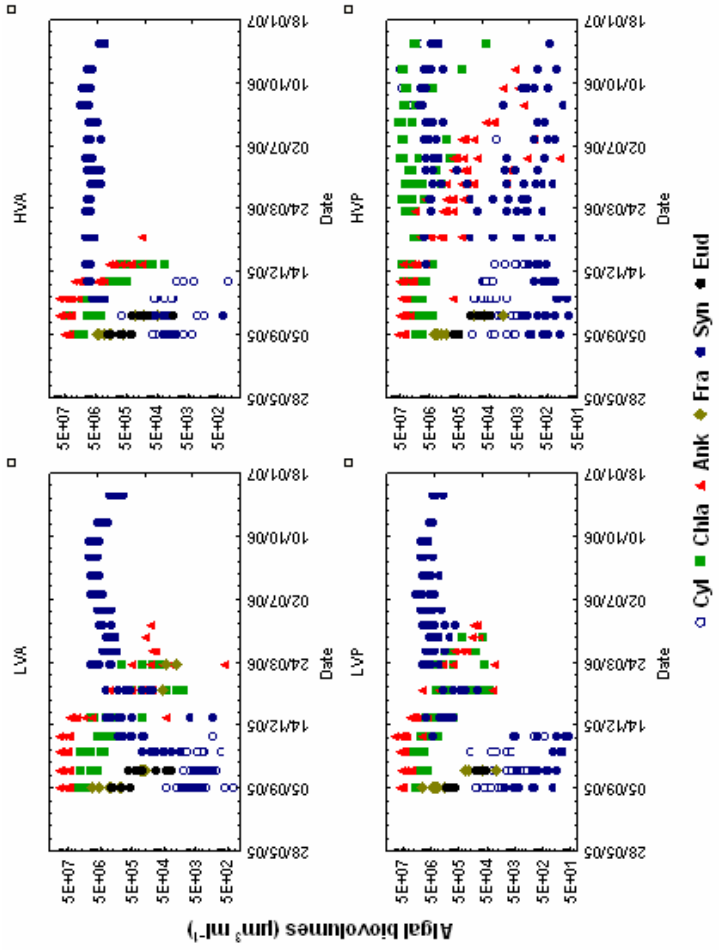


Figure 7: Continued

The temporal development of the dominant algal species is demonstrated for all replicates in Figure 8 and 9. While cf. *Synechocystis*, *Ankistrodesmus* and *Chlamydomonas* dominated, *Cylindrospermum* could be found in higher numbers until December of the first year but could not re-establish after winter except in one replicate each of the two warmed and grazed treatments, where the species reoccurred and became dominant in late summer/autumn of the second year. *Fragilaria* fell below the detection limit quickly; nevertheless this species could re-establish in all replicates of the cold mean temperature treatment without temperature variability and grazers (LSA) and formed a spring bloom from March until June after it vanished again (Figures 6-9). *Eudorina* was important until the second sampling only and vanished until the third. The time courses of the three dominating species are additionally presented single (Figure 10-12).

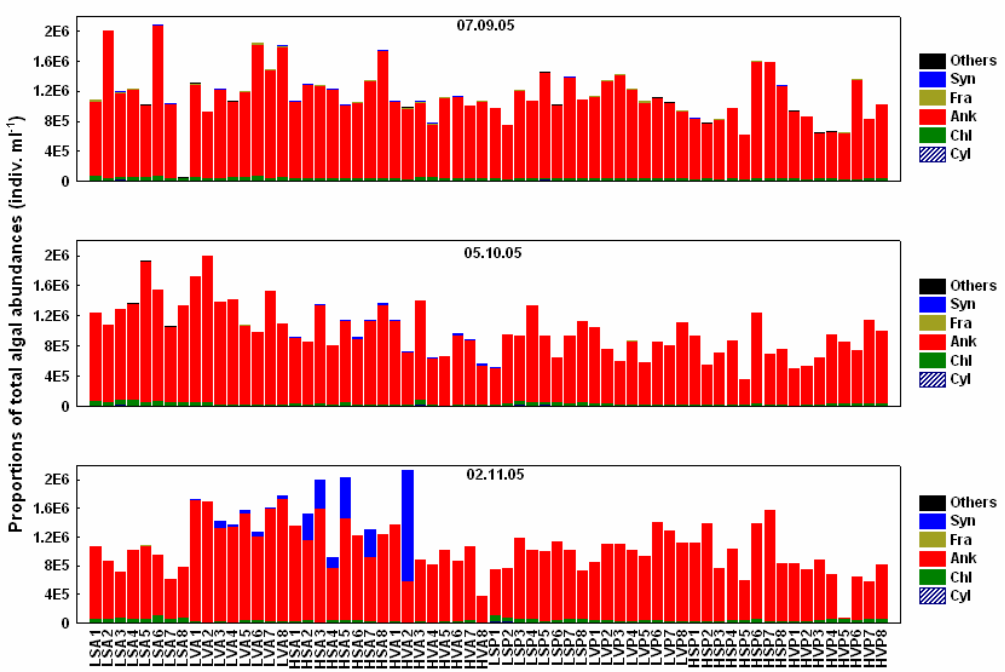


Figure 8: Community composition based on abundances over time. The most important five species are shown individually, remaining rare species including *Eudorina* are grouped in “Others”. Note the different y-axis-scaling.

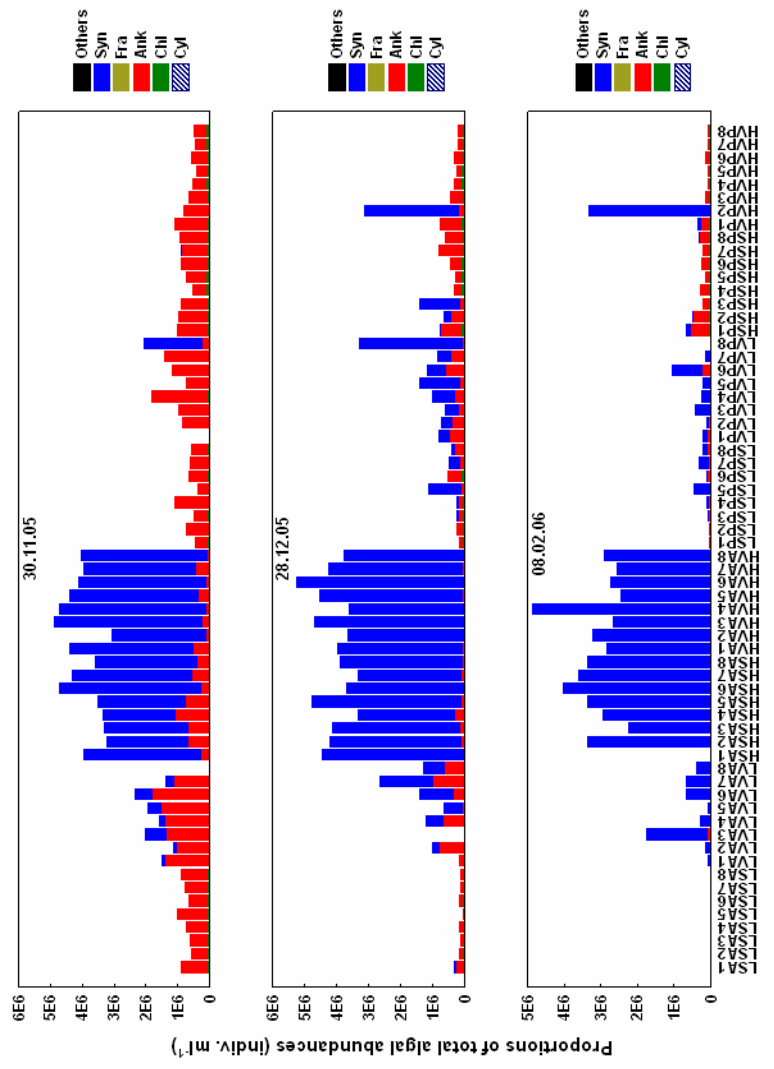
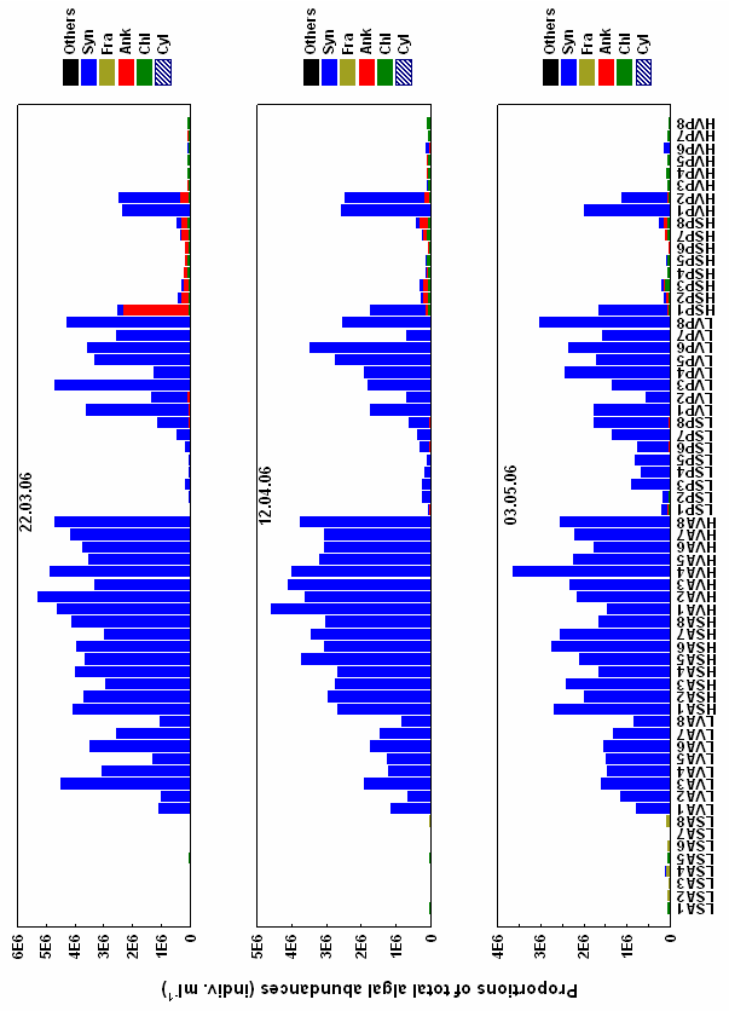


Figure 8: Continued



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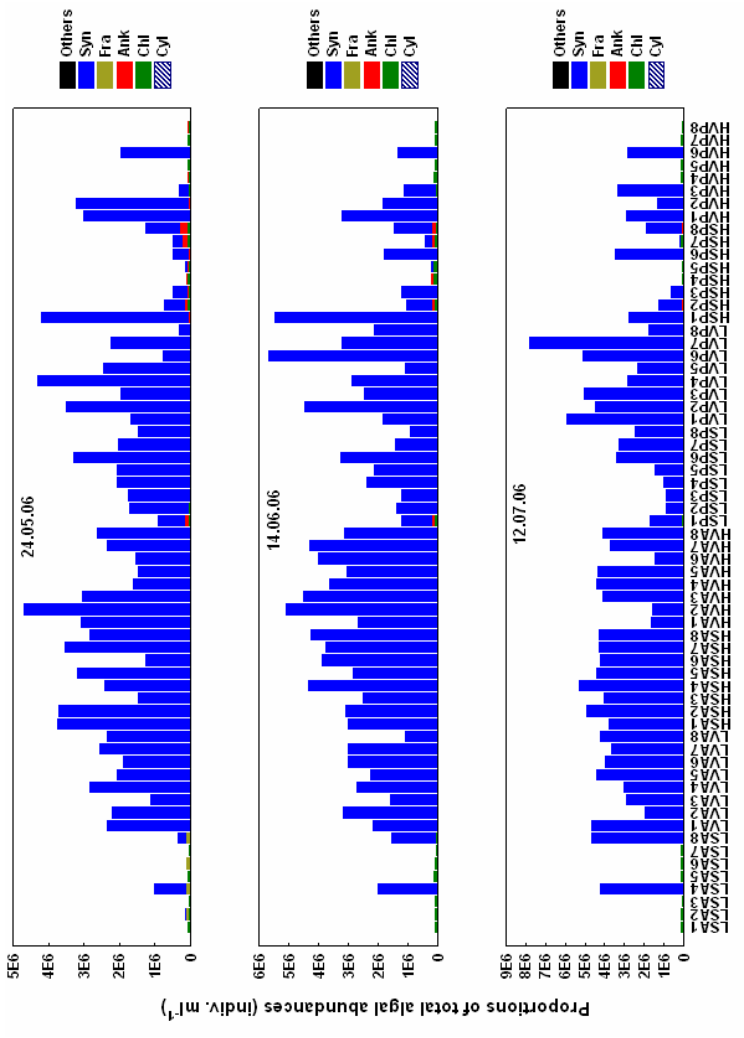
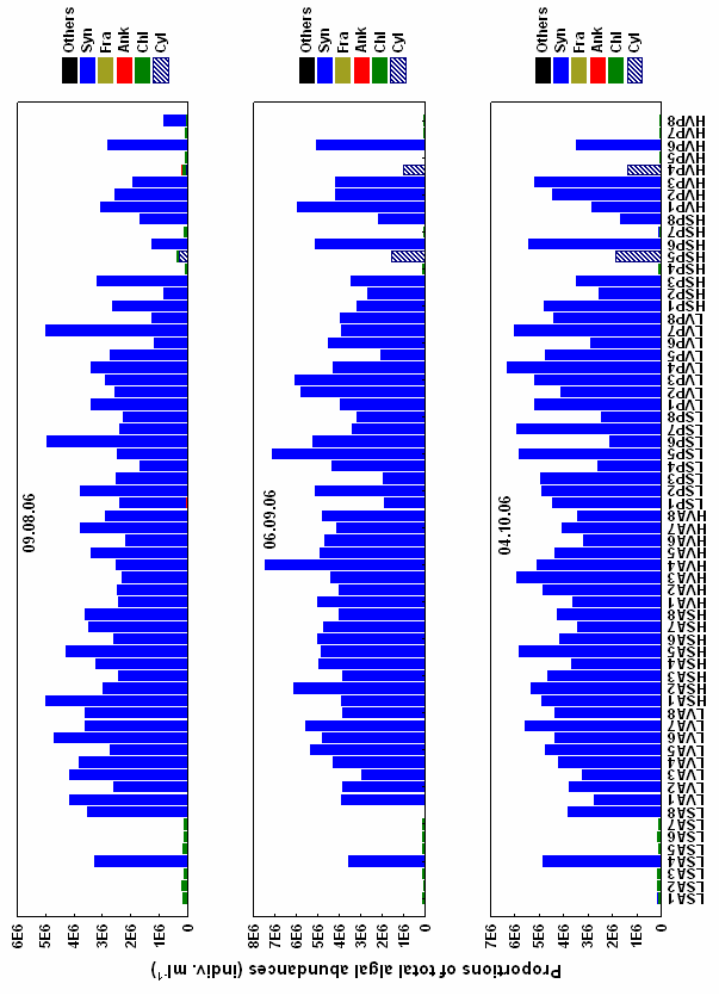


Figure 8: Continued



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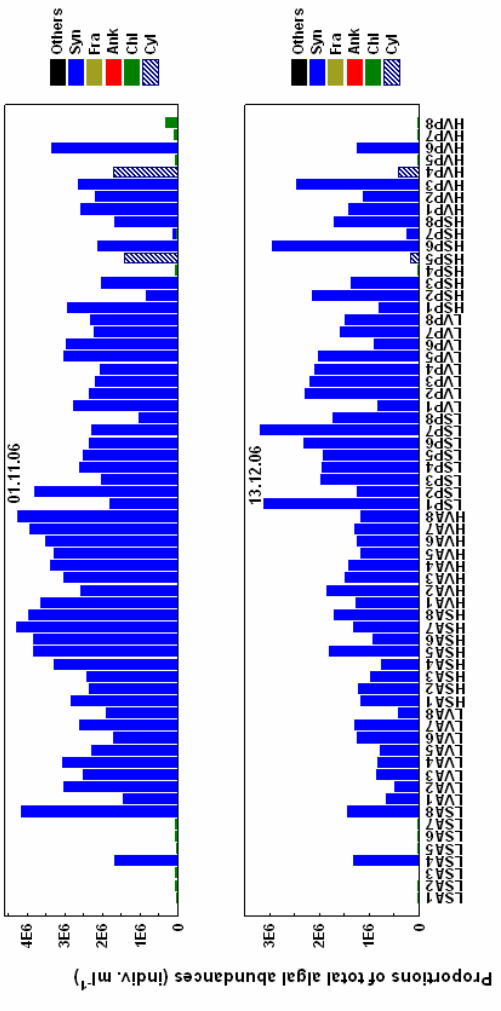

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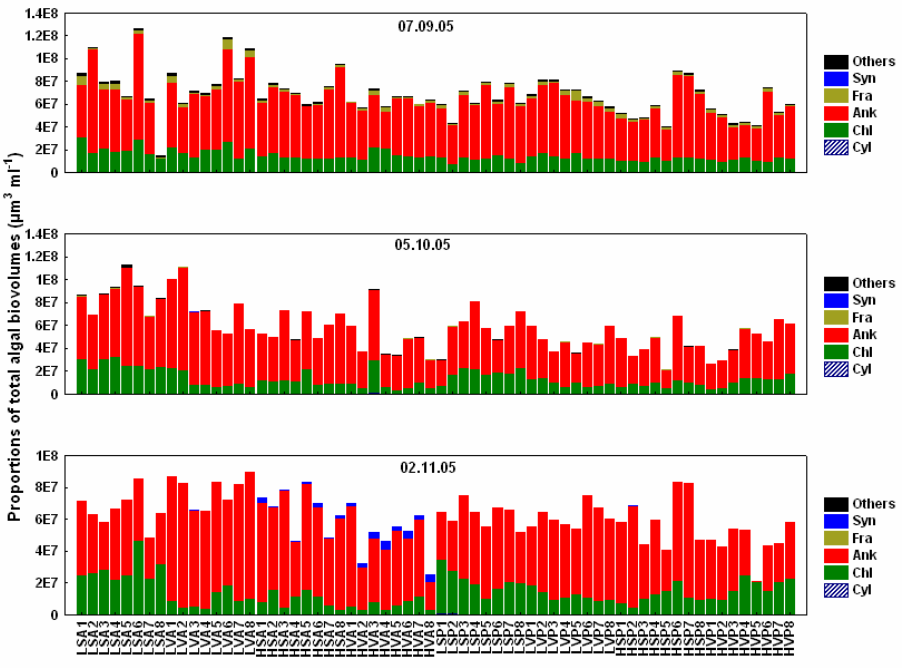
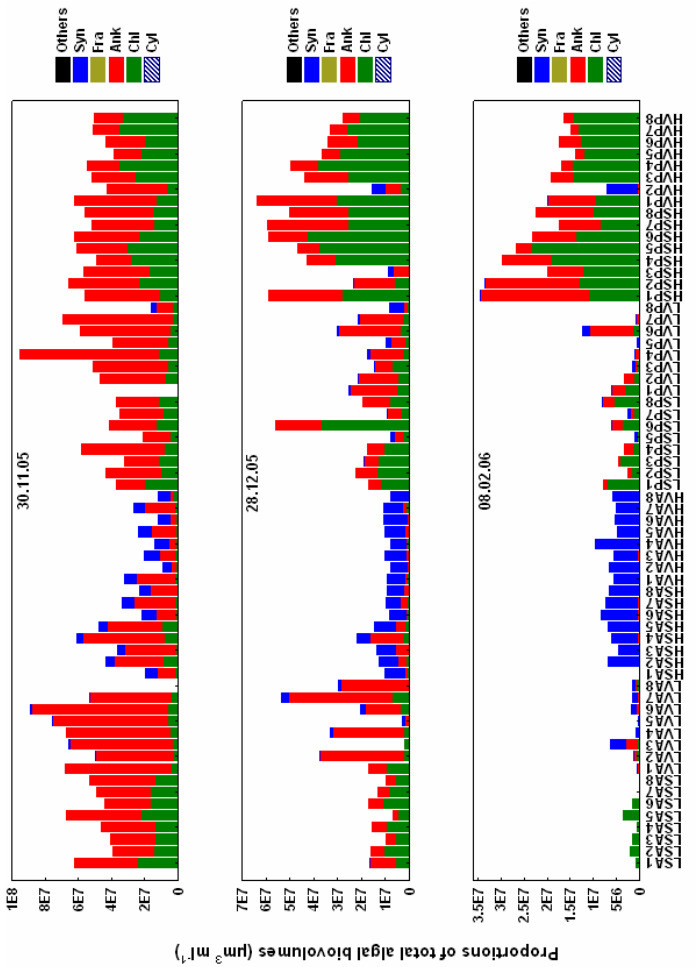


Figure 9: Community composition based on biovolumes over time. The most important five species are shown individually, remaining rare species including *Eudorina* are grouped in “Others”. Note the different y-axis-scaling.



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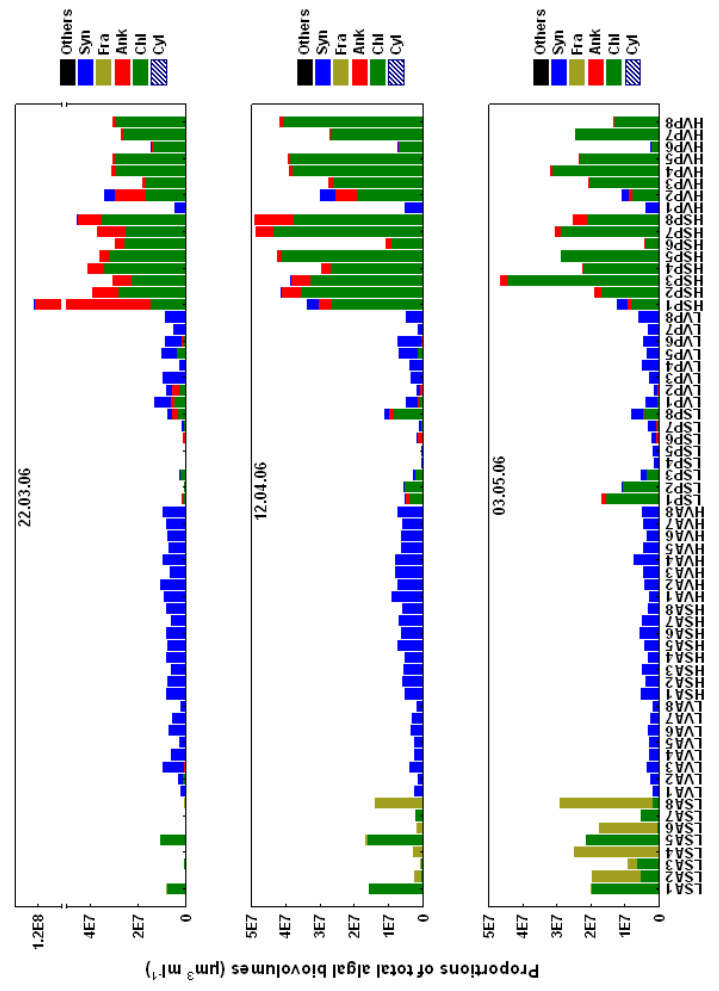

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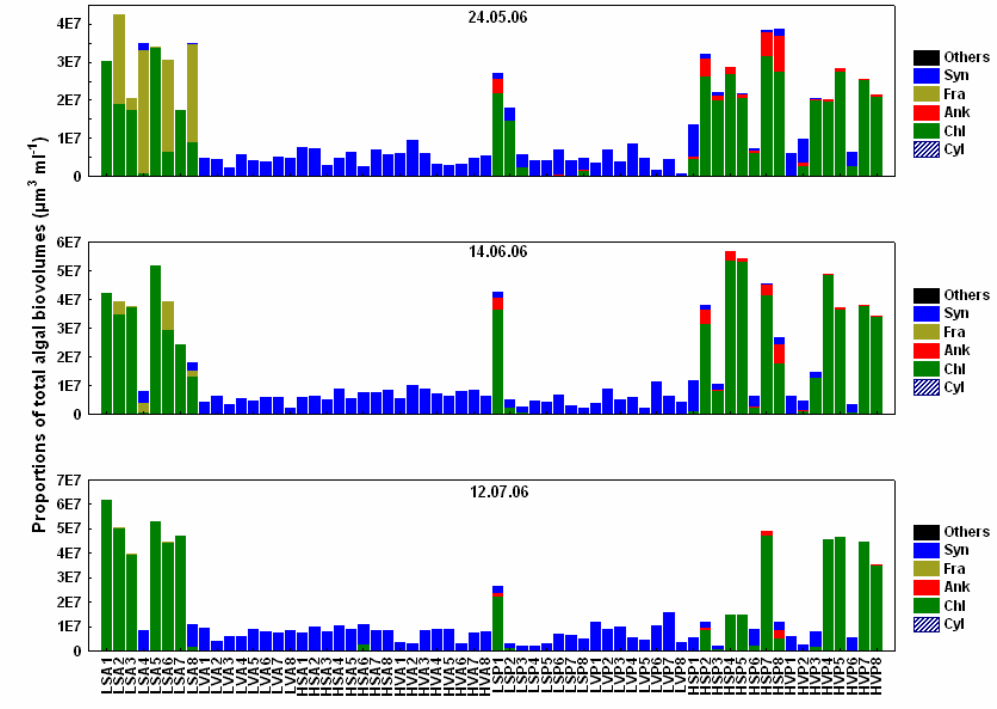

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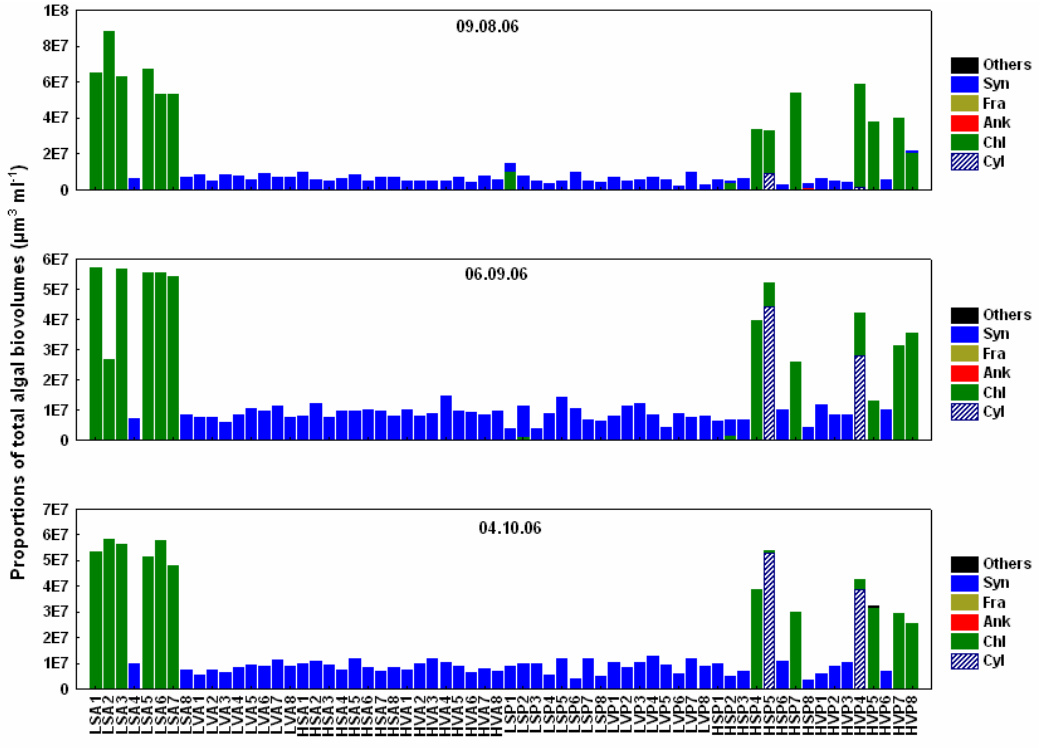

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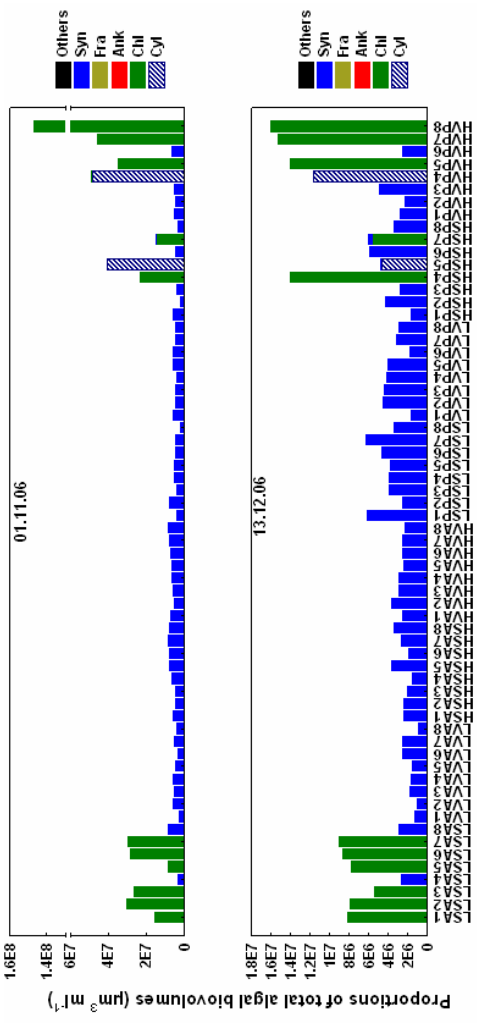


Figure 9: Continued

Single species

Ankistrosdesmus was the dominant species at the beginning of the experiment for three to four months (Figure 8). Then abundances strongly decreased until the species became undetectable, first in treatments without grazers in winter and then in treatments with grazers in spring and summer for cold and warm main temperature treatments, respectively (Figure 8).

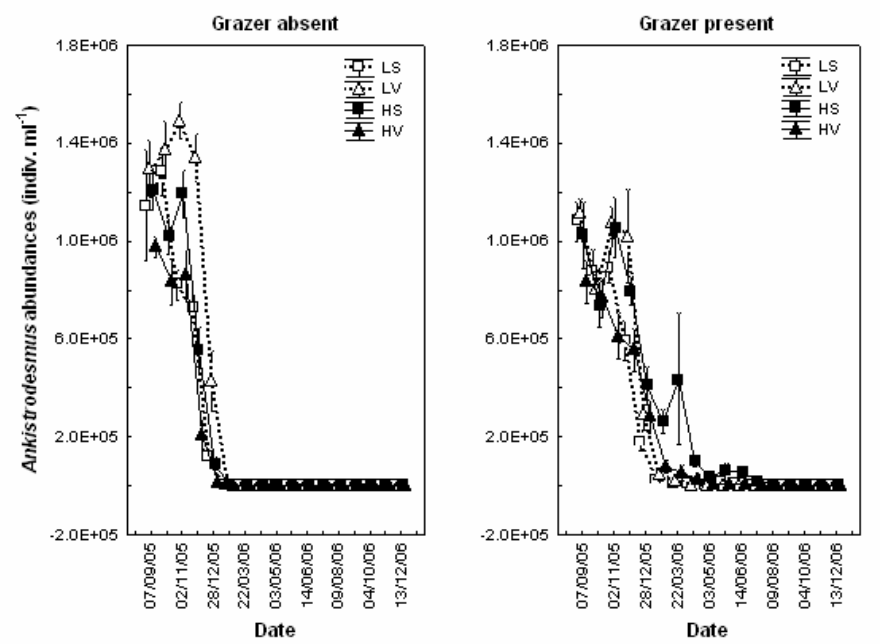


Figure 8: Development of *Ankistrodesmus* abundances over time (means and standard errors). For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

The only 1 to 3 µm small cf. *Synechocystis* could hardly be found at the beginning of the experiment, but from the first winter on numbers increased strongly and then their dynamics reflected more or less the pattern of total algal abundances thereby demonstrating the numerical dominance of this species (Figure 9). However, the timing of their success was different between treatments. In grazed treatments a decline until November could be detected, before they boomed. Within non-grazed treatments abundances of cf. *Synechocystis* immediately increased in the warm treatment, while in the cold and more variable temperature treatment they shortly declined and in the cold and less variable treatment a stronger decline until March occurred. After that they increased there also, but never reached the cell numbers of the other non-grazed treatments.

Figure 9: Development of cf. *Synechocystis* abundances over time (means and standard errors) on a logarithmic scale. For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Abundance of *Chlamydomonas* strongly decreased in non-grazed treatments and cold grazed treatments until they were nearly extinct (Figure 10). In contrast they could persist in warm temperature treatments with grazers until the end of the experiment, in some cases at the end even as the dominating species, and became the dominant algae in six out of eight replicates in the LSA treatment where they showed a summer bloom with highest abundances of all treatments. In grazed treatments they produced higher cell numbers in warm compared to cold treatments.

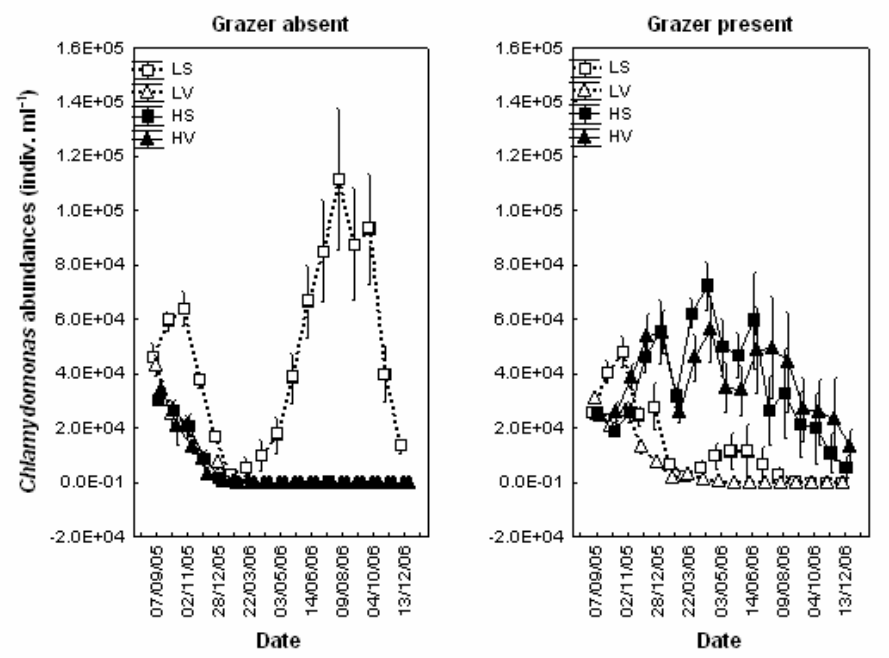


Figure 10: Development of *Chlamydomonas* abundances over time (means and standard errors). For better overview treatments with and without grazers are shown in different graphs. Open symbols and broken lines represent low temperature, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Ciliates

Urotricha furcata was not able to establish in the microcosms. *Coleps* sp. was becoming rare during autumn and vanished in the first winter which seemed to be too cold for it to persist. Lasting cells were probably washed out by dilution. Therefore, it was not possible to analyse ciliate abundances. Nevertheless their initial grazing pressure altered community dynamics which persisted throughout the whole experiment.

Discussion:

This highly controlled long-term experiment could shed further light on mechanisms of community responses to changing conditions in the context of global warming. Although the final outcome in most microcosms was a monospecific culture of one out of only two species of the initial species pool of 19 species, all factors influenced all measured variables significantly, alone and/or interacting with other factors, revealing a complex pattern of different and time dependent dynamics. In the following the effects on all variables are discussed factor by factor.

Effects of enhanced mean temperature

Changing the mean temperature had a positive effect on total algal abundances and total biovolumes but no main effect on all three diversity variables. Instead, effects of mean temperature on diversity were always dependent on the other factors. This was obvious especially for grazer presence, which changed the direction of the temperature effect on species richness from negative to positive. However, this meant rather delaying the development to monocultures than really enhancing species richness, since species had no possibility to invade. The impact of grazers on the temperature effect was similar for Shannon-diversity, even though the positive effect was not significant if based on biovolumes. Compared to grazing, temperature variability altered the influence of mean temperature on diversity only marginally, even if not significant, suggested by a negative trend of warming in less variable treatments and a positive trend of warming in high variability treatments.

Further inspection of community composition over time elucidated possible reasons for these relationships. First, it was obvious that cf. *Synechocystis* became the dominant species in most treatments which then developed to or almost to monocultures of that very small cyanophyte until the end of the experiment. In contrast, the low temperature treatment without enhanced variability and grazers (LSA) showed a different composition after the first winter. Here, cf. *Synechocystis* was present in lower numbers except for two replicates out of eight where it took over dominance in May of the second year as well. However, in the other replicates of this treatment a spring bloom of the diatom *Fragilaria* occurred and the green algae *Chlamydomonas* became the highly dominant species in summer

without excluding others completely. This treatment functioned as a control reflecting temperature conditions in present days without enhanced temperature variability and controlled also for grazer effects. Although the experimental design and the mixed algal community was very artificial, in this treatment a limited but somehow typical seasonality occurred with a spring bloom of diatoms followed by a dominance of green algae (Reynolds 2006). To a large fraction the diatom spring bloom in lakes is explained by relatively high nutrient conditions due to mixing, which also reduces sedimentation losses, combined with low light levels and reduced grazing (Reynolds 2006). Thus their temperature dependency is described to be more of indirect nature mediated by temperature induced stratification or nutrient status (Anderson 2000). This is not a plausible explanation for the bloom in these cultures, where nutrient addition and mixing is applied regularly and no stratification could occur. However, diatoms exhibit their maximum growth rates at lower temperatures compared to green algae and cyanophytes (DeNicola 1996) such that a direct temperature effect seemed to be more probable. Nevertheless, the cold non-grazed treatment with low temperature variability was the only one, where *Fragilaria* could establish in spring. In accordance with our hypothesis experimental warming shifted the community to dominance of the small cyanophyte, a group which is characterized by high temperature optima (DeNicola 1996). With higher temperatures in autumn and winter cf. *Synechocystis* could establish quickly and replace other species. This was also the case for the non-grazed cold treatment with enhanced temperature variability where a temporally limited warming occurred during each positive fraction of the applied sinus temperature curve. This was likely to be important during winter where in non variable treatments constantly 4°C prevailed, while in variable treatments oscillations between 2 and 6°C

occurred. Indeed cf. *Synechocystis* was able to increase its cell numbers here with just a short time lag compared to the warm treatments. Additionally, cyanophytes were found to increase with eutrophication (Dokulil & Teubner 2000) and also picoplankton in general was recognised to be in favour at a high trophic status (Bell & Kalff 2001). In the experiment a general eutrophic medium with a tendency to phosphorus limitation was used. However at the end of each nutrient pulse period no soluble phosphorus could be detected with our method (detection limit 5 µg L^{-1}). Picocyanophytes such as cf. *Synechocystis* have a high efficiency in nutrient uptake but can also tolerate chronical deficiency of P and N by their ability to store nutrients (Reynolds et al. 2002) which gives them a competitive advantage over other species, especially when their growth is accelerated strongly by warming. Dominance of cyanophytes resulting in summer blooms up to almost monospecific appearance have been previously described for several lakes (Dokulil & Teubner 2000; Mooij et al. 2005). Model results suggested that such summer blooms will increase with warming (Elliott et al. 2006; Elliott & May 2008; Jöhnk et al. 2008) which was supported by several field and laboratory studies (Adrian et al. 1995; Adrian & Deneke 1996; de Senerpont Domis et al. 2007a; Jöhnk et al. 2008; Weyenmeyer 2001). In contrast, Moss et al. (2003) didn't find increasing cyanophyte abundances with warming although community composition changed. But they used macrophyte dominated systems which proved resilient against such changes. In a European transect mesocosm study an increase of cyanophyte contribution to biomass was recognized but overall only slight changes in the phytoplankton communities occurred related to temperatures (Stephen et al. 2004). Additionally, impacts of warming on communities could be dependent on their disturbance history and their maturity. Such a study of

epilithic communities gave indication that well-established communities proved to be resilient against temperature changes while early successional stages responded rapidly (Baulch et al. 2005). In this context an experiment with artificial communities could be expected to show rapid and strong changes while more natural systems could be more inert. Another study using a combination of model and experimental results reported community changes of a more quantitative than qualitative nature (de Senerpont Domis et al. 2007a). Cyanophytes produced stronger responses to warming than green algae and diatoms, but successional patterns were not affected. The relevance of quantitative changes should not be underestimated since changes in evenness can also have important consequences for ecosystems as has been discussed extensively by Hillebrand et al. (2008). Thus the present experiment gives evidence that warming is likely to shift community structure to a dominance of cyanophytes, the characteristics of the impact, however, depend on the individual conditions of the system.

The fact that warming accelerated the development to monocultures and the outcome of the LSA treatment, seemed to be mainly responsible for the negative temperature effect on diversity in non-grazed treatments. This was observable for treatments without but not for treatments with enhanced variability where both, cold and warmed ones, reached the monoculture status early. In contrast, warming increased diversity in grazed treatments except for the biovolume-based Shannon-diversity, by reducing the speed to monoculture development irrespective of the temperature variability level. When grazed, more species were favoured by winter warming additionally to cf. *Synechocystis*. *Chlamydomonas* could grow to larger populations in warm treatments than in cold ones and also *Ankistrodesmus* could hold its abundances for a longer time. This

lead to a longer persistence of both species in these treatments through spring and summer and to the dominance of *Chlamydomonas* or even the second cyanophyte *Cylindrospermum* in some replicates until the end of the experiment. In cold and grazed treatments cf. *Synechocystis* could grow better during winter taking over dominance in spring and summer. This was possibly produced by the reduced grazing pressure of ciliates on cf. *Synechocystis* with cooling temperatures compared to higher grazing pressure in warmed treatments. Increased numbers of *Chlamydomonas* were subsequently combined with reduced abundances of *Synechocystis* cf. and were therefore more important for the abundance-based Shannon-diversity than for the biovolume-based, where *Chlamydomonas* became dominant in biomass. Additionally, the presence of *Chlamydomonas* was attended by the presence of further species thereby increasing diversity even if this is not automatically producing highest evenness.

Changing community composition seemed to have a great influence on the time-courses of total algal abundances and biovolumes also. Further graphical inspection of single species patterns revealed the responsibility of principally one species each for the main development in both variables. The time course of total algal abundances was mainly reflected by the development pattern of cf. *Synechocystis*. Before the cyanophyte came up, *Ankistrodesmus* was the dominant species and reflected abundance patterns most for the first months. That holds also true for total algal biovolume patterns. After that time the last were mainly reflected by the development pattern of *Chlamydomonas*, the largest species persisting.

The increasing impact of temperature on cell numbers seemed to originate strongly from the positive influence of winter warming in non-grazed treatments compared to very low numbers in

the LSA treatment. Further on, this treatment still comprised lower cell numbers after winter. By contrast, grazing switched this positive warming effect to negative by delaying the development to monocultures of cf. *Synechocystis* and no effect of winter warming on abundances was detectable. This changed during spring and summer where numbers increased stronger in cold grazed treatments attributed to higher cell numbers of cf. *Synechocystis* whereas in warm and grazed treatments *Chlamydomonas* could also grow which in turn reduced the increase of cf. *Synechocystis*.

The reasons for the impact of warming on biovolumes were more complex as for abundances. Warming enhanced abundances of either cf. *Synechocystis* or *Chlamydomonas*. Due to the size difference of both species and their consequently different contributions to total algal biovolumes this resulted in a strong positive response in grazed treatments by altering the proportions in favour of *Chlamydomonas*. Winter warming had a positive effect on biovolumes in non-grazed treatments, but this did not persist during the second summer. In the LSA treatment fewer individuals of cf. *Synechocystis* but higher numbers of *Chlamydomonas* lead to comparable biomasses as the warmed and simultaneously grazed treatments during summer and higher biomasses as in the other non-grazed treatments consisting of monocultures of cf. *Synechocystis*. Consequently, winter warming and the positive impact in grazed treatments produced the overall positive influence of warming on total biovolumes, while for non-grazed treatments the inverse summer effect was more important.

Altogether the winter conditions of the first year seemed to play a key role for the development of treatments. Differences between warm and cold treatments were distinct for all variables as were differences in community composition. When cf. *Synechocystis*

had established, differences in non grazed treatments were low; in summer no warming effect was graphically detectable. This was not that clear for warmed and grazed treatments, but here also high deviations occurred due to differences in the species that became the dominant ones. These persisting differences could be attributed to differentiation in the community composition at the beginning, since in a closed system no re-establishment of species was possible once they were extinct.

In general, warming shifted the community to smaller cells. Changed size structure by increasing temperatures have been described for marine microcosms (Sommer & Lengfellner 2008) as for freshwater diatom communities (Winder et al. 2008). This was mainly attributed to an indirect temperature effect. Nutrient uptake and growth rates in general are higher for small cells with smaller surface area to volume ratios (Litchman et al. 2006) giving them a competitive advantage when nutrient concentrations are low (Falkowski & Oliver 2007). In turn nutrient availability is reduced during stratification when the flux of nutrients from lower water layers is suppressed by the density gradient which in turn is increased by warming. This was confirmed for diatoms by Li and Harrison (2008) but they also found evidence that smaller size fractions such as nano- and picophytoplankton were directly related to temperature. This was supported by this experiment, as stratification was unlikely in the microcosms. However, other reasons for selecting small sized species as low mixing could not be excluded (Falkowski & Oliver 2007), because a general shift to small species independent of the treatment occurred and larger taxa died out first.

Effects of enhanced temperature variability

Enhanced temperature variability affected all measured variables significantly reducing total algal biovolumes and diversity but increasing total algal abundances and these impacts were modified by the level of the other factors. In general responses of total algal abundances followed contrasting patterns compared to total algal biovolumes and diversity variables. Again, this could be attributed mainly to the development patterns of the two most dominant species *Chlamydomona*s and cf. *Synechocystis* which mirrored the main patterns of total algal abundances and biovolumes respectively, as described above. Total algal abundances responded positively in enhanced temperature variability treatments, while total algal biovolumes were influenced negatively. Both responses were in general buffered by warming and grazing (the latter not significantly for biovolumes), especially in the treatment where both factors were applied. Looking at the species level, increased temperature variability favoured cf. *Synechocystis* while *Chlamydomonas* was supported in less variable environments, visible especially in cold treatments. Species richness and Shannon-diversity were reduced where cf. *Synechocystis* could get dominant while presence of *Chlamydomonas* was connected with longer persistence times of other species. This was strongest in non-grazed treatments, where most treatments developed quickly to monocultures of the cyanophyte accelerated by warming. Within the grazed treatments the warmed one without enhanced temperature variability was most species rich and showed also highest evenness within all grazed treatments. The warm treatment with enhanced variability contained similar species numbers but different relative proportions. i.e. higher amounts of *Chlamydomonas* in some treatments. Together with

similar differences in proportions of the respective low temperature treatments this lead to a negative variability effect independent of the temperature level in grazed treatments. This was significant for biovolume-based Shannon-diversity and could be detected as a trend only for the abundance-based Shannon-diversity und species richness. The differences were most obvious in winter and early spring when higher temperatures promoted algal growth. In contrast to non-grazed treatments, *Chlamydomonas* had the highest profit from winter warming. This shift was produced most likely by higher or longer persisting grazing pressure on the strongest competitor cf. *Synechocystis* in warmed treatments. Further on, increased temperature variability enhanced the decline of *Ankistrodesmus* proportions during early spring in warmed and grazed treatments leading to the dominance of either *Chlamydomonas* or cf. *Synechocystis* and in one case *Cylindrospermum*. In cold and grazed treatments cf. *Synechocystis* seemed to experience lower grazing pressure due to cold temperatures and could therefore take over dominance. This was promoted by higher temperature variability, possibly the cyanophyte could profit from the warm temperature intervals. Additionally, the remarkable difference in the community composition of the LSA treatment leading to lower overall abundances and higher diversity and biovolumes can be considered as one reason for the effect of enhanced temperature variability on all variables.

Environmental variability has been found to increase diversity in many studies resulting in hypotheses such as the Intermediate Disturbance Hypothesis (Shea et al. 2004). Differential species responses to environmental variability are considered to allow coexistence by compensatory dynamics dependent on the covariance between environment and competition (Chesson 2000).

Model predictions were confirmed by experimental investigation of long-term competition between two diatom species differing in their competitive abilities at different temperatures. Descamps-Julien and Gonzalez (2005) found out that coexistence was possible under fluctuating but not under constant temperatures. Furthermore, they could carry out that appropriate differences of functional responses of species and appropriate time scales of environmental variation seemed to be necessary. Increasing variation can result in increased probability of extinction and decreased probability of establishment and the average time to extinction (Drake & Lodge 2004). This could be a plausible explanation for the opposite impact as expected of temperature variability. Moreover, variability was applied in regular intervals and regular intensities. Jiang and Morin (2007) explored the effect of different regimes of temperature fluctuations on the coexistence of two ciliates which could not persist together under constant temperatures. The species coexisted in environments with autocorrelated fluctuations of temperature as well as in environments where temperature fluctuations were less autocorrelated. But mechanisms in both environments were different. Suggesting this relationship, not only magnitude and frequency but also autocorrelation of environmental variability can be important for its consequences on diversity. Therefore, it is not surprising that its effect in the described experiment was negative. This is supported by an investigation of the combined effects of mean and variance in aerial exposure on rocky seashore communities (Benedetti-Cecchi et al. 2006). Although larger temporal variance could reduce the effect of increasing mean intensity on parts of the community, other members were affected the opposite way.

Effects of grazers

Grazers in general increased diversity as they increased total algal biovolumes but decreased abundances. Complex interactions with the other factors could be detected, explainable by changed community composition. By shifting the community to less but also larger cells grazers increased biovolumes but reduced abundances. This was clearly to detect in warmed treatments where non grazed ones reached the monoculture status early. In contrast, in low temperature treatments grazers influenced abundances positively. However, this seemed to be strongly driven by the reduced abundances in non-grazed treatments during winter, strongly in the LSA treatment but still detectable in the LVA treatment, combined with the persisting low abundances in the LSA treatment during the rest of the experiment when compared to the grazed ones. For biovolumes, a negative grazer effect in cold treatments could not be observed because the contribution of *Chlamydomonas* in the LSA treatment to biomass was not strong enough before the second summer and winter biomasses of both cold treatments were also low.

Similarly grazers reduced total algal abundances in variable environments which was not observable in less variable ones. Mainly two treatments were responsible for that. On the one hand the negative grazing effect in treatments with enhanced temperature variability was produced to a large amount by reduced abundances in the warm treatment while in the cold treatment abundances were comparable to the respective non-grazed one. On the other hand a generally negative grazing effect in less variable environments could not be detected because of the very low abundances in the non-grazed cold one while nevertheless in warm treatments the effect occurred.

Likewise the positive grazing effect on diversity was distinct in warm but not in cold treatments independent of the variability level for all diversity variables. Within low temperature non-grazed treatments the LSA treatment showed highest diversity compared to the LVA treatment whereas in the cold grazed treatments species richness and therefore evenness was reduced early to monocultures, so that the positive grazing effect was compensated. Only biovolume based Shannon-diversity showed a positive influence of grazers in cold temperature treatments, too, even if it was still stronger in warmer ones. This can be attributed to the comparably high contribution of even low cell numbers of *Chlamydomonas* to evenness if based on biovolumes. This effect combined with higher amounts of *Synechocystis* cf. compared to the *Chlamydomonas*-dominated LSA treatment lead to even higher evenness in the respective grazed treatment (LSP). The difference between grazed and non-grazed treatments is most obvious for species richness, because in non-grazed treatments the warmed ones first became monocultures but in grazed treatments they were or would have been the last. This was mainly independent of the temperature variability treatment except for biovolume-based Shannon-diversity, where the combination of low temperature variability and grazing produced highest diversity.

Grazers were shown to increase diversity by selectively grazing superior algal competitors and preventing competitive exclusion (McCauley & Briand 1979; Sarnelle 2005). This seemed to be a plausible explanation for the patterns observed in this experiment. *Coleps* sp. is not known to be a specialist grazer and feeds on algae as well as on bacteria and flagellates. It also ingests parts of or whole ciliates and can be cannibalistic (Foissner et al.

1999). Nevertheless, in the experiment ciliates were found to also grow on the very small cf. *Synechocystis* for a long time. It seemed that they ingested them preferably enough to change the competition with other species such as *Chlamydomonas*. Higher grazing rates due to winter warming and therefore reduced abundances of the cyanophyte also fit the pattern.

However, these consequences cannot be attributed to direct grazer effects such as consumption during the whole experiment. The ciliates vanished during winter and could not re-establish. This was possibly due to the cold temperature. *Coleps* sp. is described to prefer temperatures above 10 °C even if they can be found at lower degrees down to 1°C (Foissner et al. 1999). Presumably they were washed out by the frequent dilution steps and their slow growth rates in winter. Nevertheless, there were clear and strong effects detectable and distinct differences visible in all measured variables between treatments that experienced grazing and treatments without grazing pressure. An explanation could be the closed system of the experimental set-up where something like a memory effect could have been occurred. It seemed that grazing history influenced the community after the time grazers were still active. In the first months grazers probably produced slight changes in the competition pressure for some algal species and therefore in community composition. Changed environmental conditions in winter and spring then lead to the propagation of community differences and during the experiment they could exponentiate in the closed system of the microcosms which were completely isolated from each other or from the possibility of invasion, which produced further divergence during summer. Until the end of the experiment differences became less again due to the massive dominance of mainly one species and a general species

depletion as could be expected with artificial communities in a closed system.

Altogether warming and enhanced temperature variability facilitated the development to the dominance of the small cyanophyte. Grazing could counteract these effects for a while enhancing species richness by delaying the outcome of a monospecific culture. As long as grazers were present in the cultures they fed strongly enough on cf. *Synechocystis* to reduce its competitive strength and give other species a chance. The cyanophyte was still dominant but could not exclude *Chlamydomonas* and *Ankistrodesmus* completely which lead to even higher evenness. After grazers had vanished cf. *Synechocystis* could enlarge their populations, but the competition situation had also changed, such that grazing effects propagated through time. Last, the remarkable difference in the community composition of the LSA treatment, leading to lower abundances and higher diversity and biovolumes, can be considered to have largely contributed to the impacts of all factors on all variables.

Although very simple and artificial communities in a highly controlled system were used, the experiment revealed complex interactions of mean temperature, temperature variability and grazers. It is not to deny that transferring results of this artificial system to natural communities which are more complex and affected by many more stressors is difficult. Conversely, the advantage of well controlled systems is the probability to detect effects that otherwise could be masked by noise of data or confounded by additional influences. Also direct and indirect pathways can be discriminated more easily as, for instance, direct and indirect temperature effects

on communities, which is often a delicate task in natural systems. On the other hand, artificially composed communities with low species numbers have been critized to miss important qualities such as maintaining their functionality in variable environments as stated by the insurance hypothesis (Yachi & Loreau 1999) in contrast to microcosms inoculated with natural phytoplankton. However, even in this simple system complex interactions have become apparent and relationships are even more complicated in natural habitats. Thus predictions of the consequences are not easy to be made. Studies with more natural communities or approaches indicated that nutrients or grazing are more important in structuring phytoplankton communities than temperature changes (Christoffersen et al. 2006; McKee et al. 2003; Moss et al. 2003; Stephen et al. 2004). Nevertheless, temperature was identified as important interacting factor as nutrient loading is not independent of warming. This is also valid for the relationship of light conditions and mixing with temperature regimes and the consequences for ecological systems, as well as precipitation and wind speed. Last but not least trophic interactions could complicate the pattern. However, possible mechanisms could be shown with the presented simple system. The long duration of the experiment could reveal dynamics which otherwise would not have been detected. For instance, at first it seemed that the dominant species *Ankistrodesmus*, would win the competition sooner or later, which was eventually not the case. Similarly, it could be shown that even in this system species reoccurred after a long time and could establish once more such as *Fragilaria* at its spring bloom or *Cylindrospermum* in some samples. Such aspects could often not be examined at shorter time scales of some weeks.

Conclusions:

As hypothesized warming induced species loss and increased the dominance of cyanophytes even if depending on other factors. Extinctions did not depend on the temperature regime alone. Especially phytoplankton is consisting of organisms with short generation times giving them the possibility of evolution tracking with the changing climate. Together with high dispersal rates phytoplankton has good chances to adapt to climate change, compared to other groups. On the other hand, especially this trait property can produce match-mismatches with higher trophic levels leading to changed ecosystem structure which can also imply diversity changes. However, the experiment could present complex shifts in phytoplankton communities with altered temperature regimes. This can be suggested to be even more dramatically for organisms with longer generation times. To complete the picture further investigations of climate-induced changes in several environmental parameters and their combined influences on ecosystems are necessary. Most appropriate should be a combination of natural observations of long-term data with modelling tools as well as experimental approaches from *in situ* manipulations to well-controlled systems.

Chapter 3

Complex time-dependent responses of a phytoplankton metacommunity to temperature and light in the context of climatic change

Introduction

Global warming and its consequences for biodiversity and ecosystem functioning is an important matter for human society. The International Panel on Climate Change reported an increased risk of extinction for 20 to 30 % of all plant and animal species if the temperature increase exceeds 2 to 3°C (IPCC 2007b). Biodiversity has been identified as an important driver of ecosystem functioning and consequently for goods and services provided (Hooper et al. 2005; Loreau et al. 2001). Therefore, it is important to increase the knowledge about climate-driven effects on diversity and the underlying mechanisms.

One prominent observed change induced by global warming is the shift of species` ranges to higher altitudes or latitudes (Parmesan 2006) following the shifting environmental conditions. However, the possibility to disperse is not always given or the new habitat does not match the species requirements impeding its establishment, which might lead to regional extinction. In contrast,

also increased species richness has been described for copepods (Beaugrand 2004) and for fish (Hiddink & Ter Hofstede 2008) in the North Sea due to a higher increase of warm-water species compared to the decrease of cold-water species, even if this may be temporary. However, species interactions and coexistence mechanisms can be changed and lead to endangerment of certain species or even communities or ecosystems.

Another local consequence of increased temperature are altered species interactions produced by shifts in phenology, i.e., earlier timing of breeding or flowering (Parmesan 2006; Root et al. 2003; Walther et al. 2002). Mismatches of dependent life-history events of predator and prey caused by asynchrony of their timing can have important consequences for the whole system (de Senerpont Domis et al. 2007b; Edwards & Richardson 2004; Visser et al. 1998; Visser & Holleman 2001; Visser & Both 2005; Winder & Schindler 2004a; Winder & Schindler 2004b).

The effect of altered temperature is complicated by changes in temperature variability as well as in other environmental factors such as light or precipitation. Changing variances of climatic factors on inter-annual and daily time scales are predicted (IPCC 2007c) and can be assumed as important drivers of population dynamics and interactions among species and functional groups and consequently of diversity. Several studies demonstrated the influence of the variability of environmental variables on species richness (reviewed by Shea et al. 2004). Variation in environmental factors can either reduce the fitness of species (Abrams 2004; Sommer 1995) or prevent them from competitive exclusion (Descamps-Julien & Gonzalez 2005), depending on the frequency or magnitude of the variance (Flöder et al. 2002; Gaedeke & Sommer 1986; Jiang & Morin 2007; Litchman 1998; McCabe & Cyr 2006; Sommer 1985).

Still, the combined effect of changes in the mean and in the variability of variables is poorly understood (Benedetti-Cecchi et al. 2006).

Another important factor for phytoplankton growth, if not the most important as sole energy source, is the availability of light. The amount of solar irradiance reaching terrestrial or aquatic surfaces is dependent on cloud cover. Predictions for cloud formation and increases or decreases with global warming are not clear-cut (IPCC 2007c). The trends depend on time scale, the observed part of the world and they differ between ocean and land surfaces. Species have different tolerances or sensitivities to light limitation and changing light conditions can thus be expected to change community composition. Cyanophytes often have lower light energy requirements than other algal groups (Dauta et al. 1990; Huisman et al. 1999; Passarge et al. 2006) which is speculated to be one reason for their observed dominance in some lakes leading also to blooms in summer (Dokulil & Teubner 2000). Additionally, several factors can interact. For instance, maximal photosynthetic rates and the onset of light saturation has been found to increase with temperature (Reynolds 2006) as a temperature dependent shift of the optimal light intensity (Dauta et al. 1990). Furthermore, stratification and the mixing regime is influenced strongly by temperature and in turn affects the light regime and sinking losses of algal species which can produce combined effects on communities (Diehl et al. 2002).

While many studies focused on species richness, it represents only one aspect of biodiversity. The relative proportions of species can be more essential or meaningful. Changing the dominance or evenness of species or functional groups can be more important for ecosystem function than the absence or presence of a rare species (Hillebrand et al. 2008). Moreover, these changes can occur long before a frequent or key-stone species finally has gone

extinct. Consequently, not only extinctions of species but also changed community structure should be given regard.

In nature, communities are not completely isolated from each other but connected by dispersal, resulting in the formation of metacommunities (Leibold et al. 2004). Depending on their level of connectedness and the rates of immigration and emigration different relationships of local and regional diversity can exist (Leibold & Norberg 2004). Thus extinction of a species can be prevented in a community by immigration from another community as species have the possibility to invade (Amarasekare & Nisbet 2001). These mechanisms can become important especially in the context of environmental changes by providing a community an enhanced ability to adapt to changing conditions.

Pond plankton has been identified as a good example for metacommunities (Leibold et al. 2004). Furthermore, aquatic ecosystems have been well investigated for effects of climate warming (Belgrano et al. 2004b; Drinkwater et al. 2003; Schindler 1997; Straile et al. 2003; Straile 2005). Especially phytoplankton can be considered good model organisms responding rapidly to changing environmental conditions due to short generation times and growth rates positively related to temperature (Brown et al. 2004).

The impact of climate change on a phytoplankton community was investigated in a highly controlled long-term (8 months) laboratory experiment. The single and combined effects of main temperature, temperature variability and light availability were tested. It was hypothesized that warming will decrease diversity and shift the community to species with higher temperature preferences. Increased temperature variability could possibly counteract this effect but also lead to community shifts to species with broader tolerances.

Decreased light availability could change the community composition to species with higher tolerances to light limitation.

Methods

Experimental set-up

In a long-term experiment running from May to December 2006 (8 months), mean temperature, temperature variability and light intensity were manipulated in a three factor full-factorial design. The experiment was conducted in a climate chamber under controlled conditions. The used temperatures followed seasonal curves simulating the time course of temperature in an European lake. On the one hand low temperature treatments (L) mimicked conditions in a lake at present with 4°C in winter and 20°C in summer, on the other hand high temperature treatments (H) in a lake in about the year 2100 with projected plus 2°C in summer (22°C absolute) and 4°C in winter (8°C absolute) taking the predictions for a stronger winter warming into account (IPCC 2001). Temperature curves for treatments with high temperature variability (V) were calculated by superimposing a sinus curve of ± 2°C every second week on the curves for smooth (S) treatments without high temperature variability, thereby not changing the mean temperatures. The temperatures were changed once a week and were produced by a simple cooling/heating system with four water baths, cooled with a flow-through-system by a cooling unit and adjusted with aquarium heaters. Light was provided from above in a natural spectrum using BioSun fluorescent lamps. Also light availability followed a seasonal pattern

for both day length and intensity. Intensity could be changed by moving the lamps nearer to or farther away from the experimental units (125 µmol photons m^{-2} s^{-1} to 200 µmol photons m^{-2} s^{-1}). Additionally, a dark mesh was laid over the water baths in winter (end of November, December), reducing the light intensity by 40%. The same mesh was used to shade the treatments that should experience enhanced cloud cover (C) compared to the treatments with normal (N) cloud cover. It was fixed on two stainless steel bars, which made it movable from the back to the front of the water baths. Light was not completely evenly distributed in the water baths; therefore microcosms were re-arranged in the light-field according to their treatment and additionally, C and N treatments were interchanged from the back to the front each week to compensate for such differences. Shading in winter resulted in a reduction of light intensity of about 65 % in treatments with enhanced cloud cover compared to 40% for normal conditions. Intensities varied between 200 µmol photons m^{-2} s^{-1} in summer and 75 µmol photons m^{-2} s^{-1} in winter for normal light treatments and between 120 µmol photons m^{-2} s^{-1} in summer and 45 µmol photons m^{-2} s^{-1} in winter for cloudy treatments. Each treatment combination was replicated four times. Sterile 250 ml Erlenmeyer flasks with stoppers served as experimental microcosms and were filled with 150 ml modified WoodsHole (WC) Medium (Guillard 1975) with the concentrations of the most important nutrients corresponding to a eutrophic lake with a tendency towards phosphorus limitation (50 µg P L^{-1}, 1000 µg N L^{-1}, 1500 µg Si L^{-1}). The medium was buffered and adjusted to pH 7 with hydrochloric acid. Initially, the microcosms were inoculated with 15 phytoplankton species (Table 1) representing different growth forms and taxonomical classes.

Table 1: Experimental set-up with treatment abbreviations

Factor	Abbr.							
Temp (**L**ow/**H**igh)	**L**				**H**			
Var (**S**mooth/**V**ariable)	**S**		**V**		**S**		**V**	
Light (**N**ormal/**C**loudy)	**N**	**C**	**N**	**C**	**N**	**C**	**N**	**C**
Number of replicates	4	4	4	4	4	4	4	4

Table 2: Phytoplankton species used in the experiment, their taxonomic group, and their origin

Name	Group	Strain number - source
Phacus smulkowskia	Euglenophyceae	M 2282 - CCAC
Gymnodinium sp	Dinophyta	M 2391 - CCAC
Peridinium cinctum	Dinophyta	M 1576 - CCAC
Closterium navicula	Streptophyta	M 2096 - CCAC
Staurastrum hirsutum	Streptophyta	M 2094 - CCAC
Tetmemorus laevis	Streptophyta	M 9181 - CCAC
Cosmarium biretum	Streptophyta	M 2123 - CCAC
Chlamydomonas terricola	Chlorophyta	M 1259 - CCAC
Oocystis sp.	Chlorophyta	M 1782 - CCAC
Ankistrodesmus sp.	Chlorophyta	M 2209 - CCAC
Eudorina elegans	Chlorophyta	M 0547 - CCAC
Nitzschia sp.	Bacillariophyceae	M 1771 - CCAC
Fragilaria capucina	Bacillariophyceae	M 1767 - CCAC
Cylindrospermum sp.	Cyanophyta	M 1160 - CCAC
Synechocystis-like, not further det.	Cyanophyta	Isolated by T.B.

Except for cf. *Synechocystis*, algal cultures were obtained from the Culture Collection of Algae at the University of Cologne (CCAC), grown on WC-medium for five to ten days before inoculation. Microcosms were cultured semi-continuously by exchanging 70 % of the algal suspension with new sterile medium once a week corresponding to a daily exchange rate of 10 % and an average dilution rate of 0.17 d^{-1} ($-\ln(v_t/v_0)/t$). To avoid artefacts such as wall effects via thereon growing organisms, 30 % of the algal suspension was transferred into new sterile Erlenmeyer flasks with 105 ml (70 %) fresh medium. Weekly exchange producing nutrient pulses has been found to be the best interval to maintain algal

diversity high over a long time (Flöder & Sommer 1999; Gaedeke & Sommer 1986; Sommer 1985) In this experiment all microcosms represented a metacommunity connected by dispersal. This meant that each species had the potential to invade into each microcosm if it just was present in one microcosm, thereby increasing the probability to hold high diversity over a long time. To simulate dispersal 6 % (9ml) of the total culture from each microcosm was collected in one sterile flask, and then mixed, after which 9 ml of this mixed culture were added back to each microcosm. This was done weekly until the end of August, after which dispersal was reduced to biweekly.

Sampling and measurements

Sampling was done every fourth week except in November, when diverging colour of cultures indicated dynamics in one treatment which seemed to be interesting to analyse immediately, therefore sampling was done one week earlier. Samples were taken from the remaining solution after medium exchange.

One subsample of 20 ml each was filtered onto a GF/F-filter and the filtrate was used to measure soluble reactive phosphorus. Samples were stored in a freezer at minus 20°C until measurement using the method after Grasshoff et al. (Grasshoff et al. 1983). One subsample for algal identification and enumeration was fixed with Lugol`s solution and stored in dark bottles until counting in 3 ml Utermöhl sedimentation chambers under an inverted microscope (Leica DMIRB). Algal suspensions were diluted two- to tenfold and stored over night to allow algae to settle down. For each magnification (100 times to 630 times, depending on algal concentrations and dimensions) a minimum of 400 cells or 10 counting fields were counted or, when numbers were low, half the

chamber or the whole chamber, respectively. Altogether a minimum of 800 cells was counted for each sample.

For biovolume calculations the linear dimensions of minimal 20 cells per species were measured and used in the most appropriate geometrical formulas (Hillebrand et al. 1999). Algal diversity was calculated as species richness (species number) and the Pielous` evenness Index calculated on both abundance and biovolume proportions to account for quantitative and qualitative changes in the communities.

Statistical Analysis

Repeated measures Analysis of Variance (rm-ANOVA) was used to detect significant differences between treatments as well as significant changes over time within treatments. Effects were considered significant if $p < 0.05$ and highly significant if $p < 0.001$. Mean temperature, temperature variability and light level were the factors between subjects and time as well as all interactions involving time were analysed within subjects. Prior to analyses all data were log-transformed to homogenize the variances. To check for homogeneity of variances a Cochran test was performed. As a post hoc test Tukey's honestly significant difference (HSD) was chosen to compare treatment combinations. Because the last sampling seemed to have an extraordinary influence on the results, the analyses were repeated without it. All analyses were performed with STATISTICA (2003).

Results

Experimental set-up

The cooling/heating system worked well in producing the intended temperatures with ± 0.5°C. Only few exceptions occurred .Two times the water baths for the high temperature treatments were too cold (1-4°C) for one day. Another day in July the climate chamber heated up resulting in temperatures 4-6°C above treatment levels for less than 24 hours. However, this didn't seem to have any effect on the results as no visible changes in either abundances or biomass or community composition could be detected in the samplings following these short-term events

Phosphorus

Soluble reactive phosphorus was always below detection limit (5 µmol L^{-1}) one week after the nutrient pulse before applying a new one, which indicated phosphorus limitation at that time. Thus changing conditions by nutrient pulses ranging from surplus to depletion occurred weekly.

Phytoplankton

Phytoplankton communities developed similarly in all treatments. No significant effect by any factor could be revealed for total algal abundances and species richness (Table 2). During the first 4 months the communities remained highly similar across treatments based on the high dispersal rates in the metacommunity. After changing the time interval of the dispersal manipulation to biweekly, treatments diverged, indicating that the applied dispersal intensity was indeed too high. Complex responses could be found for evenness either based on abundances and even more if based on biovolumes. Further details of the patterns are described in the following.

Table 3: Results of rm-ANOVA (including all samplings) for all measured variables. Significant results are printed in bold, trends in italic. Abbreviations: T = temperature, V = Variability, L = Light

Dependent variable		Abundance		Biovolume		Species richness		Evenness J´ Abund.-based		Evenness J´ Biovol.-based	
Effect	df	F	p	F	p	F	p	F	p	F	p
T	1	0.02	0.8895	0.78	0.3847	0.00	0.9732	7.08	**0.0137**	30.27	**0.0000**
V	1	1.47	0.2373	0.04	0.8387	1.12	0.3001	57.56	**0.0000**	1.88	0.1830
L	1	1.06	0.3131	12.55	**0.0017**	0.00	0.9759	0.10	0.7582	0.66	0.4261
T x V	1	0.28	0.5987	13.10	**0.0014**	0.00	0.9592	5.24	**0.0312**	6.20	**0.0201**
T x L	1	0.73	0.4007	1.18	0.2881	0.39	0.5392	7.06	**0.0138**	8.45	**0.0077**
V x L	1	0.03	0.8657	0.02	0.8877	0.16	0.6940	0.00	0.9996	20.58	**0.0001**
T x V x L	1	1.45	0.2405	2.21	0.1504	0.93	0.3453	0.15	0.7015	9.09	**0.0060**
Time	8	585.37	**0.0000**	397.32	**0.0000**	1046.32	**0.0000**	85.86	**0.0000**	420.25	**0.0000**
Time x T	8	13.94	**0.0000**	243.57	**0.0000**	3.87	**0.0028**	103.72	**0.0000**	27.18	**0.0000**
Time x V	8	3.80	**0.0004**	4.01	**0.0002**	2.40	**0.0408**	2.95	**0.0040**	3.53	**0.0008**
Time x L	8	1.48	0.1655	1.96	*0.0539*	3.14	**0.0106**	3.47	**0.0009**	2.36	**0.0191**
Time x T x V	8	2.60	**0.0102**	3.59	**0.0007**	0.41	0.8385	7.40	**0.0000**	2.86	**0.0050**
Time x T x L	8	1.92	*0.0592*	2.76	**0.0066**	0.98	0.4343	3.27	**0.0016**	4.34	**0.0001**
Time x V x L	8	1.41	0.1963	1.91	*0.0611*	0.31	0.9061	4.48	**0.0001**	1.40	0.1993
Time x T x V x L	8	1.69	0.1025	2.79	**0.0060**	1.10	0.3621	4.52	**0.0000**	2.18	**0.0306**

Table 4: Results of rm-ANOVA (excluding the last sampling) for all measured variables. Significant results are printed in bold, trends in italic. Df for Species Richness in interactions with time 5 instead of 7. Abbreviations: T = temperature, V = Variability, L = Light

Dependent variable		Abundance		Biovolume		Species richness		Evenness J´ Abund.-based		Evenness J´ Biovol.-based	
Effect	df	F	p	F	p	F	p	F	p	F	p
T	1	6.29	**0.0193**	148.62	**0.0000**	0.00	0.9732	52.17	**0.0000**	73.20	**0.0000**
V	1	2.40	0.1342	0.20	0.6566	1.12	0.3001	32.89	**0.0000**	3.29	*0.0822*
L	1	1.26	0.2719	9.74	**0.0046**	0.00	0.9759	0.00	0.9543	2.70	0.1136
T x V	1	0.00	0.9714	5.46	**0.0281**	0.00	0.9592	0.66	0.4241	2.35	0.1382
T x L	1	1.64	0.2120	0.20	0.6623	0.39	0.5392	8.82	**0.0067**	5.14	**0.0327**
V x L	1	0.04	0.8406	0.33	0.5718	0.16	0.6940	0.01	0.9080	18.16	**0.0003**
T x V x L	1	0.68	0.4190	0.29	0.5961	0.93	0.3453	0.02	0.8859	7.60	**0.0110**
Time	7	615.03	**0.0000**	406.07	**0.0000**	1046.32	**0.0000**	86.82	**0.0000**	343.05	**0.0000**
Time x T	7	8.45	**0.0000**	26.08	**0.0000**	3.87	**0.0028**	18.63	**0.0000**	15.75	**0.0000**
Time x V	7	3.90	**0.0006**	4.22	**0.0003**	2.40	**0.0408**	2.71	**0.0108**	3.38	**0.0021**
Time x L	7	1.57	0.1485	2.01	*0.0562*	3.14	**0.0106**	3.67	**0.0010**	1.62	0.1339
Time x T x V	7	2.42	**0.0221**	2.13	**0.0430**	0.41	0.8385	6.65	**0.0000**	2.31	**0.0284**
Time x T x L	7	1.82	*0.0862*	2.48	**0.0189**	0.98	0.4343	2.96	**0.0060**	4.32	**0.0002**
Time x V x L	7	1.34	0.2335	1.79	*0.0929*	0.31	0.9061	4.79	**0.0001**	1.46	0.1849
Time x T x V x L	7	1.66	0.1221	1.93	*0.0678*	1.10	0.3621	4.81	**0.0001**	2.27	**0.0310**

Abundance

Generally the time courses of total algal abundances of all treatments were very similar throughout the whole experiment (Figure 1). Algal numbers increased with a peak in the warmed treatments in July and in the cold treatments in September, respectively. Then abundances remained stable until they decreased from November to December. Striking was an abundance peak in November of the high mean temperature treatment with temperature variability and low light (HVC).

Repeated-measurement ANOVA revealed no significant treatment effects except for a significant change with time and interactions of mean temperature and temperature variability with time (Table 3). However, when only the last four samplings were analysed the three-way interaction became marginally significant ($p = 0.029$), but the post-hoc test (Tukey HSD) showed no differences between treatments (Figure 1 – Appendix/Chapter 3).

Figure 1: Development of total algal abundances over time on a logarithmic scale (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Biovolume

Total biovolume first increased with a peak in July in all treatments followed by a decrease in the next month (Figure 2). Total algal biovolume decreased in cold temperature treatments until November, while it was stable in warmed treatments until October and then decreased strongly until December with one exception. The high mean temperature treatment with enhanced temperature variability and low light (HVC) showed the respective peak observed for abundances in November. In contrast to warmed treatments, biovolume strongly increased from November to December in the cold treatments, thus showing a diverging pattern.

Of the three factors only light showed a significant main effect on total algal biovolume ($p < 0.05$), with reduced light intensities increasing biovolume. A significant two-way interaction of main temperature and temperature variability could be detected with a negative temperature effect in treatments without temperature variability not in treatments but with enhanced temperature variability ($p < 0.05$). When the last sampling was excluded from the analysis the interaction was only marginally significant ($p = 0.03$) and the post-hoc test (Tukey HSD: $p < 0.05$) revealed, that treatments with and without enhanced variability were not differing any more. The effect of light was not changed while mean temperature now produced a significant positive effect on total algal biovolume. The effects were time dependent (Figure 2 – Appendix/Chapter 3).

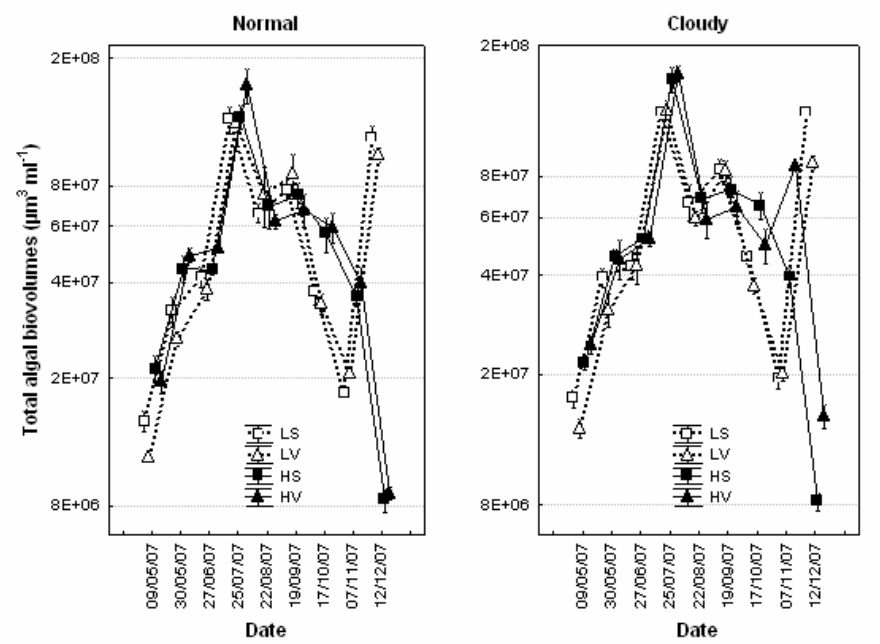


Figure 2: Development of total algal biovolumes over time on a logarithmic scale (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Diversity

Species richness

Species richness decreased continuously over time reaching a plateau of four species in June (Figure 3). A further decline was visible from September on after changing the interval for dispersal from weekly to biweekly.

However, species richness was not affected by any of the experimental manipulations. Because at three sampling dates results had no variances, not all sampling dates were analysable; the ANOVA was generated from the remaining six sampling dates only, where the last sampling date was excluded.

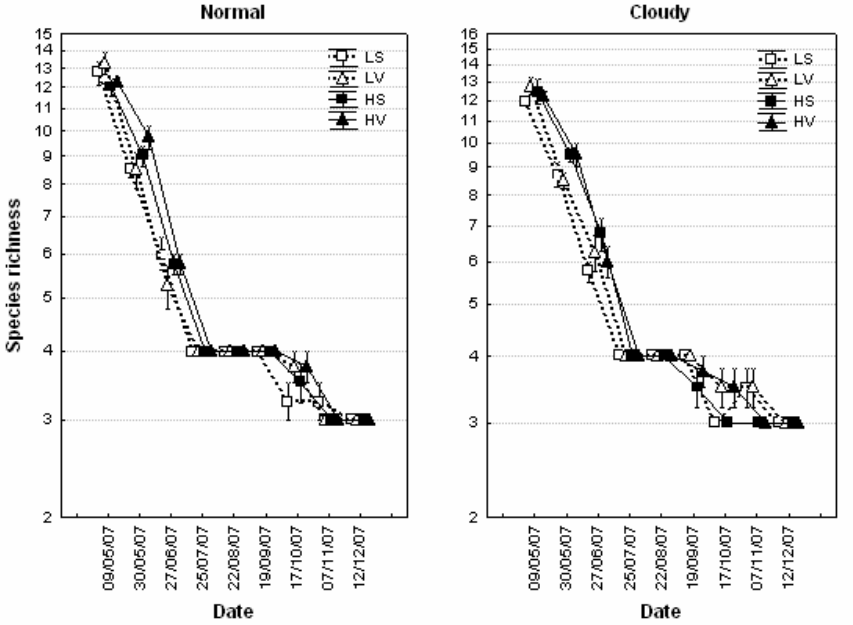


Figure 3: Development of species richness over time on a logarithmic scale (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Evenness

Evenness in the communities changed in a zigzag pattern similar for both abundance and biovolume based indices (Figure 4/5). In general evenness reached higher values when calculated from biovolumes and the zigzag pattern was more distinct.

Abundance-based evenness showed for the first two months differences between treatments, especially between cold and warm ones (Figure 4). The next three months differences were low but became larger after the change of the dispersal rhythm. During both intervals cold treatments showed lower abundance-based evenness than warmed treatments. At the last sampling date in December the pattern changed and evenness was strongly reduced in warmed treatments while it was increased in cold treatments. This resulted in lowest abundance-based evenness values during the experiment for warm treatments in contrast to highest values for cold treatments.

Biovolume based evenness decreased from one of their highest values from May until June, then increased until July followed by a decline to lowest values in September (Figure 5). From that time on, when the dispersal rhythm was changed, treatments diverged clearly between cold and warm treatments. Although in all treatments evenness increased until the end of the experiment in December warm ones showed lower values except for the last sampling date, where evenness in warm treatments further increased while it in cold treatments stagnated.

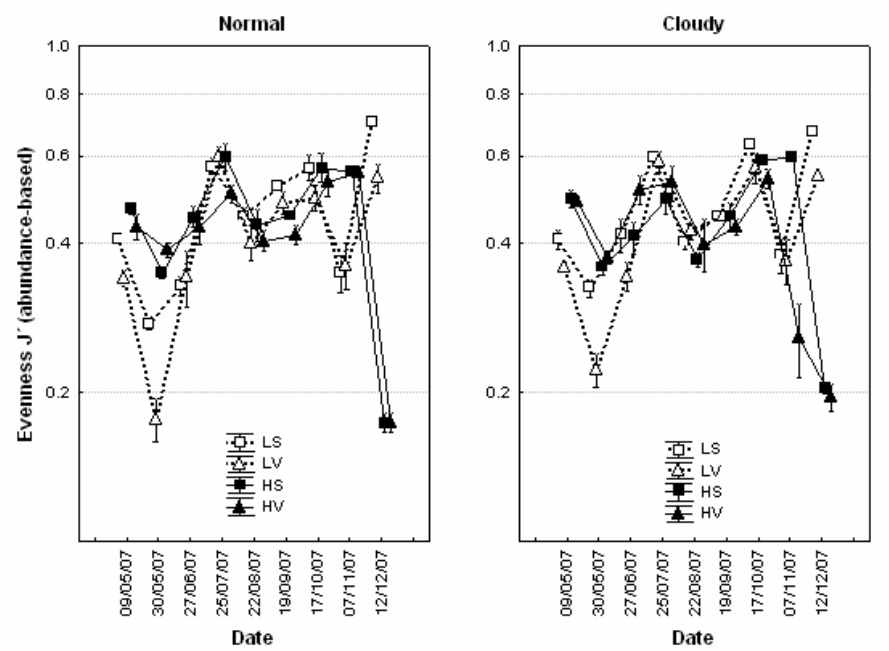


Figure 4: Development of evenness (abundance-based) over time on a logarithmic scale (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

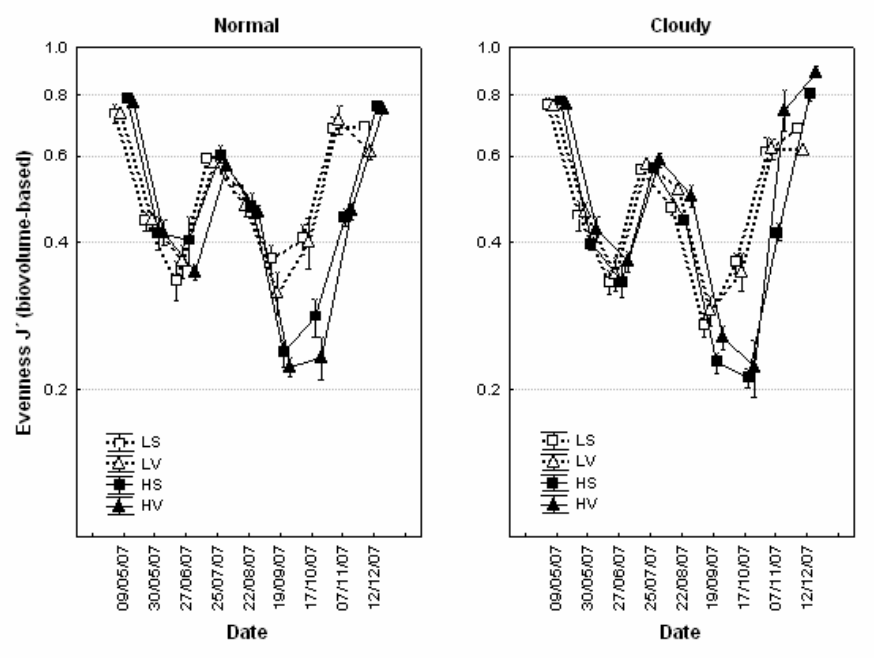


Figure 5: Development of evenness (biovolume-based) over time on a logarithmic scale (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

In general higher temperature significantly decreased evenness and increased dominance ($p < 0.05$ for abundance-based indices and $p < 0.001$ for biovolume-based indices). Only for abundance-based evenness a further negative effect of temperature variability could be found ($p < 0.001$). Light had no effect on either abundance- or on biovolume-based evenness.

Post hoc tests for the main temperature x temperature variability interaction revealed that the negative effect of enhanced temperature variability on abundance-based evenness seemed to be stronger for low temperature treatments (Tukey HSD: $p < 0.001$) than for high temperature treatments (Tukey HSD: $p < 0.05$), while the negative mean temperature effect was significant only for treatments with less variable temperature conditions (Tukey HSD: $p < 0.05$). The latter trend could also be identified for biovolume-based evenness, while enhanced temperature variability produced no significant differences in combination with mean temperature.

A significant mean temperature x light interaction occurred for both evenness indices. Post hoc tests revealed contrasting results. Based on abundances high mean temperature reduced evenness in treatments with lower (cloudy = C) light intensities, while based on biovolumes this was the case in treatments with normal (N) light intensities (Tukey HSD: $p < 0.05$).

Additionally, temperature variability and light interacted for biovolume-based indices, modifying the effects of the main factors. For treatments with low light conditions post hoc tests revealed a significant positive effect ($p< 0.05$) of enhanced temperature variability, which was in contrast to the main effect detected on abundance-based evenness. However, a negative influence under normal light conditions was not significant. Likewise, evenness was significantly reduced in treatments with lower temperature variability

when light intensities were also reduced ($p < 0.05$), but not under normal light conditions. The significant three-way interaction further revealed that reduction of evenness with reduced light level and temperature variability was distinct only with high mean temperatures. All effects were time-dependent (Tukey HSD: $p < 0.05$).

The main effects on biovolume-based evenness did not change when the last sampling was excluded. Interactions with temperature changed; the interaction with variability got lost while the interaction with light increased in strength with a negative impact of warming under both light conditions and a negative effect of increased cloudiness in cold treatments. In contrast the direction of the temperature effect changed for abundance-based evenness, also in the interaction with temperature variability and light. Therefore, the warming effect switched from a negative effect under cloudy conditions to a positive effect under normal conditions. The remaining results for the factors temperature variability and light did only change slightly by excluding the last sampling. The negative influence of higher temperature variability was detectable in warmed treatments only without the last sampling, while it could be found for both main temperature treatments when it was included, but stronger for cold ones. By excluding furthermore November data from the analysis, some effects vanished such as the interaction of all three factors and the interactions of mean temperature with light (Figure 4 and 5 – Appendix/Chapter 3).

Community composition

Four species out of the species pool persisted through the entire experiment, while the others became rare and went extinct

quickly (Figure 6-8). Community composition in different treatments developed similarly for the first 18 weeks, when dispersal events took place every week, but diverged after the dispersal rhythm was changed to biweekly. However, in all treatments *Ankistrodesmus* abundances decreased during summer and the species was counted for the last time in September/October in high main temperature treatments and October/November in low temperature treatments, respectively. *Chlamydomonas* followed this pattern, but recovered in winter, becoming even dominant with respect to biomass in the high main temperature treatment with variable temperatures and low light (HVC). Dominant throughout the whole experiment and in all treatments were the two cyanophytes *Cylindrospermum* and cf. *Synechocystis*. Cf. *Synechocystis* had highest abundances at the beginning of the experiment until it was outperformed by increasing *Cylindrospermum* in summer. During autumn *Cylindrospermum* abundances declined while cf. *Synechocystis* further increased and therefore dominated again. In high main temperature treatments *Cylindrospermum* still decreased in December, but in contrast could increase in low temperature treatments again. The development was similar for total algal biovolumes, but due to size differences of the species dominance patterns were different. *Chlamydomonas* was the largest species persisting and therefore was highly important for total algal biovolumes. With the focus on biovolumes Chlamydomonas was the dominant species at the beginning of the experiment and it still was the species with second highest total biovolumes when *Cylindrospermum* became dominant. In autumn cf. *Synechocystis* reached very high cell numbers so that even this very small species had higher biovolumes than *Chlamydomonas* in many treatments.

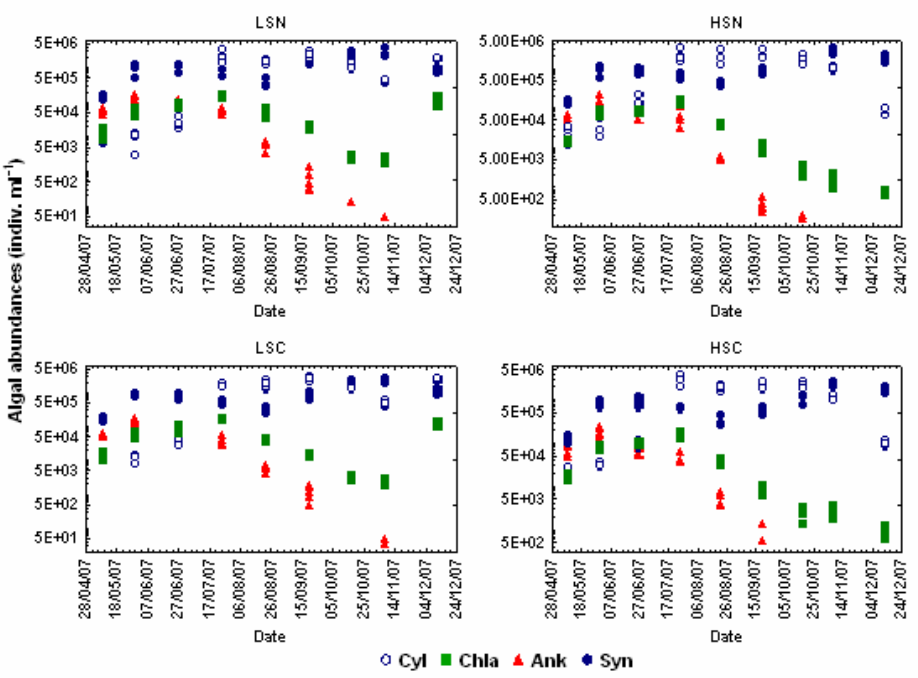


Figure 6: Community composition based on cell abundances. The most important four algal species in the four replicates at each time point are shown in one plot. Open blue circles represent *Cylindrospermu*m sp., green quarters represent *Chlamydomonas terricola*, red triangles represent *Ankistrodesmus* sp and blue circles represent cf. *Synechocystis* (L = low temp., H = high temp., S = smooth, V = variable, N= normal, C = cloudy)

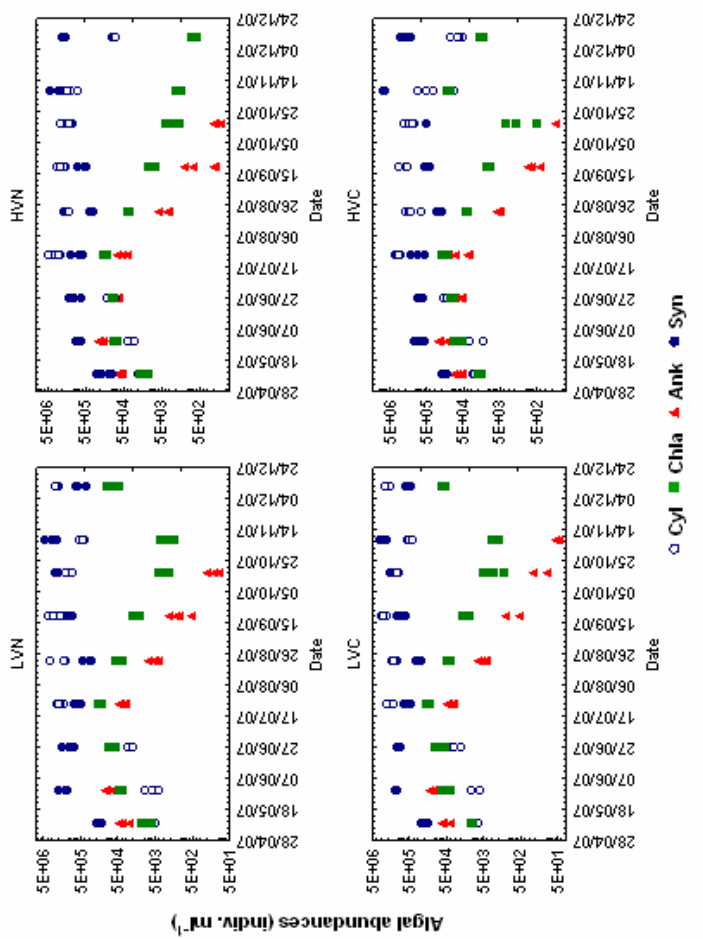


Figure 6: Continued

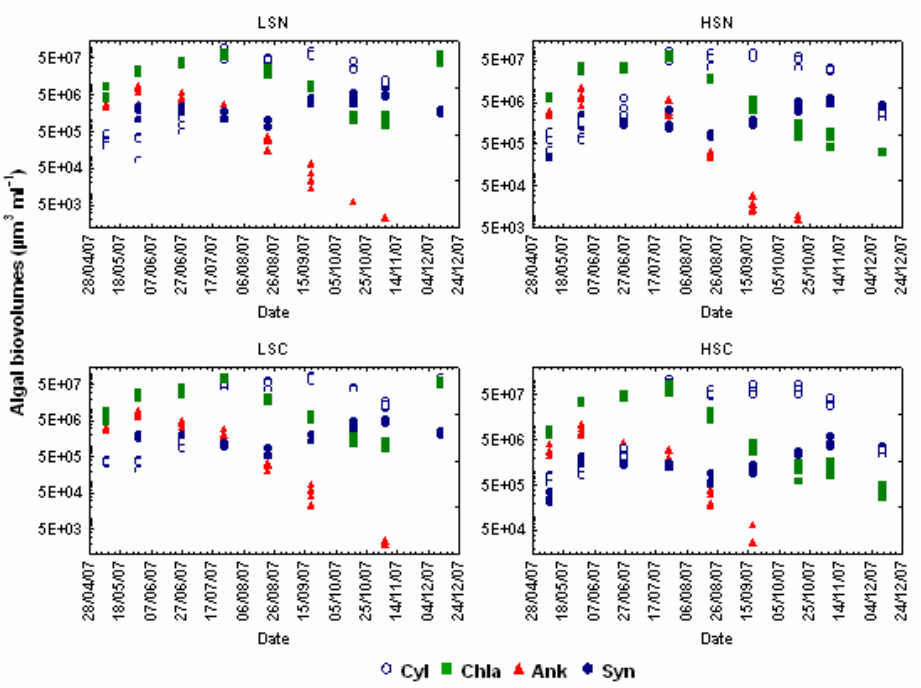
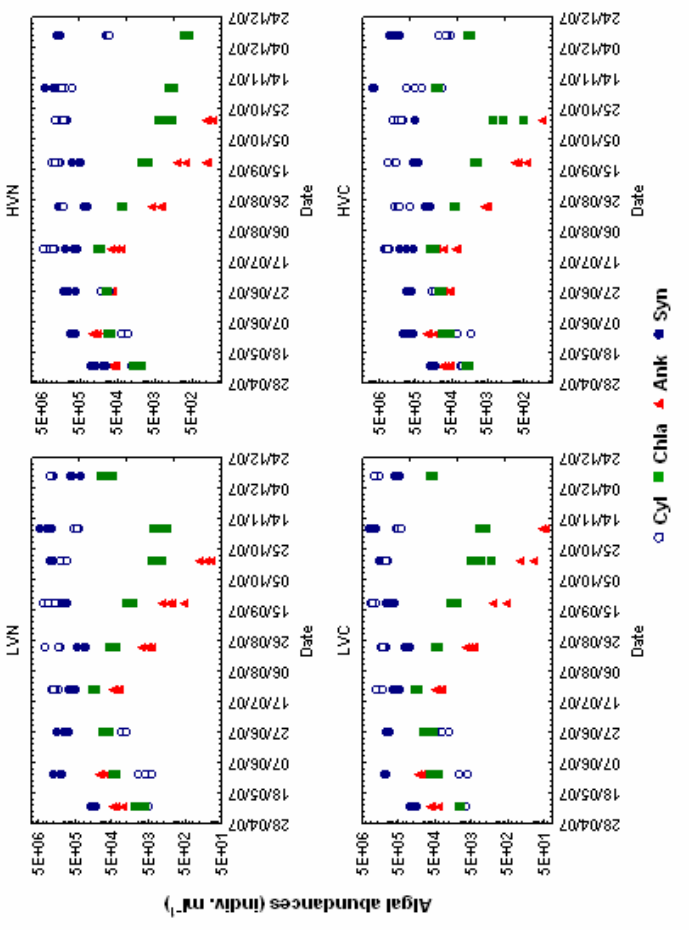


Figure 7: Community composition based on cell biovolumes. The most important four algal species in the four replicates at each time point are shown in one plot. Open blue circles represent *Cylindrospermu*m sp., green quarters represent *Chlamydomonas terricola*, red triangles represent *Ankistrodesmus* sp and blue circles represent cf. *Synechocystis* (L = low temp., H = high temp., S = smooth, V = variable, N= normal, C = cloudy).



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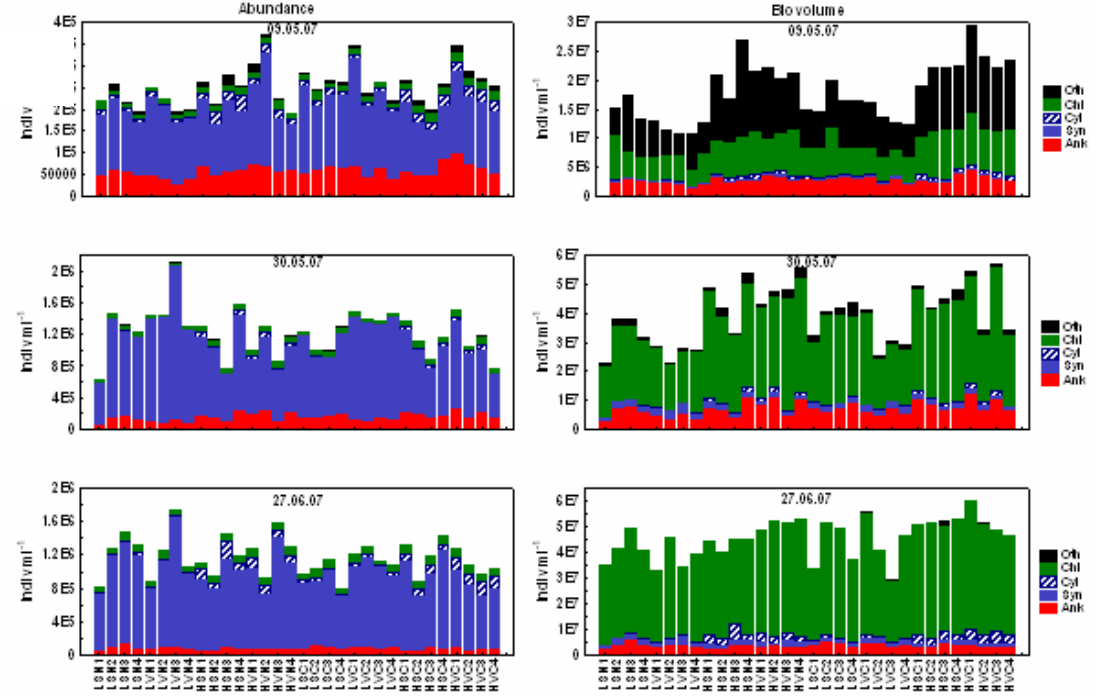
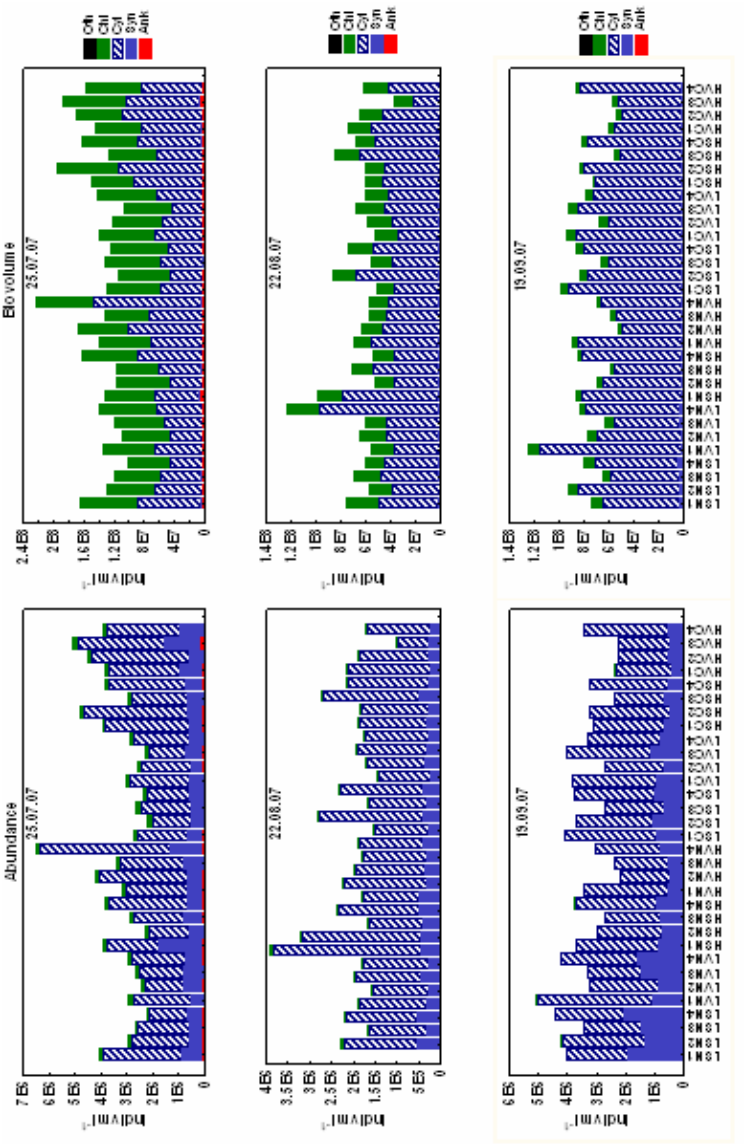


Figure 8: Community composition based on abundances (on the right) and biovolumes (on the left) over time. The most important four species are shown individually, remaining rare species including are grouped in “Others”. Note the different y-axis-scaling.



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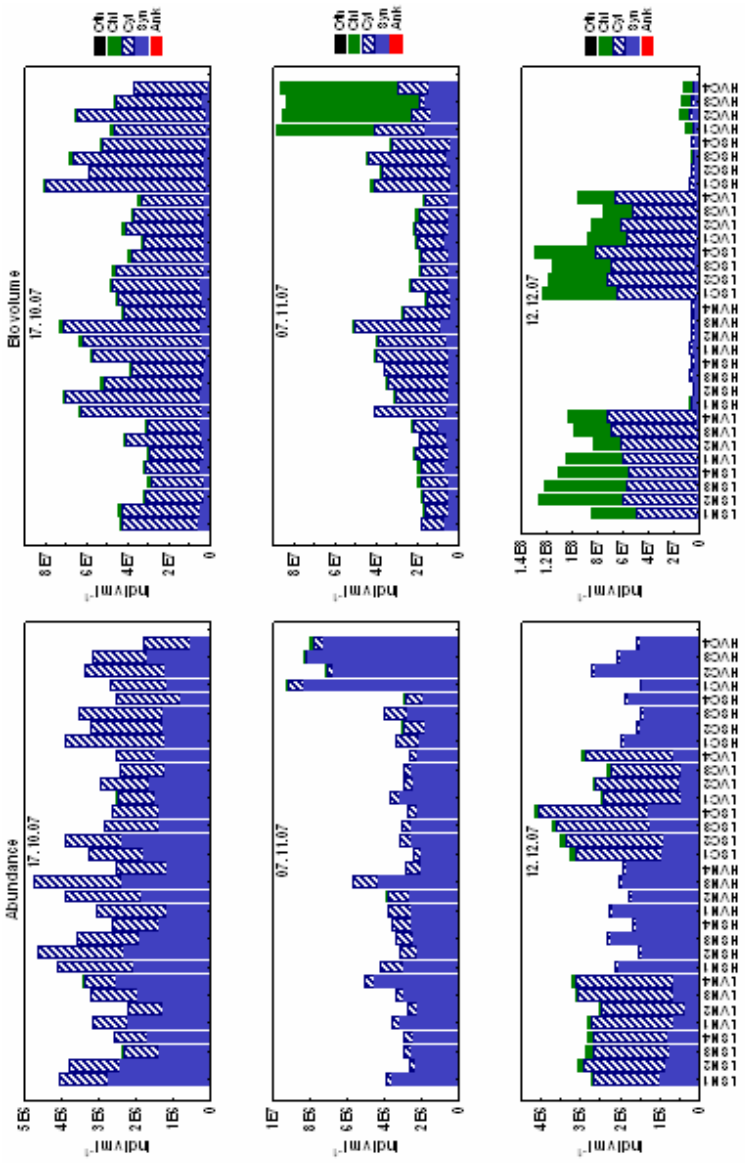

Figure 8: Continued

The biomass of *Chlamydomonas* strongly increased in warm treatments with increased variability in November, which was different to all other treatments. In December the development of *Cylindrospermum* and *Chlamydomonas* in cold treatments was strong but reduced in the HVC treatment, where as in the other warmed treatments cf. *Synechocystis* dominated, leading to low total biovolumes. Developments of the single species are described in the following.

Single species

Ankistrodesmus first increased for some weeks in all treatments, then deceased and vanished in September (Figure 9). The increase was stronger in high main temperature treatments and the decrease was more slowly in these treatments. In low main temperature treatments the increase was smaller when temperatures were variable.

Chlamydomonas showed no detectable differences between treatments except at the end of the experiment (Figure 10). The species persisted until the end of the experiment where it increased in abundances in some treatments again. This was very distinct in low main temperature treatments where *Chlamydomonas* abundances strongly increased from November to December, independent of the light conditions but more strongly when temperatures were less variable. Of the warmed treatments only the one with enhanced temperature variability but reduced light (HVC) showed a strong increase in abundances. The increase was one month earlier than in the non-warmed treatments and was reduced in December, but still a higher biomass could be detected.

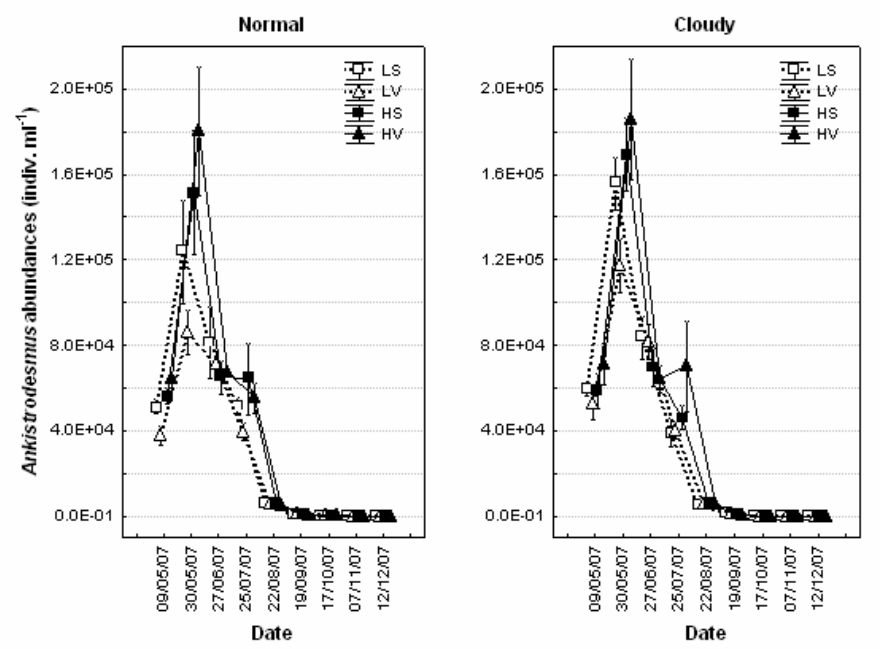

Figure 9: Development of *Ankistrodesmus* abundances over time (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments.. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

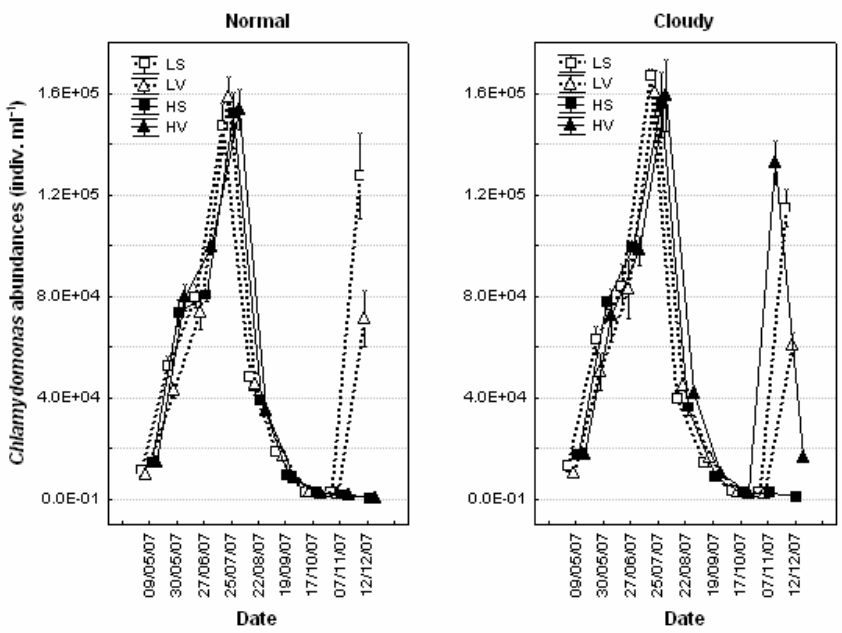

Figure 10: Development of *Chlamydomonas* abundances over time (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

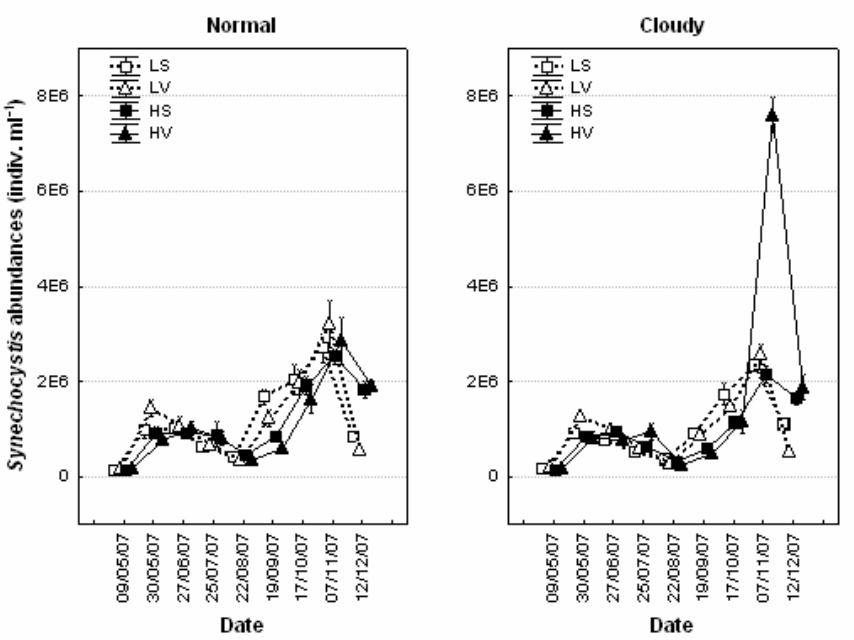

Figure 11: Development of cf. *Synechocystis* abundances over time (means and standard errors) on a logarithmic scale. For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Cf. Synechocystis showed a similar abundance peak in the warmed treatment with enhanced temperature variability and cloudy light conditions (HVC) as *Chlamydomonas* did, reaching very high numbers (Figure 11). Except for the last month and a peak in November, treatments developed similarly with one abundance peak in June, than decreased until August and increased to highest numbers in November. In December low and high main temperature treatments diverged with higher cell numbers when warmed.

The first 2 months *Cylindrospermum* was present in low numbers only, but the cyanophyte increased its numbers strongly in July in all treatments, which was stronger when warmed (Figure 12). During August and September abundances varied but stayed high, afterwards they declined again. When warmed, the decrease lasted until the end of the experiment, while non-warmed treatments showed a very strong increase from November to December.

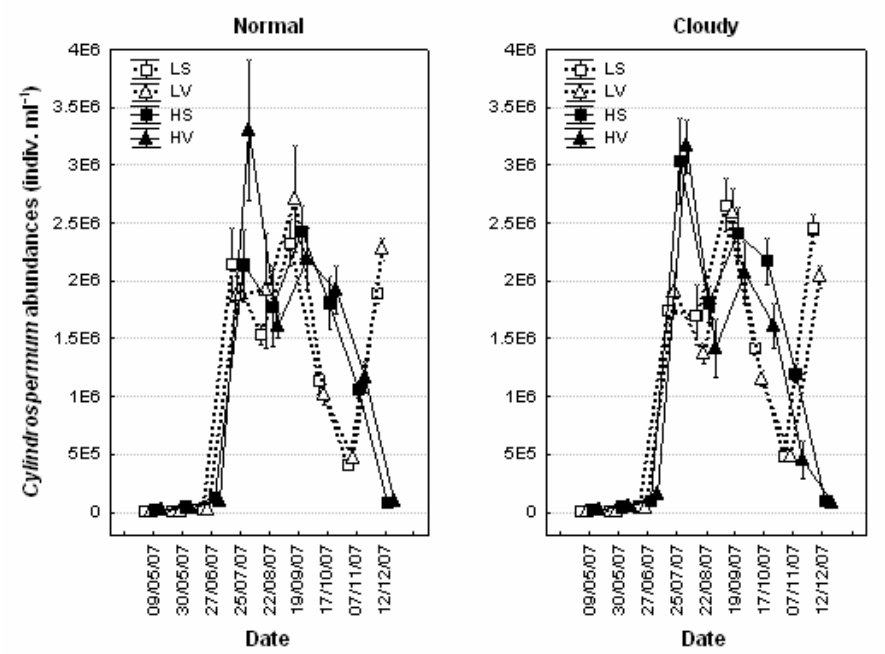

Fig.12: Development of *Cylindrospermum* abundances over time (means and standard errors). For better overview treatments with normal and cloudy light conditions are shown in different graphs. Open symbols and broken lines represent low temperature treatments, filled symbols and solid lines represent high temperature treatments. Treatments with temperature variability are represented by triangles, treatments without enhanced temperature variability by squares (LS = low temp., smooth; LV = low temp., variable; HS = high temp., smooth; HV = high temp., variable).

Discussion

While for total algal abundances and species richness no significant effects of mean temperature, the level of temperature variability and light intensity could be detected, evenness showed complex responses with interacting effects for both abundance- and biovolume-based indices. For total algal biovolume significant effects of light and an interaction between mean temperature and temperature variability could be found. In the following the effects are discussed factor by factor.

Effects of enhanced mean temperature

Although increased mean temperature did not affect most variables except evenness, compared to both other factors it had overall the strongest impact and in most interactions mean temperature was involved. In general the results were strongly influenced by the data of the last sampling. For the whole experiment increased mean temperature mainly affected and increased dominance, irrespective of being based on abundance or biovolume. When excluding this sampling, though, the increased mean temperature also positively affected total algal abundances, biovolumes and abundance-based evenness. Only main results for biovolume-based evenness did not change. However, some interactions lost their significance as all did also for other response variables.

An important role for the changes in significance patterns of mean temperature by excluding just one sampling seemed to be the

extraordinary development from the month before (November) to this last sampling in December. *Cylindrospermum* and *Chlamydomonas* strongly increased their abundances in cold treatments, while cf. *Synechocystis* decreased less and thereby was favoured in warm treatments. This led to strong effects on evenness, but different if based on abundances or on biovolumes. The very small spherical cf. *Synechocystis* became highly abundant in warm treatments and therefore strongly dominated, leading to reduced abundance-based evenness but not biovolume based evenness due to the small size of this species (1-3 µm in diameter).

The results contrast the expectation of higher abundances and biovolumes with warmer temperatures, which can be predicted based on temperature-dependent growth rates (Brown et al. 2004). Thus warming should increase cell numbers, but from November to December the opposite was observed in the treatments. Additionally, low temperatures favoured a cyanophyte, which are known to have high optimal temperatures (DeNicola 1996). Cyanophytes have often been characterized as summer species, normally flourishing in summer (Reynolds 2006; Sommer et al. 1986; Sommer et al. 1986) and often develop almost monospecific summer blooms (Dokulil & Teubner 2000). Furthermore, model results (Elliott & May 2008; Jöhnk et al. 2008) supported by several field and laboratory studies (Adrian et al. 1995) suggested that such summer blooms will increase with warming (Elliott et al. 2006). In contrast, also Moss et al. (2003) didn't find increasing cyanophyte abundances with warming although community composition changed. However, *Cylindrospermum* had generally higher abundances in warm treatments than the other way around. Also for green algae optimal growth rates have been identified between 15 to 30 ° C (DeNicola 1996), which is much higher than the mean temperatures the species experienced in the

experiment during this period. Therefore it remains unclear why these two species increased their growth rates just in the treatments and during the time with the lowest temperatures.

However, when the last sampling was excluded, the pattern was consistent with the expectations as total abundances and biovolume increased with warming. Evenness was differently affected, depending if based on abundances, positively affected by temperature, or biovolumes, negatively affected respectively. The reason for this had to be changed community composition and the different contributions of algae to abundances and biovolumes due to their sizes. These size differences and the consequently different contributions to total abundances and biovolumes also seemed to be the main reason for the significant three-way interaction demonstrating that the combination of increased variability and low light levels could counteract the negative impact of warming on biovolume-based evenness. Eliminating the last sampling from the analysis eliminated this significance and all treatments showed a significant reduced biovolume-based evenness.

Effects of enhanced temperature variability

The only variable significantly responding to temperature variability was abundance-based evenness where dominance increased with increased variability. This could be found for both average temperature regimes but was stronger in cold ones. When the last sampling date was excluded, the effect was still significant in contrast to the interaction with temperature. The effect seemed to be strongly driven by the HVC treatment in November, but also its

negative impact in low temperature treatments at the beginning of the experiment. This could be drawn back on higher abundances of the anyway dominating cf. *Synechocystis* and simultaneously decreasing abundances of *Ankistrodesmus* and *Chlamydomonas* in more variable environments. According to the relationship of metabolic rates to the surface-to-volume ratio (Irwin et al. 2006) small species have in general higher specific growth rates than large ones and respond more strongly to temperature increases (Brown et al. 2004). Probably cf. *Synechocystis*, a very small cyanophyte, could profit most from high growth rates and a strong response to temperature increases in an environment where, even if time limited, highest temperatures occurred compared to other treatments.

A three-way-interaction of both temperature-related factors with light could be revealed for biovolume-based evenness demonstrating a positive influence of increased temperature variability on evenness when the light level was low but main temperature was increased. This was not changed by excluding the last sampling. But here again the values of the HVC treatment in November played an important role, excluding this sampling let the significance vanish. However there was a trend to a general more negative impact of increased temperature variability. A plausible explanation could be increased probability of extinction and decreased probability of establishment and the average time to extinction caused by increased variation (Drake & Lodge 2004). Not only magnitude and frequency but also autocorrelation of environmental variability can be important for its consequences on diversity. Two ciliate species which did not persist under constant temperatures have been found to coexist in environments with high or low autocorrelation, but with different mechanisms working (Jiang &

Morin 2007). In this study variability was applied in regular intervals and regular intensities, such these mechanisms could not work.

Effects of light

Light reduction had a significant positive effect on algal biovolume, but no effect on the other response variables. Most studies show increased biomass production with increasing light (Bourassa & Cattaneo 2000; Cushing 1990; Hill 1996; Hillebrand 2005; Urabe & Sterner 1996). The negative effect of light on biovolume in this experiment could be aligned to the dominance of *Chlamydomonas* in the HVC treatment in November and December contributing noticeable to total algal biovolumes compared to HVN. The strength of the effect was reduced by excluding one or both samplings but was still persisting.

The light conditions could modify the effects of main temperature on evenness. The results were contrasting for abundance- and biovolume-based evenness. Increased main temperature decreased abundance-based evenness under cloudy conditions, while it decreased biovolume-based evenness under normal conditions. Additionally, increased temperature variability increased biovolume-based evenness in warm treatments when light levels were low. Excluding the last sampling from the analysis could again demonstrate the large influence of the responses in December. Based on abundances under both light conditions the warming effect switched to positive, but this was stronger when normal light conditions were applied. This probably was largely produced by the negative effect of the HVC treatment with its dominance of the small cf. *Synechocystis*, thereby reducing the overall positive effect on

evenness. Indeed, the interaction vanished when November was also excluded from the ANOVA. The picture yielded for biovolume-based evenness was similar. The HVC treatment as the sole warm one with increased evenness due to its comparable higher content of the largest species persisting *Chlamydomonas* reduced the overall negative impact of warming with more cloudy conditions. By excluding the both last samplings from analysis the significance of the interaction got lost. This was the case also for the positive effect of increased temperature variability under low light levels and the interaction of all three factors. In contrast, only the negative effect of cloudy conditions in treatments without enhanced temperature variability persisted. Most times evenness was slightly lower under cloudy conditions; this became stronger in September to November. However, differences were minimal. Although most times only slight changes in community compositions occurred with reduced light intensity it could not be ruled out that in the development in November light conditions played an important role in addition to the temperature regime. Cyanophytes have been described to be more adapted to low light intensities (Hill 1996) and cf. *Synechocystis* possibly could profit at that time. On the other hand chlorophytes seemed to be less adapted and *Chlamydomonas* could increase also its abundances. Effects of light in the field have not been described for light intensity as sole. An important factor seemed to be the mixing depth and intensity which has consequences for the light regime and for sinking losses, the last differently for different species, and such can lead to changed communities (Diehl et al. 2002; Huisman et al. 2004; Winder & Hunter 2008). The mixing regime in turn is influenced strongly by temperature which can produce effects of combined mixing and light regime on communities and an additional direct effect by temperature of the same magnitude (Tirok & Gaedke 2007).

Missing effects of light thus could be attributed to missing mixing and sinking losses.

The loss of significances by removing the sampling from analysis demonstrated to a large extent the combined effects of increased temperature, enhanced temperature variability and reduced light levels on community composition in November. It can only be speculated how this affected particular species. Cf. *Synechocysti*s has very low critical light intensities (Dauta et al. 1990) and cyanophytes were found to increase their maximum growth rates more strongly than green algae and diatoms (Coles & Jones 2000; Reynolds 1997). Additionally both factors interact as a shift of optimal light intensities with temperature (Dauta et al. 1990). Thus cf. *Synechocystis* could be expected to be favoured by higher temperatures and low light conditions over the other species except for possibly *Cylindrosperm*um, the second cyanophyte. Indeed, generally both cyanophytes dominated, however without revealing a clear picture. Both species increased by warming, but in December *Cylindrospermum* reached higher abundances in cold treatments. In contrast cf. *Synechocystis* dominated in warm ones as expected.

However, differences were sometimes low and differed between samplings sometimes showing contrasting dynamics. One probable explanation for missing effects could be that treatment effects were flattened by high dispersal rates more and more in the first four months. It seemed that after changing the dispersal rhythm to biweekly, differences between treatments developed again and could establish. This clearly indicates that dispersal rates were too high and suppressed impacts of the manipulated factors. The role of dispersal rates on communities was discussed by Leibold et al. (Leibold et al. 2004; Leibold & Norberg 2004) in context with the

metacommunity concept. Moderate dispersal could produce rescue effects preventing species from local extinction which was the intention of using metacommunities in the experiment to allow species to re-establish, when environmental conditions (temperature) has changed. High dispersal could lead to mass effects supporting stable populations which otherwise would not have been self-sustaining. Consequently, lower dispersal rates at the first four months also would have probably resulted in stronger differences of treatments and developments in community composition. Nevertheless, also at the beginning treatments showed contrasting dynamics. As demonstrated for total algal abundances varying responses in different seasons with different directions could lead no overall effect of the factor. This also shows the importance of the time-dependency of the patterns. The dynamics that became apparent over time would probably not have been found on shorter time scales.

Overall, the strongest effects detected which were independent of the dynamics in November and December were the stimulated growth by warming (abundances and biovolumes), which affected abundance-based evenness positively and biovolume-based evenness negatively due to species specific responses to warming, and the positive effect of enhanced cloudiness on total algal biovolumes. Generally this experiment demonstrated that even in artificial communities which are not completely isolated from each other effects of warming, increased temperature variability and light reduction were low. Apart from warming which enhanced growth of phytoplankton by stimulating several species, diversity was only marginally affected. While species richness showed no responses to any factor, most effects with most interactions could be detected for

evenness. Also other studies using a combination of model and experimental results reported community changes of a more quantitative than qualitative nature (de Senerpont Domis et al. 2007a). This supports stating that increased attention should be expended to dominance patterns in contrast to constrict on species richness. Apart from the earlier response of proportional community composition compared to species richness, changes in dominance can have far reaching consequences for the system (Hillebrand et al. 2008). Effects on diversity were time-dependent and species-specific making predictions difficult. This would be even more complicated in natural systems were more species are involved and several additional factors such as nutrients or grazers are play a role and have been identified as sometimes more important than for instance temperature (Christoffersen et al. 2006). Furthermore, also for light the rule of variability in light intensities was examined and found to strongly affect diversity and community composition (Flöder et al. 2002; Flöder & Burns 2005; Litchman 2003; Litchman & Klausmeier 2001; Litchman 1998).

In the experimental system used for this investigation with the possibility of dispersal in a metacommunity, treatments were not much distinguishable for a long time. High dispersal rates reduced extinction and even large changes in community composition. This could act as a rescue effect against regional extinction. Likewise high dispersal rates of phytoplankton offer good chances to adapt to climate change by range shifts and short generation times give the possibility to evolution tracking with the changing climate.

General Discussion

The aim of this study was to shed light on impacts of climate change on the diversity of aquatic organisms. It profited from combining well controlled laboratory experiments with natural long-term field data analyses. Additionally, different aquatic organism groups were investigated to detect possible general patterns.

Effects of warming could be detected in all three investigations. Macroinvertebrates in Swedish lakes did not respond in a simple direct way, but nevertheless 6% of the variation in community composition of that group could be attributed to temperature (see Chapter 1). Many species could be identified that were correlated to high or to low temperatures, respectively. However, responses were very species-specific and more or less independent from their taxonomic attribution.

Species-specific responses could also be found in the experimental studies with phytoplankton. In general, the artificial communities were composed of the same species in both experiments, which suggested that the same species should coexist under competition. This was supported by an experiment where extinct species were introduced again in the established community: these introduced species all went extinct again, even if abiotic conditions were changed (Biermann 2008). However, one important difference occurred between the two long-term experiments: in the first experiment (Chapter 2), cf. *Synechocystis* was the only cyanophyte establishing throughout the experiment, whereas in the second experiment *Cylindrospermum* coexisted with cf. Synechocystis (Chapter 3). Both species showed contrasting responses to treatments. Such species-specific responses to

warming have also been described in the field for copepods (Gerten & Adrian 2002) and phytoplankton (Thackeray et al. 2008) and could be attributed for instance to cell size in diatoms (Winder et al. 2008) or body size and the fastness of life-cycles in fishes (Perry et al. 2005).

Consequently, investigations of climate impacts on species diversity should account for species-specific responses. Certainly this complicates predictions about changes in communities to future climate change. Furthermore, results of Chapter 1 support the scale dependency of community patterns. Influences of the large-scale atmospheric system, the North Atlantic Oscillation, could not be detected, nevertheless temperature influenced community composition. However, several studies observed coherence of community responses on the large scale (Livingstone 2008; Livingstone & Padisák 2007; Straile 2002).

Complications also could arise by the recognized complex structure of responses in the experimental systems (discussed in Chapter 2 and 3). Dynamics differed between seasons as well as between species. Especially in the second experiment responses occurred contradicting the expectations.

The different approaches of the analyses have differing advantages and disadvantages. While in natural data clear relationships are not easy to detect, artificial systems suffer from their distance to natural complexity. By comparing the results, however, general patterns can be distinguished. Hence, warming affected the community composition of benthic macroinvertebrates (Chapter 1) and increased extinction rate of phytoplankton in closed communities, which was further increased by increased temperature variability but counteracted by grazing (Chapter 2). Moreover, warming shifted the community to smaller cells as has been observed in nature (Winder et al. 2008) and in marine mesocosm experiments (Sommer & Lengfellner 2008). Increased temperature and temperature variability predominantly acted negatively on diversity, but also increased evenness could be determined when based on abundances of algae (Chapter 2 and 3). However, biovolumes have higher relevance because size differences in species are dampened.

The long duration of both experiments was new for this kind of cultures. Season-dependent dynamics could be shown which with shorter durations of some weeks would not have been detectable (Chapter 2 and 3). The first and the second experiment (Chapter 2 and 3) were similar in their set-up and treatment levels, but began at a different time of the year. The first one started in August with generally warm but than decreasing temperatures and the second one at the end of April with further on increasing temperatures. Possibly this lead to slight differences in community development such as the establishment of *Cylindrospermum*, but generally the same species revealed as coexisting over a long time.

While in the first experiment communities were completely closed after inoculation, all treatments and replicates formed a

metacommunity connected by dispersal in the second experiment. This should have increased the general diversity and the possibility for species to re-establish in treatments where they have gone extinct, when conditions changed to their advantage (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002; Mouquet & Loreau 2003). However, during the first half of the experiment dispersal was too high, so that influences of the manipulated factors became unimportant and treatments converged in their responses due to mass effects (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002; Mouquet & Loreau 2003). The fact that dispersal rate was too high was supported by diverging composition in treatments when the interval of dispersal was reduced. Nevertheless, interpretation of the results became difficult. While in the first experiment manipulation clearly produced significant responses in all variables, effects were often minimal or missing in the second experiment. This was not necessarily due to a deficiency in the experiment, but could also give evidence that responses in the field would be dampened and masked or annihilated by other mechanisms than dispersal.

Another difference of both experiments was the manipulation of light. While the first experiment was subjected to a constant light and dark rhythm over the whole time, light intensity and day length followed a seasonal pattern additional to manipulating light as a factor with low and high intensities. Not many effects could be detected although light is the most important resource for phytoplankton and community composition could be expected to change by competition for it (Huisman et al. 1999). Additionally, light interacts with the second factor temperature (Dauta et al. 1990; Reynolds 2006).

In contrast, the third factor manipulated in the first experiment was grazer presence and it could be shown that grazers indeed have the potential to change competition patterns and

community composition. This may also have important implications for changes occurring with global warming when grazers could counteract loss of species by reducing the success of otherwise dominant forms (McCauley & Briand 1979). Revealing a high degree of interactions even in well controlled simple systems further emphasizes the need for further investigations including several not independently acting factors such as nutrients, stratification and the cascading of effects through the trophic levels.

Changes in communities induced by global warming remain difficult to predict. The presented study all in all supported that changes occur and ecosystems change. Anyhow relationships are not simple and how changes exactly occur could be differently generated by species-specific responses, changed interactions and complex dynamics.

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Appendix

Chapter 2

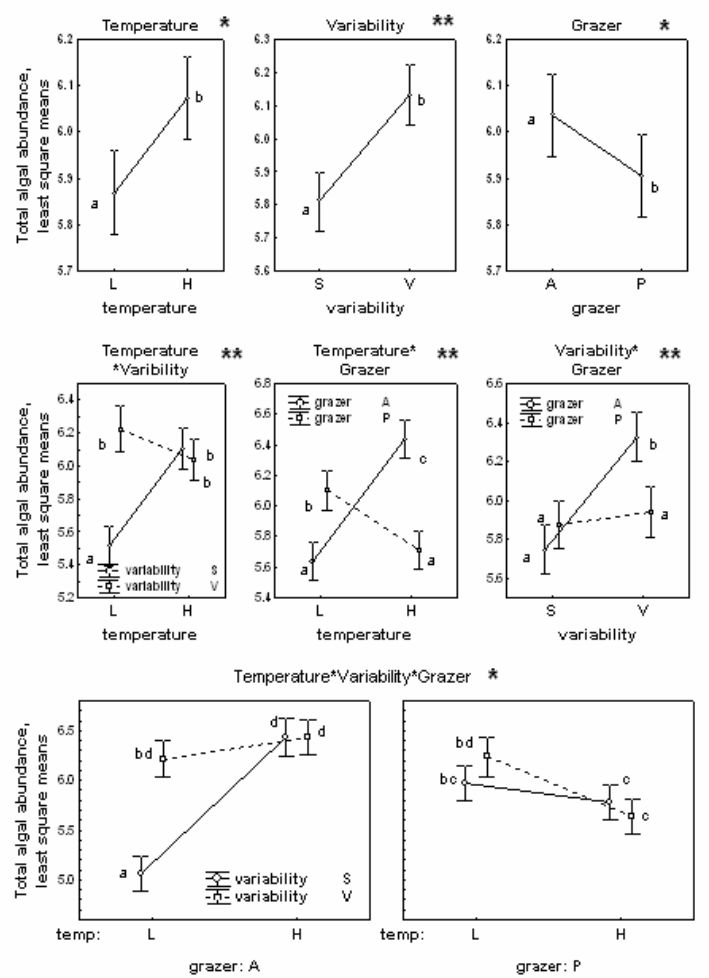

Fig. 1: Graphical visualization of single effects and interactions of all factors on total algal abundances. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

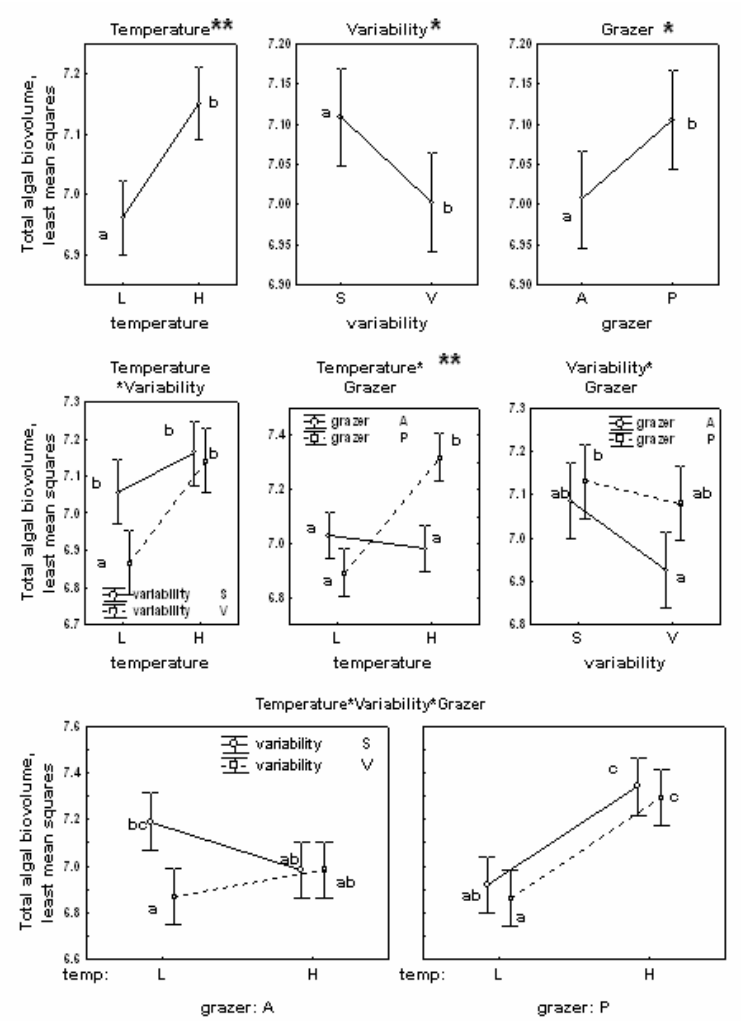

Fig. 2: Graphical visualization of single effects and interactions of all factors on total algal biovolumes. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

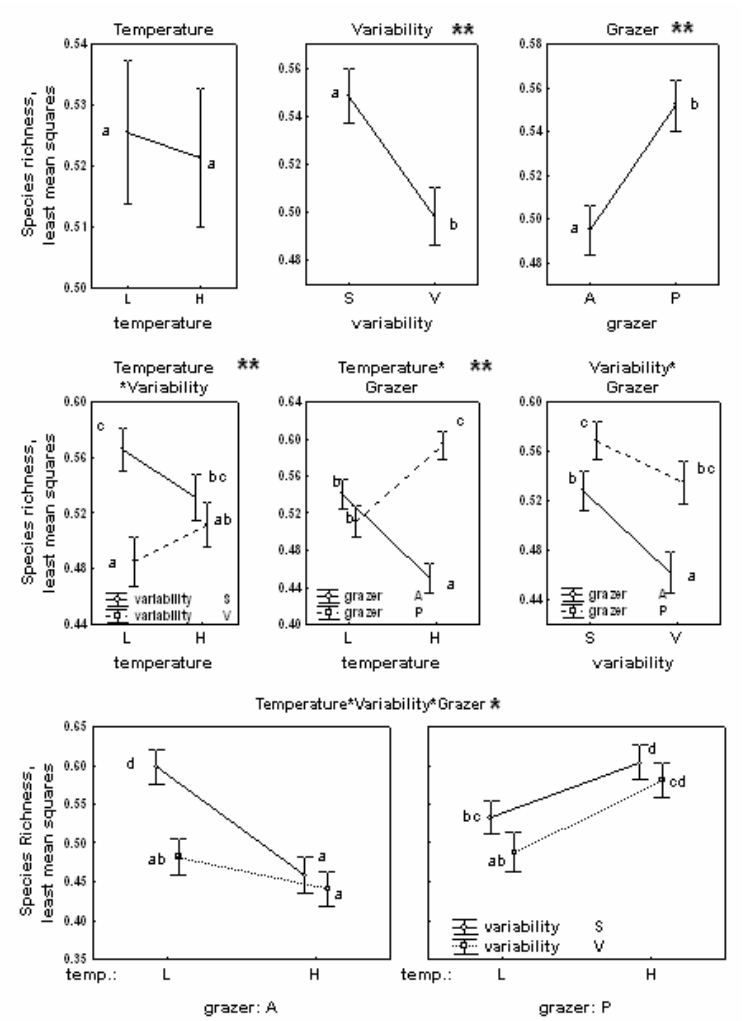

Fig. 3: Graphical visualization of single effects and interactions of all factors on species richness. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

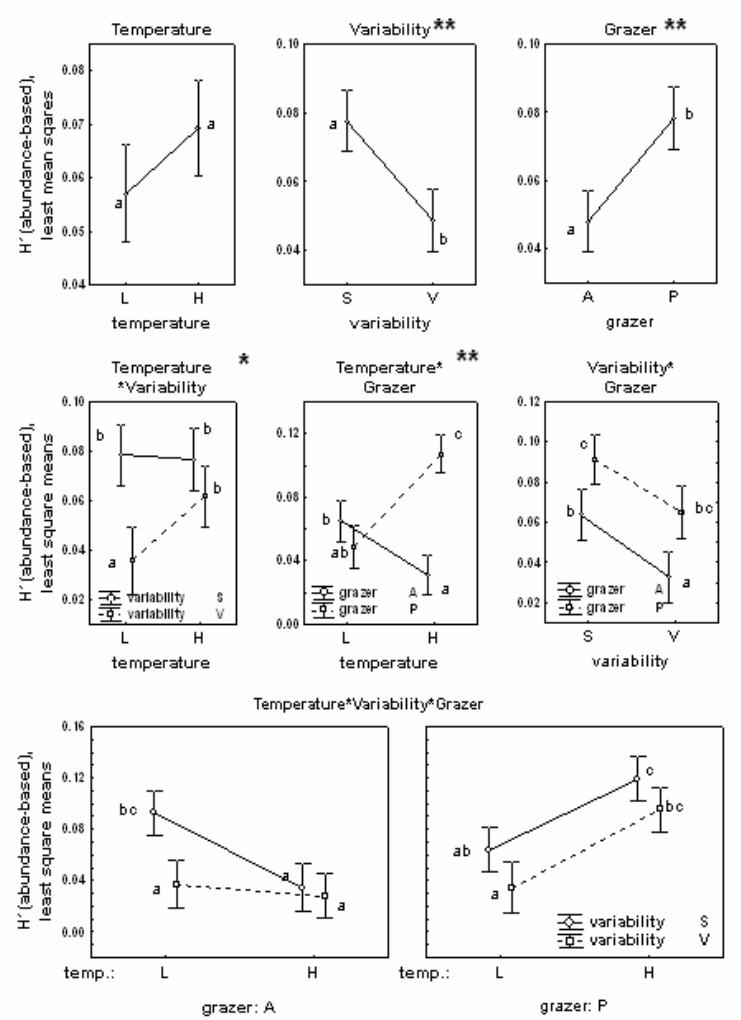

Fig. 4: Graphical visualization of single effects and interactions of all factors on abundance-based Shannon-diversity. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

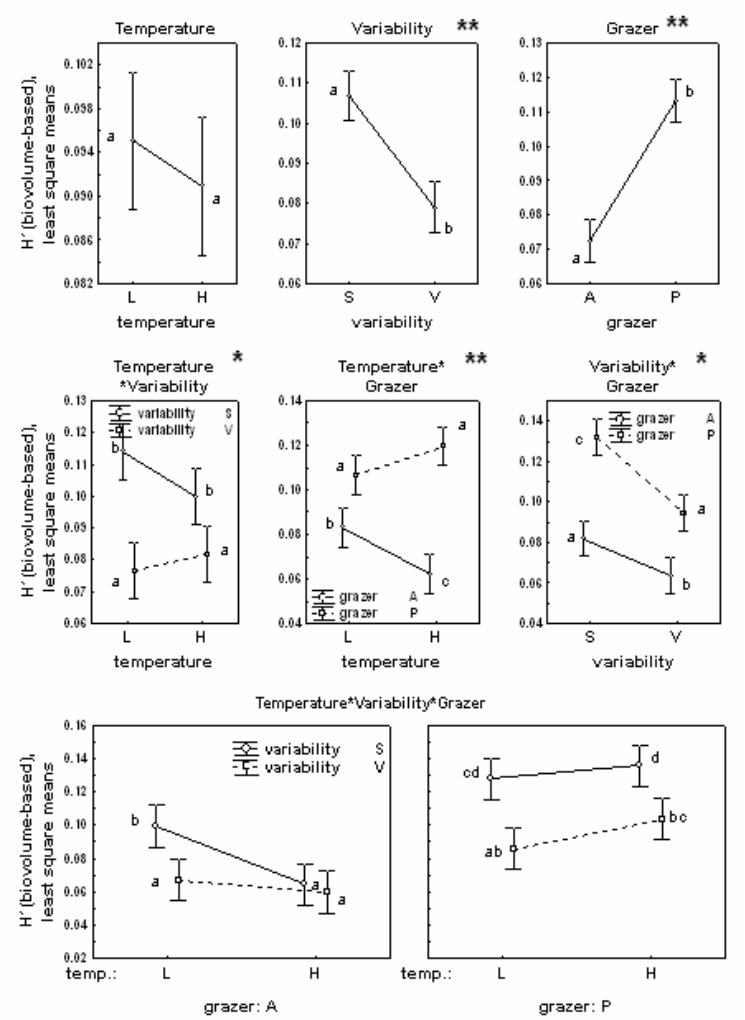

Fig. 5: Graphical visualization of single effects and interactions of all factors on biovolume-based Shannon-diversity. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

Chapter 3

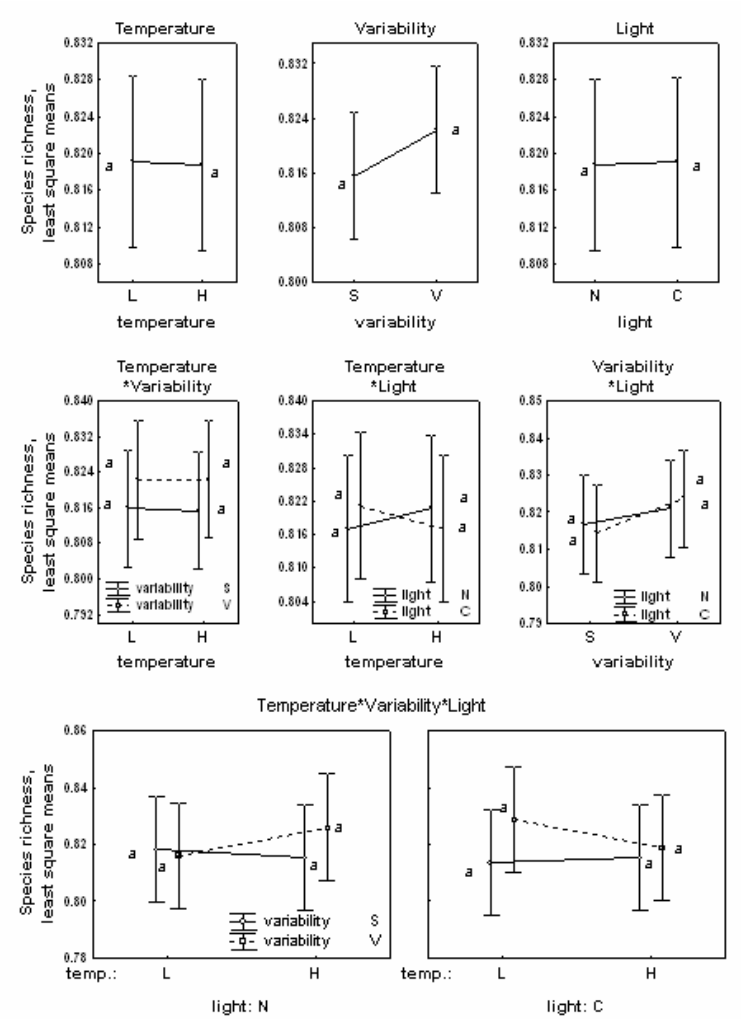

Fig. 1: Graphical visualization of single effects and interactions of all factors on species richness. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

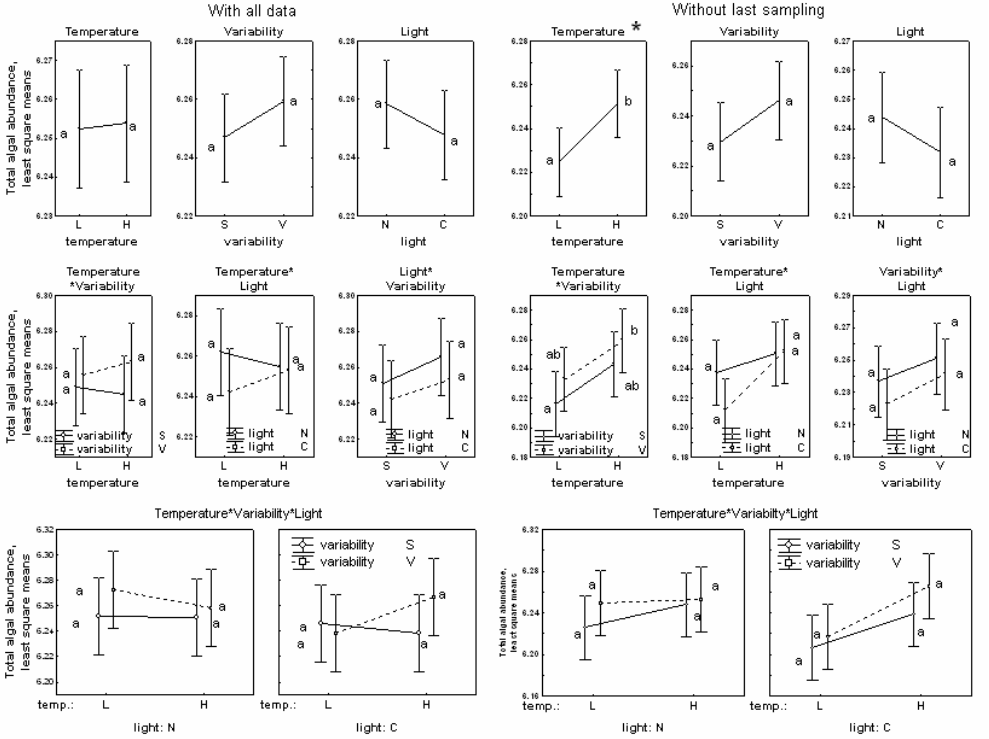

Fig. 2: Graphical visualization of single effects and interactions of all factors on total algal abundances. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

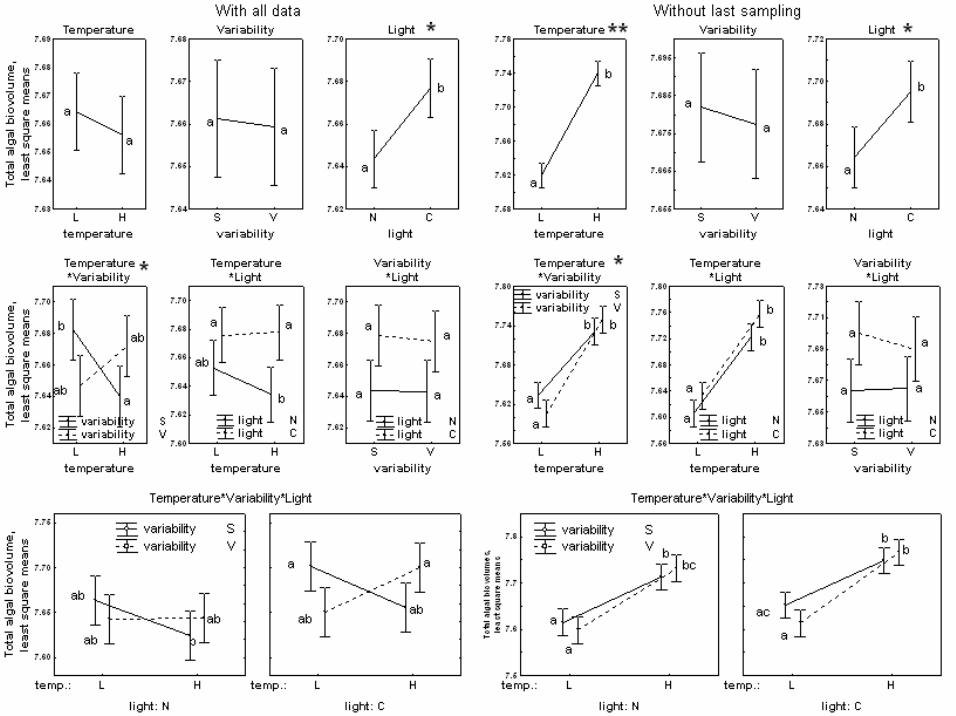

Fig. 3: Graphical visualization of single effects and interactions of all factors on total algal biovolumes. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

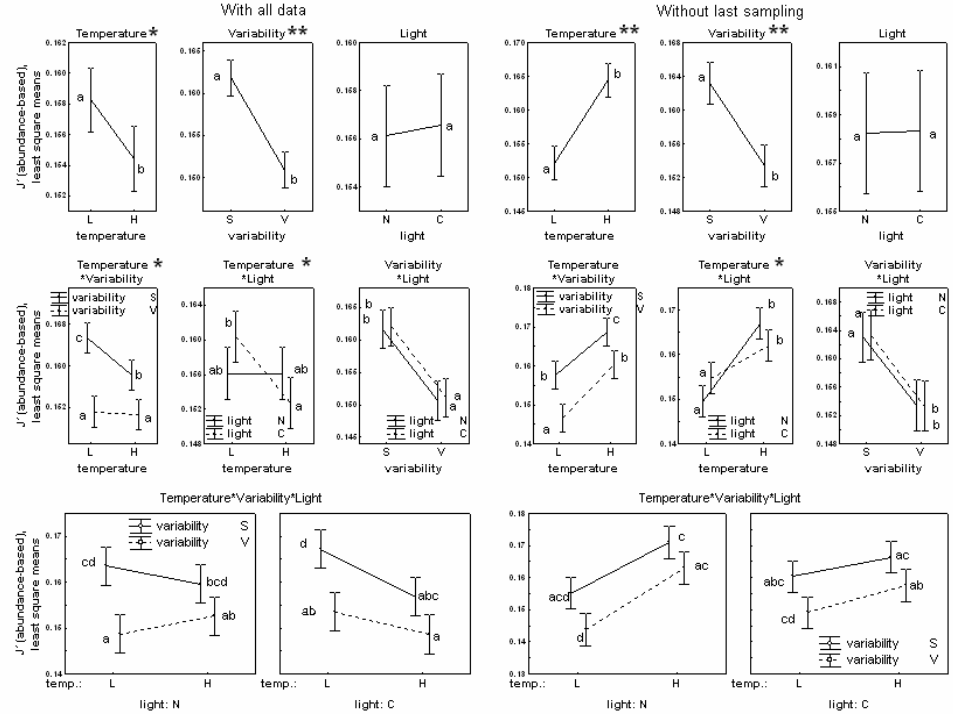

Fig. 4: Graphical visualization of single effects and interactions of all factors on abundance-based evenness. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

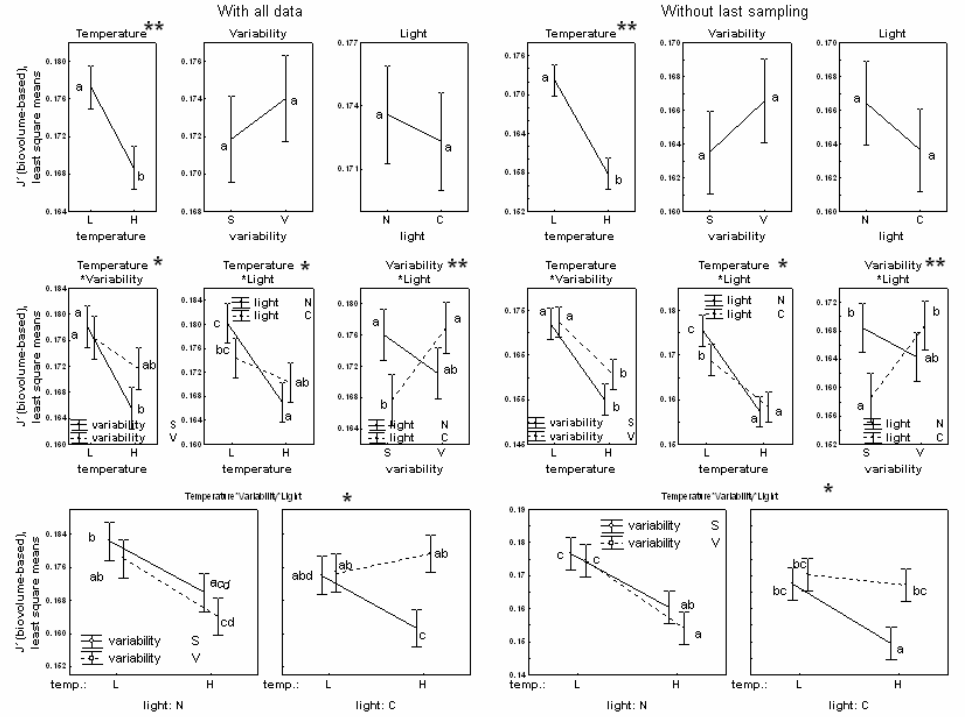

Fig. 5: Graphical visualization of single effects and interactions of all factors on biovolume-based evenness. Significant effects are marked with one asterisk, highly significant results with two asterisks. Results of post-hoc tests (Tukey-HSD) are presented by groups indicated with letters.

Erklärung:

„Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Tabellen, Karten und Abbildungen -, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von unten angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Prof. Dr. Helmut Hillebrand betreut worden."

Tanja Burgmer

Teilpublikation

Burgmer Tanja, Hillebrand Helmut, Pfenninger Markus; Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates; Oecologia (2007); 151:93 - 103; DOI 10.1007/s00442-006-0542-9

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