Effects of warming on the phytoplankton succession and trophic interactions

Dissertation
in fulfilment of the requirements for the degree “Dr. rer. nat.”
of the Faculty of Mathematics and Natural Sciences
at Kiel University

submitted by
Aleksandra Magdalena Lewandowska

Kiel, 2011

First referee: Prof. Dr. Ulrich Sommer

Second referee: Prof. Dr. Helmut Hillebrand

Date of the oral examination: 18.03.2011

Approved for publication: 18.03.2011

Signed: Prof. Dr. Lutz Kipp, Dean

Here are things known, and there are things unknown,
and in between are the doors

Jim Morrison

CONTENTS

SUMMARY

There is now a good evidence of ecological impacts of recent climate change on ecosystems worldwide. A major challenge in climate change research on phytoplankton succession is to understand the multiple factors, which drive ecological changes in phytoplankton communities. Increasing sea surface temperature is likely to alter phytoplankton bloom dynamic, phenology and community structure. Recent studies on the global primary production showed decline in size and productivity of marine phytoplankton in relation to climate warming. Reorganisation of phytoplankton community with warming can change community interactions and energy flow through the whole marine food web.

The aim of this study was to examine the impact of light and temperature on the spring phytoplankton bloom and disentangle direct and indirect effects of warming on phytoplankton. I conducted two indoor mesocosm experiments with the natural winter plankton community from the Kiel Bay, Baltic Sea. In the first experiment the combined effects of the factors light and temperature were tested and in the second experiment the factors temperature and zooplankton density were crossed. Additionally, I also included the data from four earlier experiments performed with the same experimental system in a metaanalysis on the effects of warming on primary productivity and an analysis of the pathways between temperature, diversity and productivity of phytoplankton.

In the first chapter of this thesis, I described the results of performed metaanalysis and presented the interactions between temperature, phytoplankton diversity and primary productivity. This analysis allowed me to expand an earlier experimental work on the overall effects of warming on phytoplankton succession. I found a general direct positive temperature effect on the specific primary productivity and an independent positive effect of phytoplankton species richness on the net and specific primary productivity. I concluded, that there are other factors than temperature (e.g. grazing, nutrient limitation), which might affect phytoplankton diversity and change diversity-productivity relationship.

My experimental work, presented in chapters 2 and 3, focused on combined light and temperature or consumer density and temperature impacts on the phytoplankton succession. Overall, the phytoplankton bloom started earlier in warmer conditions. Surprisingly, light intensity within the range studied (32 to 64% of sea surface irradiance on cloudless days) had only a weak effect on phytoplankton bloom phenology and

community composition, whereas the temperature effects were stronger. In general, I observed a decline of phytoplankton standing biomass and a decline in phytoplankton size with warming, which effects were related to increased grazing pressure under higher temperature. Higher consumer activity changed community composition and dominance of phytoplankton species and increased phytoplankton diversity (richness and evenness). In the chapter 3, I show that warming can shift community composition of copepods, the main phytoplankton grazers. Furthermore, the identity of copepods could be meaningful for changes in phytoplankton diversity. Thus, I suggested that the species specific interactions might be crucial to understand changes in phytoplankton community in response to climate warming.

To summarize my experimental studies and data analyses, I developed a conceptual model of temperature impacts on biotic interactions in marine plankton. In this model temperature can directly act on specific primary productivity and indirectly (via consumers) affect phytoplankton biomass and diversity. I concluded that the primary productivity in marine pelagic ecosystem depends on the relative strength between direct and indirect temperature effects and on the consumer-producer interactions.

My work, described in this thesis, highlights the importance of the complex studies on phytoplankton community for understanding ecological processes in aquatic ecosystems and their response to predicted climate warming. This complexity might be achieved by combining field work with experimental studies and testing multiple factors, which affect phytoplankton community.

ZUSAMMENFASSUNG

Es gibt heutzutage eindeutige Beweise für die Auswirkungen der Klimaveränderung auf Ökosysteme weltweit. In Bezug auf die Erforschung der Folgen des Klimawandels für die Phytoplanktonsukzession ist es wichtig, die multiplen Faktoren zu verstehen, die die ökologischen Veränderungen in der Phytoplanktongemeinschaft steuern. Ansteigende Temperaturen der Meeresoberfläche können Phänologie, Dynamik und Gemeinschaftsstruktur der Phytoplanktonblüte beeinflussen. Aktuelle Studien über die globale Primärproduktion haben gezeigt, dass Produktion und Größe des Phytoplanktons mit der Erwärmung des Klimas abnehmen. Eine Reorganisation der Phytoplanktongemeinschaft durch die Erwärmung kann die Interaktionen mit anderen trophischen Ebenen und den Energiefluss durch das gesamte marine Nahrungsnetz beeinflussen.

Das Ziel dieser Studie war, den Einfluss von Licht und Temperatur auf die Frühjahrsblüte des Phytoplanktons zu untersuchen und die direkten und indirekten Effekte der Erwärmung auf das Phytoplankton voneinander zu trennen. Ich habe zwei Indoor-Mesokosmenexperimente (2008 und 2009) mit den natürlichen Frühjahrsplanktongemeinschaften aus der Kieler Förde (Ostsee) durchgeführt. Während des ersten Experiments waren die Faktoren Licht und Temperatur und während des zweites Experiment die Faktoren Temperatur und Zooplanktondichte getestet. Zusätzlich habe ich die Daten aus vier vorherigen Experimenten (2005-2007) benutzt, die mit demselben Mesokosmensystem durchgeführt worden waren, um eine Metaanalyse der Erwärmungseffekte auf die Primärproduktion durchzuführen und die Abhängigkeit zwischen Temperatur, Diversität und Produktivität des Phytoplanktons zu testen.

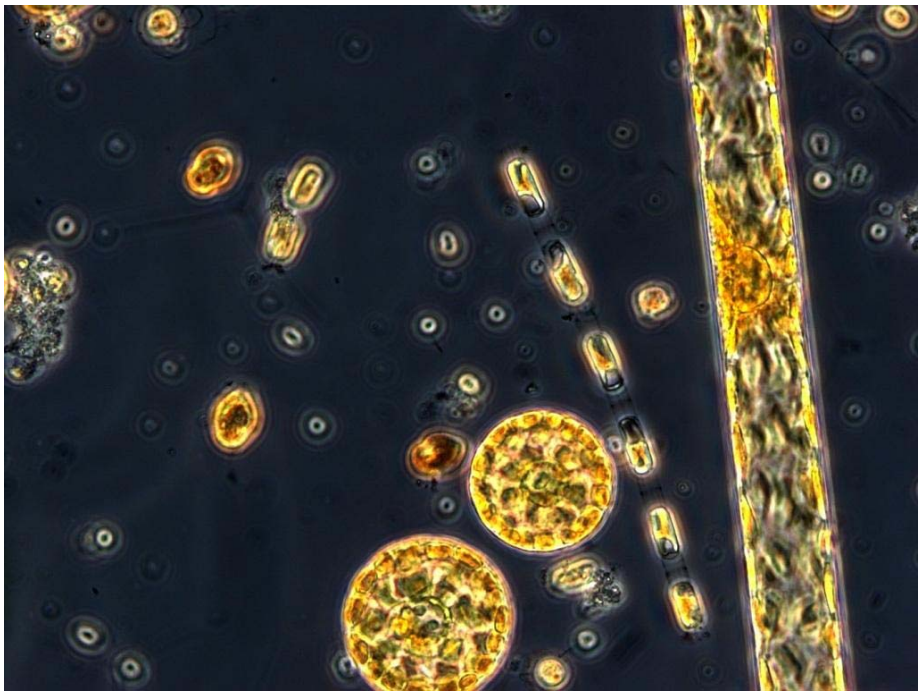
In dem ersten Kapitel dieser Doktorarbeit werden die Ergebnisse der Metaanalyse vorgestellt und die Interaktionen zwischen Temperatur, Phytoplanktondiversität und Primärproduktion beschrieben, um die generelle Effekte der Erwärmung auf die Phytoplanktongemeinschaften zusammenzufassen und die experimentelle Arbeit erweitern. Ich habe einen generellen direkten positiven Temperatureffekt auf die spezifische Primärproduktion gefunden und einen davon unabhängigen positiven Effekt der Artenanzahl des Phytoplanktons auf die spezifische und Nettoprimärproduktion. Außerdem konnte ich feststellen, dass es außer der Temperatur andere Faktoren (z. B. Fraßdruck der Konsumenten, Nährstofflimitierung) gibt, welche die

Phytoplanktondiversität sogar stärker beeinflussen können und wodurch sich die Interaktion zwischen Diversität und Produktivität ändert.

Der Schwerpunkt meiner experimentellen Arbeit (Kapiteln 2 und 3) lag auf der Kombination der Temperatureffekte mit den Lichteffekten bzw. mit den Fraßdruckeffekten auf die Phytoplanktonsukzession. Generell hat die Algenblüte unter wärmeren Bedingungen früher angefangen. Lichtintensität innerhalb des getesteten Bereichs (von 32 bis 64% der Oberflächeneinstrahlung an wolkenlosen Tagen) hatte einen unerwartet geringen Effekt auf die Phänologie der Phytoplanktonblüte und -zusammensetzung. Gleichzeitig waren die Temperatureffekte stärker. Generell habe ich unter wärmeren Bedingungen geringere Biomasse und kleinere Größen des Phytoplanktons gemessen. Diese Effekte konnten mit einer erhöhten Fraßaktivität des Zooplanktons verbunden sein. Die hohe Fraßaktivität der Phytoplanktonkonsumenten hat die Zusammensetzung und Dominanzstruktur des Phytoplanktons verändert und die Phytoplanktondiversität (Artenzahl und Gleichverteilung) erhöht. Ich habe gezeigt, dass die Erwärmung die Zusammensetzung der Copepoden, den wichtigsten Phytoplanktonkonsumenten, beeinflussen kann. Außerdem kann die Identität der Copepoden für die Veränderungen der Phytoplanktondiversität eine Rolle spielen. Ich schlage deshalb vor, dass artspezifische Interaktionen sehr wichtig sein können, um den Einfluss des Klimawandels auf die Phytoplanktongemeinschaften zu verstehen.

Meine experimentellen Studien und Datenanalysen zusammenfassend, habe ich am Ende der Arbeit ein konzeptionelles Model erstellt, welches Temperatureinflusse auf die biotischen Interaktionen innerhalbes Meeresplanktons beschreibt. In diesem Model hat die Temperatur einen direkten Einfluss auf die spezifische Primärproduktivität und einen indirekten Einfluss (durch den Fraßdruck) auf die Biomasse und Diversität des Phytoplanktons. Ich bin zu dem Schluss gekommen, dass die Primärproduktivität in den pelagischen Meeresökosystemen von der relative Stärke der direkten und indirekten Temperatureffekten und von den Konsumenten-Produzenten Interaktionen abhängig ist.

Die Ergebnisse meiner Arbeit, die ich hier vorlege, unterstreichen die Wichtigkeit von komplexen Phytoplanktonstudien, um die Effekte der vorhergesagten Klimaerwärmung auf die ökologischen Prozesse in aquatischen Ökosystemen zu verstehen. Diese notwendige Komplexität könnte durch die Kombination von Feldstudien mit Laborexperimenten, welche multiple Faktoren auf die Phytoplanktongemeinschaft berücksichtigen, erreicht werden.



Microscopic view of the spring phytoplankton

GENERAL INTRODUCTION

Phytoplankton responses to the recent climate warming

Marine phytoplankton contribute approximately 50 % of the global primary production (Falkowski and Raven 2007) and are the basis of the pelagic food web. They are responsible for most of the transfer of carbon dioxide (CO_2) from the atmosphere to the ocean and even small changes in the phytoplankton productivity might affect atmospheric CO_2 concentrations. In the context of global warming and increasing anthropogenic CO_2 emission (IPCC 2007) marine phytoplankton draw increasingly more attention nowadays.

The Intergovernmental Panel on Climate Change (IPCC) presented several scenarios of global warming depending on the CO_2 concentration in the atmosphere. According to these forecasts, future warming between 1.1 ºC and 6.4 ºC until the end of the 21st century is expected, with the most probable scenarios predicting a temperature increase ranging from 1.7 ºC to 4.9 ºC temperature increase (A1B scenario, IPCC 2007). Recent observations confirm rising sea surface temperature (SST), however ocean temperature measurements from 2004 – 2008 suggest a substantial slowing of the increase in global ocean heat content (Trenberth et al. 2009).

Latest oceanographic studies predict a decline of marine phytoplankton biomass (Boyce et al. 2010) and primary productivity (Behrenfeld et al. 2006) in response to increasing SST. Experimental mesocosm studies provided similar results (Sommer and Lengfellner 2008, Lassen et al. 2010). As the sea surface warms up, the water column becomes increasingly stratified, which reduces vertical mixing and nutrient transfer to the upper layer (Doney 2006). On the one hand low nutrient supply in the surface waters limits phytoplankton growth. On the other hand warming increase reproduction rates and grazing activity of the phytoplankton consumers (Sommer and Lengfellner 2008, O'Connor et al. 2009), which might complementarily reduce phytoplankton biomass.

More stratified, nutrient limited waters favour small phytoplankton species over larger ones, which require more nutrients (Bopp et al. 2005). Furthermore, the metabolic theory states that the individual body size decreases with increasing temperature, what is associated with faster generation times under higher temperature (Atkinson et al. 2003). Warming strengthened selective feeding of zooplankton on large phytoplankton (O'Connor 2009) and faster sinking of the large phytoplankton cells with increasing

temperature due to increasing potential for building aggregates (Piontek et al. 2009) might be the other reasons of the phytoplankton size decline.

Beside phytoplankton size, warming might also reorganize phytoplankton community structure affecting species diversity. It is commonly known that warmer regions are characterised by higher numbers of species (richness) and recent studies confirm a positive relationship between temperature and species richness across marine ecosystems (Tittensor et al. 2010). Less is known, how warming affects phytoplankton evenness (a contrary term to dominance, which describes distribution equitability among species). It was shown that warming decreased evenness in terrestrial plant communities (Walker et al. 2006). If this is true for phytoplankton too, it might have a negative consequences for ecosystem stability, because highly dominated communities are suspected to be less resistant to disturbances like acidification, invasion etc. (Hillebrand et al. 2008). Effects on phytoplankton diversity are however strongly related to consumers presence and nutrient enrichment.

The phenology of the phytoplankton bloom is the other challenge in the research on climate change. A number of long-term studies have shown that changes the in timing of phytoplankton blooms are related to increased water temperature (Edwards and Richardson 2004, Thackeray et al. 2008, Wiltshire et al. 2008, Koeller et al. 2009). The spring phytoplankton bloom might occur later in the season, if more consumers survived after warm winter (Wiltshire et al. 2008). Earlier phytoplankton bloom in temporal and high latitudes (where light is limiting) might be caused by an earlier onset of thermal stratification in the water column (Thackeray et al. 2008, Koeller et al. 2009). Shallow mixed layer depth (MLD) increases light availability for phytoplankton, what might initiate algae growth, if nutrients are not limiting (Thackeray et al. 2008). On the other hand, wind activity is predicted to increase in parallel to the sea surface warming (IPCC 2007), what may strengthen mixing of the water column and delay the spring phytoplankton bloom like it was reported by Edwards and Richardson (2004). Both direct climatic drivers (e.g. thermal stratification, earlier ice-break, increased water temperature) and indirect drivers (e.g. grazing pressure, changes in nutrient supply) can affect phytoplankton phenology and the response might strongly differ between regions and ecosystem types (Ji et al. 2010).

Trophic reorganisation of the pelagic ecosystem in response to warming

Climate warming can differentially influence species within a community having impact on their interaction strength. Increased water temperature might affect both: nutrient uptake by phytoplankton (bottom-up processes) and activity of higher trophic levels (top-down control). Furthermore zooplankton feeding preferences might strongly reorganize phytoplankton composition and community structure.

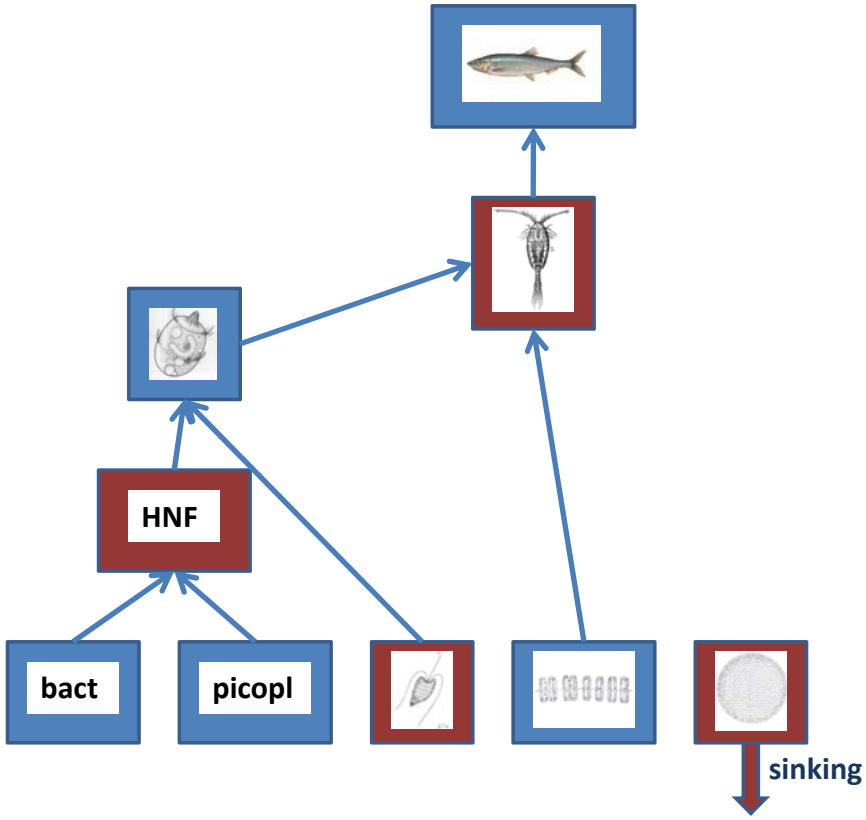


Fig. 1. Simplified pelagic food web with a focus on possible warming driven trophic reorganisation. Red boxes represent potential increase in biomass with warming. The relationships between all trophic levels are explained in text.

It is suspected that the strength of consumer control over primary producers will increase with warming (O'Connor 2009). A model presented by Thebault and Loreau (2003) predicts that consumers control only edible producers, whereas inedible plants are dependent of nutrient concentration. Thus phytoplankton composition and evenness might determine the relative strength of bottom-up and top-down processes (Hillebrand et al. 2007). In such a case warming might lead to the decline of edible phytoplankton species due to increased grazing pressure and increased relative abundance of inedible species

changing phytoplankton diversity (particularly evenness) and community composition. For instance enhanced copepod grazing activity, especially in a system where pelagic fish (the main copepod consumer) is overexploited, might reduce the biomass of edible diatoms, promoting the dominance of nanoflagellates. Besides diatoms, copepods would reduce the number of ciliates, whereby heterotrophic nanoflagellates (HNFs) would increase their biomass (Fig. 1). As a consequence the phytoplankton community might shift towards nanoflagellates dominated system. Furthermore very large diatoms, which are inedible for copepods might also grow rapidly, which would enhance phytoplankton sinking rates and carbon export to the bottom.

As the heterotrophic organisms are more temperature dependent than autotrophic ones (Brown et al. 2004), warming might cause a mismatched phenological shifts between different trophic groups, where some species respond to the temperature changes faster than the others. This pattern was originally described by Cushing (Cushing 1990) as the match-mismatch hypothesis. He stated that the survival of organisms depends of possibility to match their prey at the right time of their life cycle. For example Edward and Richardson (2004) showed that planktonic phenological shifts led to the mismatch between trophic levels and functional groups in the North Sea. Similarly Beaugrand et al. (2010) reported that changes in copepod phenology reduced recruitment success of Atlantic cod.

Phytoplankton drivers other than temperature increase

Phytoplankton growth depends of nutrient availability, underwater light and other environmental factors like water temperature, salinity, wind velocity, consumers pressure etc. (Tab. 1). Whereas some phytoplankton drivers (e.g. nutrients, light) are mostly responsible for their replication rates, other factors (e.g. grazing, sedimentation) affect phytoplankton loss. Balance between replication and loss processes is crucial to understand phytoplankton bloom dynamic and it might be driven by temperature changes.

Light as a factor essential to photosynthesis is a major driver of phytoplankton growth. At low irradiance levels, photosynthetic rates are linearly proportional to irradiance. As irradiance increases, photosynthetic rates rise to a saturation level with maximal phytoplankton production. Further increase of irradiance leads to photoinhibition of phytoplankton growth (Jassby and Platt 1976). Whereas the initial slope of the photosynthesis-irradiance relationship is not temperature dependent, at

saturated light warming can promote phytoplankton growth (Falkowski and Raven 2007). It has been also shown experimentally that daily and seasonal irradiance changes affect phytoplankton competition and nutrient uptake (Litchman et al. 2004).

Table 1: Phytoplankton drivers and their effects

direct drivers	**effects on phytoplankton quantity**	**effects on phytoplankton quality**
Nutrients	determines the phytoplankton growth	affects competition for nutrients and PUFAs content
Light	determines the phytoplankton growth and photoinhibition	affects competition for light, PUFAs and pigment content
Temperature	affects metabolic rates	affects PUFAs content, different temperature optima determine species composition
Grazing	affects biomass loss	selective feeding affects size, species composition and diversity
Salinity	-	affects size and species composition
indirect drivers		
Mixing depth	determines nutrient and light availability	
Ice cover	determines light availability and salinity	
Wind speed	regulates mixing processes	
Temperature	affects grazing pressure, thermal stratification determines MLD	
Light	affects nutrient uptake	

Macro- and micronutrients such as nitrogen, phosphorus, silicate, iron etc. are essential resources for phytoplankton and their limitation decreases the efficiency of biomass production. Phytoplankton nutrient uptake and growth are described as a function of internal and external nutrient concentrations (Dropp 1974) and differ strongly between species (Litchman and Klausmeier 2008). Velocity adapted species with high maximum uptake rates and growth rates are able to grow fast in nutrient rich ecosystem, whereas storage adapted and affinity adapted species with low growth rates or low nutrient uptake affinity would have a competitive advantage in nutrient limited ecosystems (Reynolds 2006). Thus nutrient limitation affects not only the efficiency of photosynthesis, but might be crucial to understand phytoplankton competition between species.

Grazing is an important driver of phytoplankton loss. Copepods are the major consumers of marine phytoplankton and respond strongly to temperature, food quantity and food quality like e.g. the content of polyunsaturated fatty acids (PUFAs). Copepods are mostly omnivores feeding on phytoplankton and ciliates between 500μm^3 and 1000 μm^3 particle volume (Sommer and Sommer 2006). Copepods food selection does not only depend on food size. Some species prefer feeding on non-motile pray like diatoms (suspension feeders), another copepods feed mostly on motile pray like ciliates or flagellates (raptorial feeders). Thus phytoplankton response to grazing pressure depends not only on consumer density and activity, but also on their feeding strategies.

In a nutrient-rich ecosystem, where light availability determines phytoplankton growth, grazing is the major factor, which reduces phytoplankton biomass. The relative strength of the factors light and grazing is therefore crucial for phytoplankton bloom dynamics. How climate warming might affect this interaction needs, however, better understanding. Relationship between physical growth conditions and phytoplankton biomass was formulated by Sverdrup (Sverdrup 1953) as the critical depth hypothesis, which states that there exists a critical mixing depth at which phytoplankton growth is matched by losses of phytoplankton biomass. If the mixing depth exceeds the critical depth, the phytoplankton biomass decreases as a result of insufficient light dose which limits phytoplankton growth. Bahrenfeld (2010) proposed an alternative dilution-recoupling hypothesis to explain the balance between phytoplankton growth and loss based on phytoplankton-grazer interactions and physical processes affecting this balance. According to this theory phytoplankton-grazer interaction is attenuated (diluted), when stratification of the water column is minimal and as stratification is established, grazing increases reducing phytoplankton biomass. Both hypotheses, based on different parameters, link the phytoplankton growth with stratification of the water column, which is predicted to change as a consequence of climate warming.

AIM OF THE STUDY

The aim of this study was to explore direct and indirect effects of increased temperature on phytoplankton production, species composition and phenology and to evaluate the relative strength of different phytoplankton drivers. To reach this goal I conducted two independent indoor mesocosm experiments with the natural winter plankton community from the Kiel Fjord, Baltic Sea. The first experiment conducted in 2008 focused on the combined effect of light intensity and increased temperature on the phytoplankton spring bloom. The second experiment conducted in 2009 addressed the effects of warming and grazing pressure on the phytoplankton succession. In addition I performed a metaanalysis of the effect of temperature increase on the phytoplankton productivity during the spring bloom using experimental data since 2005 to 2009.

Chapter 1

In the first chapter I present results of a metaanalysis of the effect of increased temperature on primary production across six mesocosm studies to test how phytoplankton productivity might change in response to predicted climate warming. Subsequently I related the effects to the light intensity and copepod grazing pressure. I expected that warming will positively affect phytoplankton productivity, light intensity will strengthen and grazing pressure attenuate the temperature effect. To test a hypothesis that temperature indirectly affects primary productivity due to increase of phytoplankton diversity, I performed a path analysis. I suspected that indirect temperature effect on primary productivity (via diversity changes) might be stronger in relation to the direct temperature effect on primary productivity.

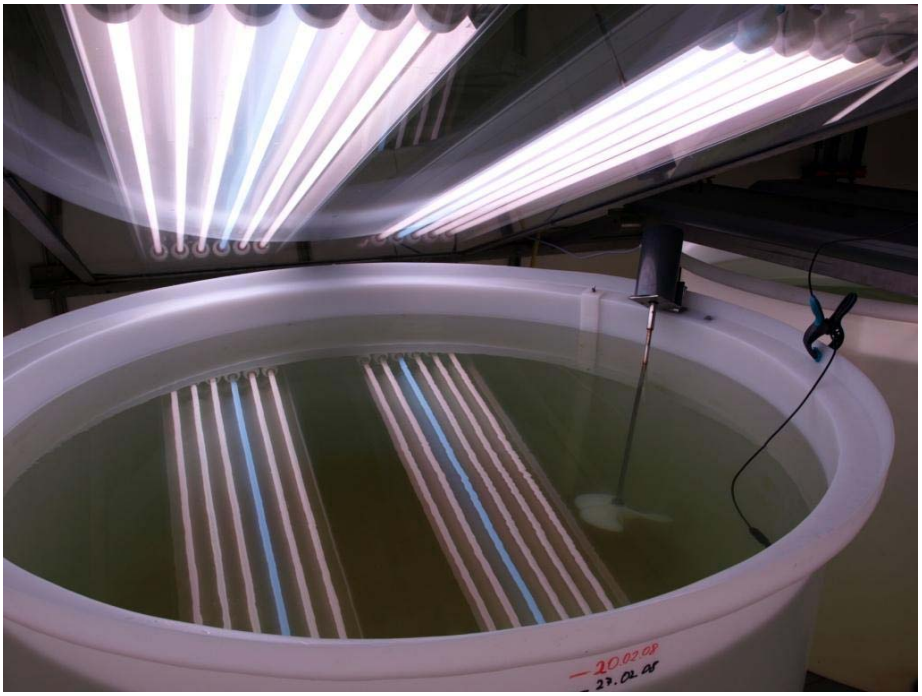
Chapter 2

In the second chapter my main objective was to combine light intensity and temperature in a factorial design to compare directly the strength of the positive light effect and the negative temperature effect on the timing of the phytoplankton bloom. Because light as an essential factor for photosynthesis was suspected to be a major driver of phytoplankton growth, I predicted a positive relationship between light and phytoplankton biomass and delay of phytoplankton bloom timing as the light intensity decreases. I also hypothesized that the light intensity effects will be weaker under warmer

conditions, because grazing activity of phytoplankton consumers would increase with increasing temperature leading to faster reduction of the phytoplankton biomass.

Chapter 3

In the second chapter I concluded that the light intensity had a weaker effect on phytoplankton than expects and temperature was the major factor, which affected the phytoplankton bloom. I assumed that temperature effect on phytoplankton was mostly indirect via enhanced grazing activity of copepods – the main phytoplankton consumers. Thus the next experiment and the chapter 3 focus on the temperature effects combined with the effect of copepod grazing, where grazing pressure was manipulated due to introduction of different copepod densities to the mesocosms, when the experiment started. Because I previously observed a shift in copepod composition, which I associated with warming, I also supposed that this taxonomic shift of consumers might have an impact on phytoplankton diversity due to the genus specific feeding strategies of copepods.



Indoor mesocosm system at IFM-GEOMAR in Kiel

CHAPTER 1

Responses of primary productivity to increased temperature and their implications for the phytoplankton diversity

ABSTRACT

In order to examine the effects of warming and diversity changes on primary productivity, we conducted a metaanalysis on six independent indoor mesocosm experiments with a natural plankton community from the Baltic Sea. We showed, how the temperature effects on primary productivity are influenced by light intensity and zooplankton density and analysed pathways between temperature, diversity and productivity elucidating direct and indirect effects of warming on primary productivity during the spring phytoplankton bloom. Our findings indicate that warming directly affected biomass specific primary productivity, which was more pronounced under low grazing pressure. On the other hand, primary productivity per unit volume did not respond to temperature, because of a negative temperature effect on biomass. Primary productivity response to temperature changes depended on light limitation in a unimodal shape. The path analysis demonstrated that phytoplankton species richness had a positive impact on both net primary productivity and specific primary productivity, while evenness had a negative effect on the net primary productivity. Both richness and evenness were not affected by temperature. Thus, we suggest that diversity effects on primary productivity can depend on other factors than temperature such as grazing, sinking or nutrient limitation, which, however, are temperature dependent. In conclusion, the relative importances of direct and indirect temperature effects determines primary productivity response to warming.

INTRODUCTION

The world's oceans have been warming over the last decades and numerous field and experimental studies have been performed to examine phytoplankton temperature responses (Behrenfeld et al. 2006, Sommer and Lengfellner 2008, Boyce et al. 2010, Finkel et al. 2010, Sommer and Lewandowska 2010). Most of the recent work on temperature driven phytoplankton changes examine the impact of predicted warming on phytoplankton productivity or seasonal patterns. However, studies, which link primary productivity and diversity effects to increasing temperature are very rare (Beaugrand et al. 2010, Burgmer and Hillebrand in press), although the relationship between productivity and diversity has been broadly discussed outside the climate change context (Worm and Duffy 2003, Grace et al. 2007, Stachowicz et al. 2007, Cardinale et al. 2009).

Warming is suspected to increase specific primary productivity directly acting on photosynthetic carbon assimilation by phytoplankton (Falkowski and Raven 2007). Recent oceanographic studies, however, have shown that increasing sea surface temperature (SST) has caused a global decline in phytoplankton productivity (Behrenfeld et al. 2006, Boyce et al. 2010), which was tentatively explained by limited nutrient supply due to increasing water column stratification (Doney 2006).

Increasing temperature has been reported to have a positive effect on the number of species (richness) in marine environments (Beaugrand et al. 2010, Tittensor et al. 2010) and in some terrestrial ecosystems (Menéndez et al. 2006). By contrast, Walker et al. (2006) found decreased plant richness with warming in tundra ecosystems. The relationship between temperature and evenness (a measure of how equitable biomass or abundance is distributed among species) has received less attention. Nonetheless a metaanalysis across the tundra biome (Walker et al. 2006) showed that warming decreases evenness in plant communities.

The diversity-productivity relationship has been frequently discussed in the literature leading to the conclusion that productivity increases with species richness, because communities with a high number of species are more likely to contain and become dominated by highly productive species (selection effect, Cardinale et al. 2009). The relationship between evenness and productivity is less well understood and the available studies lead to divergent predictions. Some authors found a positive effect of evenness on plant biomass in a grassland ecosystem (Wilsey and Potvin 2000), whereas others (Mulder et al. 2004) gave a contrary example. Polley et al. (2003) found no effect

on the biomass production and suggested that the evenness-productivity relationship strongly depends on the identity of the dominant species and on the relative importances of complementarity (niche differentiation between species) and selection effects.

Most of the experiments, which examine the impact of temperature and producers diversity on productivity, use standing biomass or chlorophyll content as a proxy for primary production (Cardinale et al. 2006, Boyce et al. 2010). However, primary productivity and producer biomass are separate ecosystem functions (Stachowicz et al. 2007), with productivity measuring carbon flux and biomass measuring carbon accumulation. Thus results of different studies might diverge depending on the measured parameters.

The first aim of our study was to test the impact of warming on net primary productivity (PP) and biomass specific primary productivity (PP:B) using a metaanalysis approach on six independent mesocosm experiments conducted in Kiel, Germany within the project AQUASHIFT. Analysis of individual experiments already showed a decline of phytoplankton standing biomass as an effect of warming and enhanced grazing pressure (Sommer and Lengfellner 2008, Sommer and Lewandowska 2010), whereas phytoplankton biomass responses to the light intensity changes were not very conclusive (Sommer and Lengfellner 2008, Lewandowska and Sommer 2010). Thus, in this study we tested both grazing and light intensity effects on the primary productivity response to warming across the AQUASHIFT experiments.

The second aim of this paper is to illustrate the interaction pathways between temperature, phytoplankton diversity and primary productivity to find out if observed phytoplankton productivity changes are a direct effect of temperature increase or rather an effect of changing phytoplankton diversity with warming. We hypothesise that different pathways are relevant for PP compared to PP:B.

METHODS

Experimental design and laboratory techniques. Mesocosms of 1400 L volume and 1 m depth were set up in temperature controlled rooms. Mesocosms were filled with the natural plankton communities (containing phytoplankton, bacteria and protozoa) from the Kiel Fjord, Baltic Sea. Mesozooplankton was added from net catches at typical overwintering concentrations (Tab. 1-1, Behrends 1996). During the first experiment (2005) an additional 300 L “benthos”-chamber was connected in circular flow to each main mesocosm. The “benthos”-chambers contained sediment and mussels in

order to supply the plankton community with larval stages of benthic organisms. The "benthos"-chambers were omitted during the following experiments, because no larvae of benthic organisms were observed to play a role in the system.

Table 1-1. Experimental design of studies included in analyses.

Experiment	Temperature (ºC)	Light intensity (% I_0)	Initial copepod abundance (ind. L^{-1})
2005	0, 2, 4, 6	16	16
2006-1	0, 2, 4, 6	100	5.5
2006-2	0, 2, 4, 6	64	8.5
2007	0, 2, 4, 6	32	4.5
2008	0, 6	32, 48, 64	8
2009	0, 6	48	1.5, 4, 10

Temperature and light were computer programmed to simulate daily and seasonal variability. There were four temperature scenarios (each replicated twice) tested in the experimental period 2005 – 2007 and two temperature scenarios tested during the experiments 2008 and 2009 (Tab. 1-1). In the experiment 2008 the factor temperature was crossed with the factor light intensity, in the experiment 2009 with the factor copepod density. The coldest treatment (baseline, ΔT=0ºC) during each experiment corresponded to the decadal mean (1993 – 2002) of the SST in Kiel Bay starting from February 15th. In order to simulate predicted warming (IPCC 2007), temperature was elevated 2 ºC, 4 ºC and 6ºC above the baseline, symbolized by the notations ΔT=2ºC, ΔT=4ºC and ΔT=6ºC in the text. For the analysis in this paper we used only data for ΔT=0ºC and ΔT=6ºC to allow straightforward comparisons between experiments.

Light conditions mimicked daily and seasonal irradiance patterns according to the model presented by Brock (1981). The daily light cycle equal approximately 10 h for our experimental periods, however the day length change during the course of the experiments, according to the natural changes. We reduced light intensity to 16%, 32%, 48% and 64% of the sea surface solar irradiance calculated for cloudless days (I_0) in order to test different light scenarios (Tab. 1-1) related to underwater attenuation and cloud cover. During the experiment 2006-1 light intensity was not reduced (100% I_0).

Phytoplankton samples were taken three times per week from the mid depth of the mesocosms, fixed with Lugol's iodine and counted using an inverted microscope (Utermöhl 1958) for species >5 µm and flow cytometry technique (FACScalibur, Becton Dickinson) for species <5 µm cell size. Phytoplankton biomass was estimated from

carbon content (Menden-Deuer and Lessard 2000) after approximation of cell volumes to geometric standards (Hillebrand et al. 1999).

Primary productivity (PP) was measured by the ^{14}C incorporation method after Gargas (1975). We used 4µCi ^{14}C-bicarbonate per 30 ml sample. Duplicate samples were incubated together with a blank (dark) sample during 3-4 h around noon inside each mesocosm at mid depth. Afterwards samples were filtered through cellulose-nitrate membrane filters (0.2 µm pore size), filters were fumed with HCl and fixed with scintillation cocktail (Lumagel). A liquid scintillation counter (Tricarb counter, Packard) was used to measure radioactivity. Productivity per day (µg C L^{-1} d^{-1}) was calculated from productivity during the incubation time by adjusting for the light received during incubation in relation to the total daily light dose.

Data analysis. Biomass specific primary productivity per day (PP:B) was calculated as net primary productivity as µg C L^{-1} d^{-1} (PP) divided by total phytoplankton biomass as µg C L^{-1} (B). If not stated otherwise we used the mean values of PP and PP:B from the bloom start to the point of the maximal productivity for further analysis. We did not include values of primary productivity after the productivity maximum to avoid an impact of nutrient limitation which might have occurred from the peak onwards. In addition we conducted the same analysis based only on the maximum primary productivity (PP_{max} and $PP:B_{max}$), which are reported in the Appendix (Fig. A1, Tab. A1) for comparison.

To examine an impact of simulated warming on PP and PP:B, we conducted a metaanalysis on six independent experimental datasets. We used log response ratios to analyse relative effects of warm temperature treatments (ΔT = 6ºC) over ambient temperature treatments (ΔT = 0ºC) for each experiment. Afterwards we calculated an overall effect size (with the inverse of variance as a weight) across all studies and tested for significance. Variation in effect sizes was further analysed by the categories light intensity and initial copepod density in order to detect significant differences between groups (analysis of heterogeneity). Light intensity and initial copepod density from factorial studies (experiments 2008 and 2009 respectively) were entered as additional independent variables in a heterogeneity analysis for a better representation of general trends. Data points from factorial experiments were proved to have no significant impact on general trends (see Appendix Table A2).

A structural equation model (SEM) based on a correlation matrix in "R" (version 2.12.0) was used to check for relationships between temperature, mean primary productivity (PP and PP:B) and phytoplankton diversity parameters (richness and evenness) across all experiments. Because of identical counting efforts between all experiments, richness (S) could be approximated as the number of phytoplankton species identified and Pielou's index (Smith and Wilson 1996) was used to estimate phytoplankton evenness (J).

RESULTS

Effects of warming on primary productivity

Across all experiments warming caused positive changes in phytoplankton primary productivity. We observed a slightly positive, however not significant, temperature effect on PP and a significant positive response of PP:B to enhanced temperature (Tab. 1-2). Similar effects of warming were observed on maximal net primary productivity (PP_{max}) and biomass specific maximal primary productivity ($PP:B_{max}$, see Appendix Fig. A1, Tab. A1) .

Table 1-2. Summary of results from metaanalysis of temperature impact on net primary productivity (PP) and biomass specific primary productivity (PP:B).

	PP	PP:B
Overall effect	0.15	0.42
Variance	< 0.01	< 0.01
Standard deviation	0.39	0.28
+95% confidence interval	0.47	0.65
-95% confidence interval	-0.16	0.20

The primary productivity response to increased temperature varied strongly between the single experiments (Fig. 1-1). Temperature had a negative effect on PP during experiments with low light intensity (experiments 2005 and 2007, light intensity 16% I_0 and 32% I_0 accordingly) and a positive effect on PP during all other experiments with higher light intensities. Effects of warming on PP:B were positive for each study except for experiment 2006-2, which was characterised by a high initial phytoplankton biomass and PP_{max} was reached shortly after the beginning of the experiment.

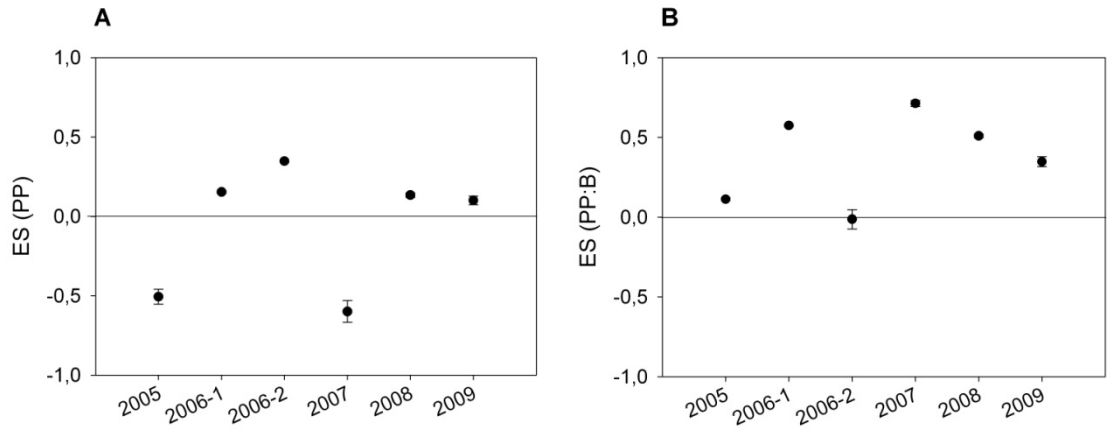


Figure 1-1. Average effect sizes (±95% confidence intervals) of increased temperature on net primary productivity (A) and biomass specific primary productivity (B) for each experiment used in analysis.

We found a significant relationship between the effect size of warming on PP and light intensity (Fig. 1-2, *2nd order polynomial regression*, F = 9.489, r^2 = 0.79, P = 0.02). No correlation was found between the effect size of warming on PP:B and light intensity (P > 0.05). Effect sizes of warming on PP did not show any response to changes in grazers abundance (P > 0.05), whereas effect sizes of warming on PP:B showed a negative, however not significant, trend in response to increasing initial copepod density (Fig. 1-3, *linear regression*, F = 3.732, r^2 = 0.38, P = 0.1).

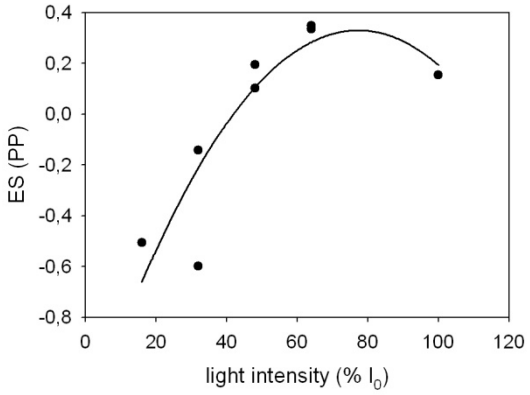


Figure 1-2. Impact of light intensity on the effect sizes of warming on net primary productivity (PP). Polynomial regression according to the equation: $y = -1.25 + 0.04x - 0.003x^2$ (F = 9.489, r^2 = 0.79, P = 0.02).

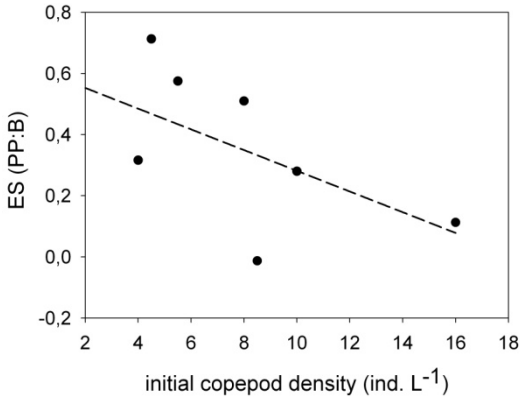


Figure 1-3. Impact of initial copepod abundances on the effect sizes of warming on biomass specific primary productivity (PP:B). Linear regression according to the equation: y=0.62– 0.03x (F = 3.732, r^2 = 0.38, P = 0.1).

Temperature-productivity relationship pathways

Hypothetical temperature-productivity pathways with standardised correlation coefficients are illustrated in Fig. 1-4. A chi-squared test showed no significant deviation between the observed correlation matrix and that predicted by the proposed SEM ($\chi^2 = 0.26$, df = 1, $P = 0.61$), suggesting that the model presented a suitable description of the variables. The proposed SEM described 99% of data variability ($R^2 = 0.99$).

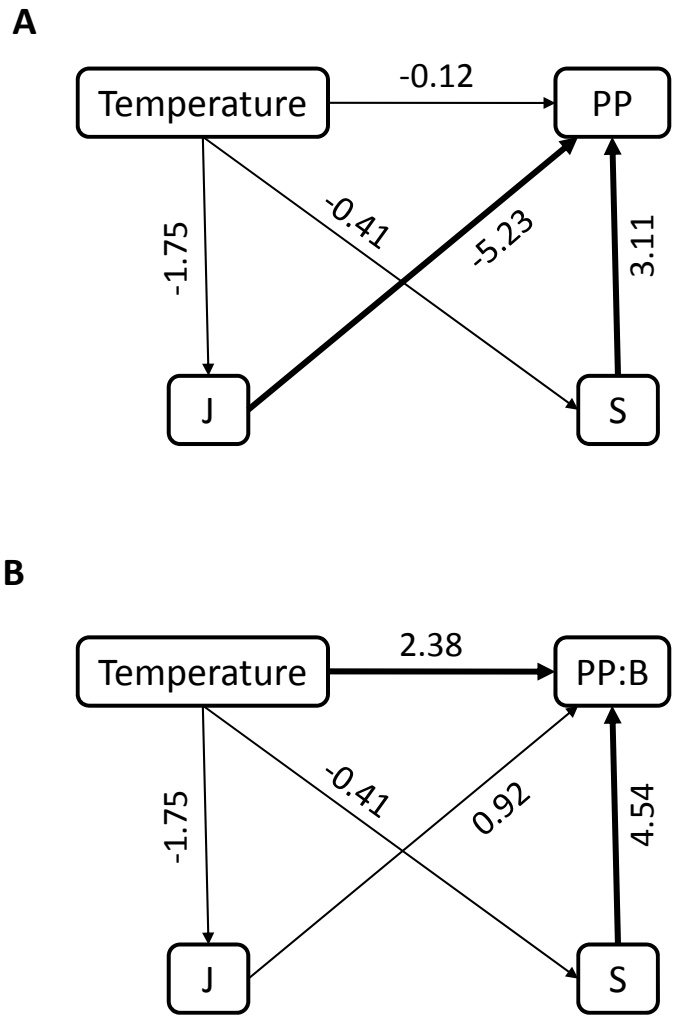


Figure 1-4. Results of the Structural Equation Model (SEM) used to illustrate effects of temperature (T) and phytoplankton diversity (richness, S; evenness, J) on A) net primary productivity (PP) and B) biomass specific primary productivity (PP:B). Significant ($P > 0.05$) relationship pathways are marked with bold arrows, given are standardized correlation coefficients. Metrics of overall model fit suggest that the models cannot be rejected ($\chi^2 = 0.25$, $P = 0.61$).

The SEM did not indicate significant pathways between temperature and PP, neither directly nor indirectly through diversity, which was true for evenness as well as richness (Tab. 1-3). However there was a direct impact of richness and evenness on PP, but both effects had opposite sings (Fig. 1-4A). Phytoplankton evenness had a negative impact on PP ($P < 0.001$), whereas phytoplankton species richness positively affected PP ($P = 0.002$).

Table 1-3. Unstandardized path coefficients (standardized values are shown in Fig. 1-4) between temperature (T), net primary productivity (PP), biomass specific primary productivity (PP:B), phytoplankton species richness (S) and phytoplankton evenness (J).

Pathways	Estimate	SE	*P*
T → PP	-0.014	0.116	0.9
S → PP	0.349	0.112	0.001
J → PP	-0.608	0.116	< 0.001
T → PP:B	0.311	0.131	0.02
S → PP:B	0.572	0.126	< 0.001
J → PP:B	0.120	0.131	0.4
T → S	-0.066	0.160	0.6
T → J	-0.270	0.154	0.08

The pathway between temperature and PP:B was a direct relationship and was not mediated via diversity (Fig. 1-4B). Temperature significantly increased PP:B ($P = 0.02$). In addition, there was a positive, independent impact of richness on PP:B ($P < 0.001$). Phytoplankton evenness had no significant effect on PP:B ($P > 0.05$).

DISCUSSION

Temperature impact on primary productivity

Temperature is suspected to increase specific primary productivity due to increasing carbon incorporation rates (Falkowski and Raven 2007). In parallel, however, temperature positively affected phytoplankton loss processes caused by zooplankton grazing (O'Connor et al. 2009), sinking (Piontek et al. 2009) and respiration (Falkowski and Raven 2007) thus diminishing net primary productivity. Our metaanalysis indicates that warming has a significantly positive effect on PP:B, which is related to copepod

density (Fig. 1-3). Under high grazing pressure (high copepod density) the temperature effects on PP:B were rather weak and under lower copepod density the effects of warming on PP:B became stronger. This is in agreement with the results reported by Burgmer and Hillebrand (in press), who used microcosms to examine the combined effect of temperature and consumer pressure on freshwater phytoplankton. They showed that algae biomass decreased with warming only if consumers were present, whereas warming led to an increase of algae biomass in the absence of the consumer pressure. Although not significant, our results might suggest that 1) grazing activity, not density of copepods determine the PP:B response to increased temperature, 2) other processes than grazing, such as nutrient limitation, strong aggregation and sinking of phytoplankton affect PP:B response to warming.

We did not find a significant response of PP to warming, which was probably caused by the compensation of increased PP:B and decreased B due to higher grazing activity in warmer conditions. A negative effects of temperature and grazing pressure on B were reported by Sommer and Lewandowska (2010) for the experiment 2009. A similarly negative response of phytoplankton biomass to increased temperature was observed for all experiments included in our metaanalysis (Sommer and Lengfellner 2008, Lewandowska and Sommer 2010).

Temperature effects on PP depended on light intensity (Fig. 1-2). Under light limited conditions, temperature had a negative effect on PP, because warming strongly increases grazing activity of phytoplankton consumers (O'Connor et al. 2009) and community respiration, as reported by Wohlers et al. (2009), whereas the carbon incorporation process is limited by light (MacIntyre et al. 2002). Under light saturated conditions in the nutrient rich ecosystem, warming led to increase of PP, because photosynthetic activity of phytoplankton is not light limited and carbon loss due to respiration or zooplankton grazing is balanced by an increase in carbon incorporation rates. Thus the temperature effects on the net primary productivity depend on the relative strength of increasing photosynthetic activity and phytoplankton loss processes like community respiration, grazing or sinking.

Linking temperature and diversity effects on primary productivity

The path analysis confirmed our previous results that temperature has a direct positive impact on PP:B (Fig. 1-4B). In addition, PP:B increased with increasing species number (richness), probably as a result of niche complementarity and selection effects,

which favoured highly productive species (Grace et al. 2007). We did not observe a significant response of PP:B to evenness, suggesting that the co-dominant species in the more even communities were as productive as the single dominant species in the communities with low evenness.

The SEM indicated no significant effect of warming on PP (Fig. 1-4A), which stays in agreement with our metaanalysis (Tab. 1-2). Phytoplankton species richness significantly increased PP, similar to richness-PP:B relationship. Phytoplankton evenness in our studies had a negative effect on PP, which confirms results presented by Mulder et al. (2004), but contradict others (Wilsey and Potvin 2000, Bruno et al. 2005). As suggested by Polley et al. (2003) the relationship between evenness and productivity depends on the relative importance of selection and complementarity effects. If the selection effect prevails and a single dominant species successfully competes for the resources, increase in phytoplankton evenness will decrease primary productivity and the dominant species will largely control ecosystem functions. Thus, the identity of a dominant phytoplankton species in such a case might affect primary productivity more strongly than diversity, as suggested by Bruno et al. (2005).

Surprisingly temperature did not affect phytoplankton diversity, neither richness nor evenness. Although the slightly negative response of phytoplankton diversity to increased temperature agrees with the predictions of species loss with climate warming (Worm et al. 2006), these effects were not significant. It should be noted, that all experimental temperatures were low (< 9°C) and thus probably no species was excluded by exceeding its upper temperature limit. Accelerated competitive exclusion under warmer temperatures was also less probable, because increased grazing pressure at higher temperatures should have decreased competitive pressure. On the other hand, highly sensitive species might have been excluded earlier by stronger grazing. Overall, these counteracting processes might have cancelled each other out, in spite of being temperature dependent individually (Hillebrand et al. 2007).

In conclusion, our analyses indicate that warming has a direct positive impact on PP:B while at the same time negatively affecting standing phytoplankton biomass (B). Thus the temperature effect on PP depends on the relative strength of increased PP:B with warming and decreased B with increased grazing pressure under warmer conditions. Moreover, primary productivity response to increased temperature depends on light limitation. Hence future studies on the impact of warming on phytoplankton should,

beside temperature effect, consider changes in the light conditions. Temperature did not affect phytoplankton diversity, but species richness directly increased primary productivity in our study, probably as result of the strong selection effect. Thus we suggest that experimental studies on species specific interactions might help to understand temperature-diversity-productivity relationship and phytoplankton community response to recent climate changes.

ACKNOWLEGMENTS

This study was founded by DFG (German Research Fundation) within the priority program 1162 ´AQUASHIFT´. T. Hansen, H. Tomanetz, R. Koppe and C. Meyer are acknowledged for their technical assistance. We thank K. Gocke for his help with measurements of primary productivity. M. Winder is acknowledged for her constructive comments and help with data analysis.

CHAPTER 2

Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton

ABSTRACT

We examined the simultaneous effect of climate warming and light availability on the phytoplankton spring bloom using 1400 l (1 m depth) indoor mesocosms. The timing of the spring bloom was advanced both by warming and higher light intensity, but the influence of temperature on the phytoplankton community was stronger than the light effect. Warming affected phytoplankton directly and indirectly via enhanced grazing pressure at higher temperatures. Warming resulted in markedly lower phytoplankton biomass and a shift towards smaller cell sizes. It also led to changes in the community structure of phytoplankton and zooplankton. Among phytoplankton, large-celled diatoms were most negatively affected by warming. Overwintering zooplankton species (*Oithona*, *Pseudocalanus)* remained dominant in the cold treatments, while they were replaced by late spring or summer species (*Acartia*, *Centropages*, *Temora)* in the warmed treatments. Our results show that understanding food web interactions might be very important to the study of the effects of climate warming on pelagic ecosystems.

INTRODUCTION

Global warming is considered to be one of the most important chronic factors driving future ecosystem changes. Aquatic ecosystems have a climate-buffering capacity due to their impact on the global carbon cycle (biological CO2-pump), and each disturbance may irretrievably change the functioning of the Earth ekosystem (Schiermeier 2006).

The temperature of ocean surface waters is predicted to increase by 1 to 6°C within the 21st century, depending on the climate scenario (IPCC 2007). As a consequence of this warming, the structure of Marine ecosystems is expected to change. Drastic changes in phytoplankton community structure provoke a chain reaction in marine food webs and might result in the removal of top predators or herbivores (Smetacek and Cloern 2008). However, marine ecosystems are also controlled by top-down processes. Warming might affect the abundance of top predators and herbivores and change grazing pressure. Strong top-down effects of marine fishes on zooplankton with warming have been shown by Mueter et al. (2009), but the relative strength of bottom-up and top-down control in the marine environment across all trophic levels needs to be better understood.

The spring phytoplankton bloom is one of the most important seasonal patterns in pelagic food webs, supplying energy to the higher trophic levels after winter (Townsend et al. 1994). Suspected shifts in the timing of spring blooms (Edwards and Richardson 2004) may cause a mismatch between food supply by phytoplankton and food demand by zooplankton according to the match-mismatch hypothesis (Cushing 1990), thereby disturbing the energy flow through the system.

In deep, well-stratified water bodies, seasonal warming and the seasonal onset of higher light availability are coupled triggers of the spring bloom, because thermal stratification increases the mean light exposure of phytoplankton cells circulating in the mixed water layer (Sverdrup 1953). In shallower, well-mixed water bodies or in systems where non-seasonal haloclines restrict mixing even in winter, the spring bloom can start before the onset of thermal stratification (Reynolds 2006, Sommer et al. 2007, Sommer and Lengfellner 2008). Under such conditions, seasonal phytoplankton growth can start at extremely low temperatures because light-limited photosynthesis is rather insensitive to temperature (Tilzer et al. 1986). However, trophic interactions should be strongly modified, because heterotrophic processes tend to be more sensitive to temperature (Rose

et al. 2009). Thus, we can suspect that warming without increasing light availability will lead to higher grazing rates by overwintering zooplankton that will not be balanced by a concomitant increase of primary productivity. An earlier onset of grazing might reduce the size of the phytoplankton community before light conditions permit the built-up of the phytoplankton spring bloom, thus leading to food shortage for zooplankton (Durant et al. 2005), particularly for the starvation-sensitive larval stages.

Although numerous experiments on the response of natural phytoplankton communities to light intensity or temperature changes have been published (Keller et al. 1999, Huisman et al. 2004, Elliott et al. 2006), tere are few studies where both factors are addressed with experiments (Berger et al. 2007, Sommer and Lengfellner 2008). Several field observations have shown that increasing temperature provoked changes in community structure and dynamics of the phytoplankton bloom (Winder and Schindler 2004, Thackeray et al. 2008, Nixon et al. 2009). A strong impact of light on the phytoplankton spring bloom was observed by Berger et al. (2007) in their *in situ* enclosure experiments of a freshwater ecosystem. They did not observe any temperature effect on phytoplankton biomass or bloom timing, although the abundance of mesozooplankton changed with warming. Our previous experiments (Sommer and Lengfellner 2008) with an indor mesocosm system with the natural plankton community from the Baltic Sea (mesozooplankton added from net catches at the same concentration as the present study, see 'Materials and methods') suggested a weak temperature effect on the timing of the phytoplankton spring bloom, but a strong temperature effect on phytoplankton biomass and composition. Three experiments performed in different years under different light regimes preliminarily suggested a strong light effect on timing, phytoplankton biomass and composition (Sommer and Lengfellner 2008); however, these studies were not a factorial combination of light and temperature within the same experiment and therefore not a rigorous test of the relative importance of light and temperature effects. Therefore, in the present study we utilized an experimental design of 2 temperature scenarios ($\Delta T = 0$ and 6°C) and 3 light regimes (32, 48 and 64% of sea surface irradiance) in a factorial combination to test the relative importance of climate warming and light availability on the phytoplankton spring bloom.

MATERIALS AND METHODS

Experimental design. Twelve mesocosms were deployed in 4 climate chambers where temperature could be programmed. Light could be regulated individually for each mesocosm. We tested 2 temperature and 3 light scenarios, resulting in 6 treatment combinations; each treatment was duplicated. Each mesocosm was 1400 l in volume and 1 m deep, with a gently moving propeller that mixed the water column. Mesocosms were filled with the natural winter plankton community containing algae, bacteria and protozoa from Kiel Bight, Baltic Sea. Mesozooplankton dominated by *Oithona* sp. was added from net catches at a natural concentration of ca. 10 ind. l^{-1} (Behrends 1996). Initial nutrient concentrations were 13.8 µmol l^{-1} nitrate, 0.9 µmol l^{-1} phosphate, 30.0 µmol l^{-1} silicate and 0.9 µmol l^{-1} ammonium. Such concentrations were high enough to preclude nutrient limitation until the biomass peak was reached.

The temperature program was derived from the decadal mean (1993 to 2002) of water surface temperatur es in Kiel Bight. We used 2 temperature regimes (Fig. 2-1): (1) baseline (i.e. 0°C elevation above the decadal mean, $\Delta T = 0°C$) and (2) +6°C above the baseline ($\Delta T = 6°C$), in agreement with the most drastic climate scenario presented by IPCC (2007).

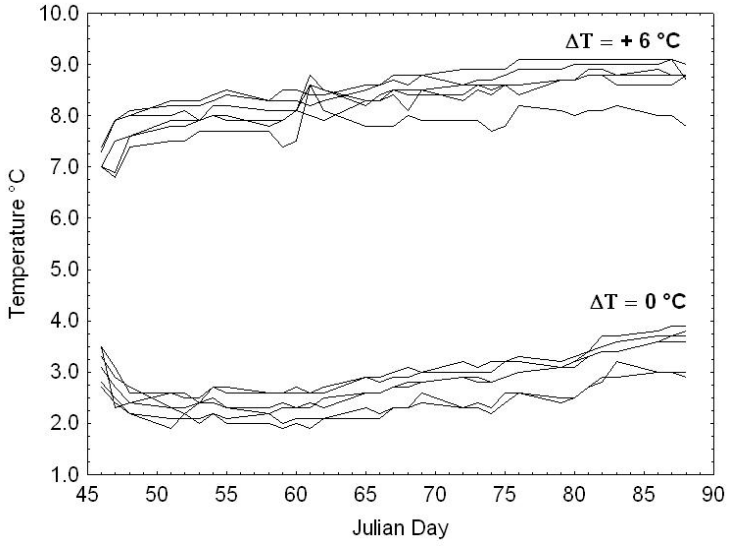


Figure 2-1. Temperature profiles for all 12 mesocosms. ΔT: elevation of temperature.

Light conditions mimicked daily irradiance curves and seasonal light patterns according to the astronomic model by Brock (1981). We reduced the natural irradiance to 32, 48 and 64% of sea surface irradiance (I_0) on cloudless days to test 3 light scenarios. The highest I_0 (64%) was based on a mixed water column mean light intensity during

cloudless days at 10 m mixing depth (depth of the halocline *in situ)* and a vertical attenuation coefficient (*k*) of 0.18 m^{-1}. The 32% I_0 corresponded to 50% light reduction by cloud cover or any combination of less clouds and a higher attenuation coefficient.

The light system was controlled by a computer program (GHL, Prometeus). The starting date for the light and the temperature programs was set at 15 February (day of year [DOY] 46).

Sampling and plankton estimation. Water temperature, fluorescence, pH and nutrient concentrations were measured every day to monitor the system. Samples for phytoplankton counts were taken 3 times per week from the mid depth of mesocosms and fixed with Lugol's iodine. Samples for flow cytometry and primary production measurements were taken at the same time and measured immediately. Mesozooplankton samples were taken weekly using a net (12 cm in diameter, 64 μm mesh size), fixed with Lugol's iodine and counted with a binocular microscope (Leica MS5).

Phytoplankton were counted using the inverted microscope method (Utermöhl 1958). For cells smaller than 5 μm, flow cytometry (FACScalibur, Becton Dickinson) was used. Flow cytometric phytoplankton categories were distinguished by size and pigment fluorescence (chlorophyll *a* and phycoerythrin). Cell volumes were calculated after approximation to geometric models (Hillebrand et al. 1999) and converted into carbon content as described by Menden-Deuer and Lessard (2000).

In order to provide a simplified image of phytoplankton composition, phytoplankton species were aggregated into functional groups (see Table 3): microdiatoms, nanodiatoms, bentho-pelagic diatoms, nanoflagellates, dinoflagellates and picoplankton. Microdiatoms were classified as species >20 μm, nanodiatoms were classified as species <20 μm and bentho-pelagic diatoms were distinguished separately. Nanoflagellates did not include dinoflagellates, which were grouped separately. Species <2 μm were classified as picoplankton.

Measurements of primary production. Primary production was measured by the ^{14}C incorporation metod after Gargas (1975). ^{14}C-bicarbonate with 4 μCi per 30 ml sample was used. Duplicate samples, as well as a blank (dark) sample, were incubated during 3 to 4 h inside the mesocosms at mid depth. Following incubation, samples were filtered through cellulosenitrate membrane filters (0.2 μm pore size). Filters were fumed with HCl and fixed with Lumagel scintillation cocktail. Radioactivity was measured by a liquid scintillation counter (Tricarb counter, Packard).

Statistical analyses. To test light and temperature effects, we used general regression models (best subsets, R^2) using STATISTICA 6 with temperature as the categorical factor and light as the continuous factor. If not stated otherwise, statistics were based on maximal phytoplankton biomass to exclude the effect of pseudoreplication by interdependent measurements over time.

Timing of the phytoplankton bloom was defined by cardinal points: beginning of the bloom (BB), the day when the community biomass was at a maximum (MB) and end of the bloom (EB). Species-specific biomass was transformed according to standard normal variation. BB and EB were the days corresponding to the first and third quartiles, respectively, of the maximal biomass.

We compared the taxonomic phytoplankton composition in the mesocosms by conducting analysis of similarities (ANOSIM) and multidimensional scaling (MDS) using PRIMER 5, based on the Bray-Curtis dissimilarity coefficient.

RESULTS

Time of the bloom

The phytoplankton bloom started about 1 wk earlier under warmer conditions (Table 2-1). We found a significant effect of warming on BB ($p < 0.001$, $r = 0.92$), MB ($p < 0.001$, $r = 0.79$) and EB ($p < 0.05$, $r = 0.81$). The MB at the lower temperature level ($\Delta T = 0°C$) was achieved at DOY 65 for 48 and 32% of I_0 and at DOY 62 for the highest light intensity (64% of I_0). In the warmer treatments ($\Delta T = 6°C$), MB was achieved at DOY 58, 60 and 62 depending on the light conditions ($p < 0.001$, $r = 0.79$ for interaction between temperature and light intensity, see also Table 2-1). The bloom duration was similar among all treatments and did not depend on temperature or light ($p > 0.05$, average duration time: 27 ± 2 d).

Phytoplankton growth and cell size

Growth dynamics of the phytoplankton in our experiment were typical for the spring bloom with an exponential increase, a short peak and decline of biomass until the clear water phase was achieved (Fig. 2-2, see also Reynolds 2006). Small species like picoplankton and nanoflagellates predominated at the beginning and the end of the experiment. During the bloom period there was a shift towards dominance by diatoms with smaller species at the beginning and a subsequent succession towards larger ones.

Table 2-1. Date of the spring phytoplankton bloom (day of year). ΔT: elevation of temperature; I_0: percentage of sea surface irradiance tested; BB: beginning of the bloom; MB: day of maximal biomass; EB: end of the bloom.

ΔT	I_0	BB	MB	EB
0°C	32%	58 58	65 65	83 83
	48%	53 55	65 65	81 83
	64%	58 55	62 62	86 81
6°C	32%	51 48	62 62	79 79
	48%	48 48	60 60	76 69
	64%	48 48	58 58	74 76

Primary production started to increase earlier in warmer conditions, but it did not achieve higher maximal values in warmer mesocosms than in the colder ones (Fig. 2-3). There was no significant difference in maximal primary production between the 2 temperature conditions ($p > 0.05$). However, the primary production/biomass ratio (P/B) was slightly higher under warmer conditions relative to colder conditions (warmer: $P/B = 0.28\ d^{-1} \pm 0.09$; colder: $P/B = 0.19\ d^{-1} \pm 0.05$; $p = 0.048$). We found that light had a positive, though insignificant ($p > 0.05$), effect on primary production during the bloom in the warmer mesocosms. After the bloom, primary production decreased rapidly in the warmer mesocosms, whereas a more gradual decline in the colder mesocosms was observed (Fig. 2-3). These changes in primary production corresponded to changes in microdiatom biomass (Fig. 2-4).

Table 2-2. Mean cell size (pg C $cell^{-1}$) of phytoplankton under the different light and temperature conditions. ΔT: elevation of temperature; I_0: percentage of sea surface irradiance tested. Values represent the mean size of phytoplankton cells for each mesocosm during the bloom time period.

	I_0		
ΔT	32%	48%	64%
0°C	35 41	34 46	38 38
6°C	21 25	7 23	27 41

At elevated temperatures (ΔT = 6°C), lower total biomass ($p < 0.001$, $r = –0.83$) and higher picophytoplankton biomass ($p < 0.001$, $r = 0.25$) were observed (Fig. 2-2), suggesting a shift to smaller cell sizes with warming. Indeed, the mean cell size was smaller under warmer conditions ($p = 0.01$, $r = 0.69$; Table 2-2).

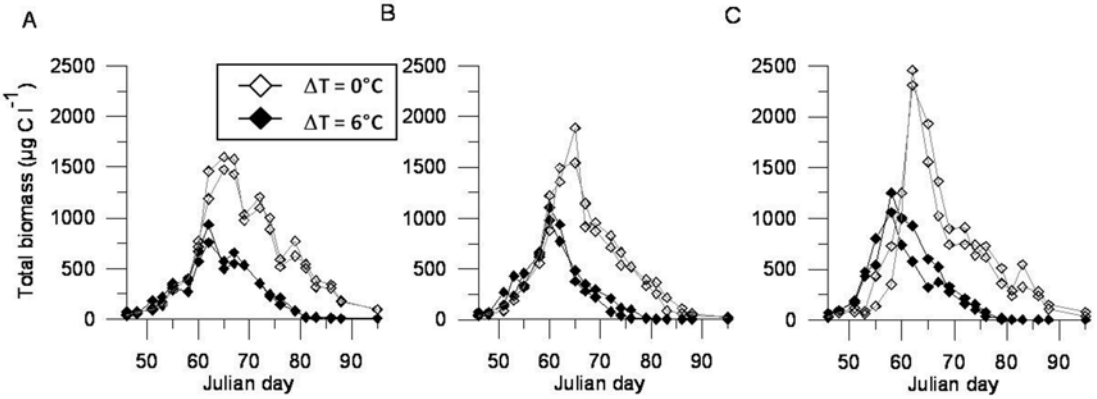


Figure 2-2. Total biomass of phytoplankton under the different light and temperature conditions. (A) 32% of sea surface irradiance (I_0); (B) 48% of I_0; (C) 64% of I_0. Open and filled symbols correspond to different temperature regimes (ΔT = 0 or 6ºC, respectively).

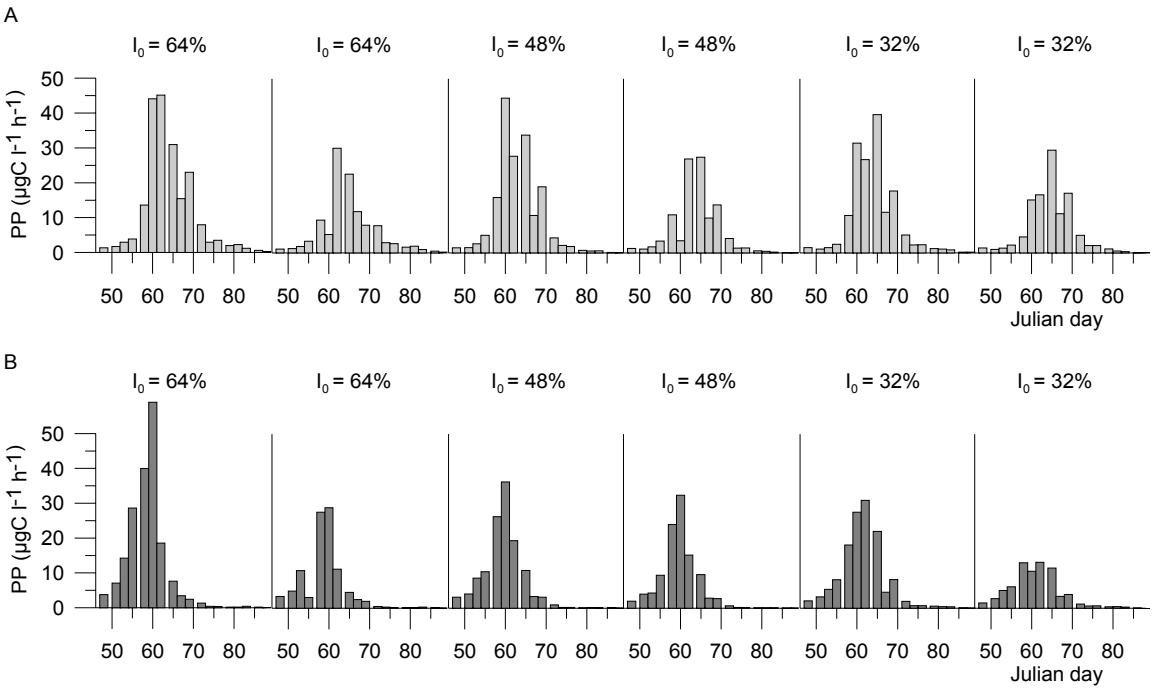


Figure 2-3. Primary production (PP) under (A) control conditions and (B) elevated temperature with different light scenarios (32, 48 and 64% of sea surface irradiance) in the 12 mesocosms.

Phytoplankton community structure

Twenty phytoplankton species were counted using inverted microscopy and flow cytometry. Additionally, the smallest fraction (picoplankton, <2 µm) was distinguished without species identification. Picophytoplankton were present in all treatments, but varied in abundance between colder and warmer mesocosms (Table 2-3). Phytoplankton biomass was dominated by diatoms. Diatoms differed in size (microdiatoms, >20 µm; nanodiatoms, 2 to 20 µm) and function (planktonic and bentho-pelagic diatoms, the latter were an indicator of algal growth on mesocosm walls).

Table 2-3. Functional groups of phytoplankton. m-diat: microdiatoms; n-diat: nanodiatoms; b-diat: benthic diatoms; n-flag: nanoflagellates; dino: dinoflagellates; pico: picoplankton. Rare species (only single cells) are marked with + and – for presence and absence, respectively.

phytoplankton groups	mean maximal abundance (cell ml^{-1} ± SD)		% of maximal total biomass (± SD)	
	ΔT = 0°C	ΔT = 6°C	ΔT = 0°C	ΔT = 6°C
m-diat				
Ceratulina pelagica	6 ± 4	+	+	no
Chaetoceros curvisetus	478 ± 199	60 ± 50	2 ± 1	+
Coscinodiscus sp.	+	+	+	+
Proboscia alata	57 ± 13	34 ± 10	+	1 ± 1
Pseudonitzschia sp.	2420 ± 733	3373 ± 1309	1 ± 0	2 ± 2
Rhizosolenia setigera	3 ± 1	6 ± 5	21 ± 2	20 ± 8
Thalassionema nitzschioides	225 ± 69	330 ± 34	1 ± 1	3 ± 2
Thalassiosira nordenskioeldi	74 ± 15	145 ± 74	1 ± 0	3 ± 2
Thalassiosira rotula	464 ± 170	17 ± 8	39 ± 6	3 ± 1
n-diat				
Chaetoceros minimum	4454 ± 1278	2889 ± 1107	2 ± 1	1 ± 1
*Skeletonema costatum**	32366 ± 4418	46877 ± 11911	19 ± 5	55 ± 8
b-diat				
Nitzschia acicularis	65 ± 48	77 ± 33	+	+
n-flag				
Dinobryon balticum	904 ± 199	84 ± 28	no	no
Rhodomonas sp.	244 ± 218	79 ± 41	3 ± 3	1 ± 1
Teleaulax amphioxeia	531 ± 111	592 ± 151	6 ± 4	4 ± 4
Tetraselmis sp.	3 ± 3	21 ± 14	no	no
dino				
Ceratium tripos	+	+	no	+
Gymnodinium ostenfeldi	21 ± 13	9 ± 2	+	+
Gyrodinium fusiforme	+	+	no	no
Heterocapsa rotundata	1662 ± 523	1837 ± 732	4 ± 2	3 ± 3
pico				
Picoplankton from flow cytometry counting (not identified)	45390 ± 10152	159960 ± 60116	+	4 ± 4

* undefined real chain length

The diatom *Skeletonema costatum* was the most abundant species under all conditions (Table 2-3). It played a major role in forming the bloom, achieving 55 ± 8% of maximal total biomass in the warmer mesocosms and 19 ± 5% of maximal total biomass in the colder mesocosms. In the cold mesocosms, *Thalassiosira rotula* and *Chaetoceros curvisetus* were also highly abundant species, as opposed to in the warmer mesocosms (Table 2-3). We counted 30 times more *T. rotula* and 10 times more *C. curvisetus* in colder mesocosms than in warmer mesocosms. In the colder treatments ($\Delta T = 0°C$), *T. rotula* (39 ± 6% of maximal total biomass) formed the bloom together with *S. costatum* and *Rhizosolenia setigera*, whereas under warmer conditions ($\Delta T = 6°C$) *T. rotula* played only marginal role in forming the bloom (3 ± 1% of maximal total biomass).

Bloom-forming species (*Skeletonema costatum*, *Rhizosolenia setigera*, *Thalassiosira rotula)* showed highly significant (*R. setigera* and *T. rotula*, $p < 0.001$; *S. costatum*, $p < 0.01$) responses to warming (Table 2-4). The biomass of other diatoms also varied significantly between the 2 temperature levels, except for the pinnate diatoms *Pseudonitzschia* sp., *Thalassionema nitzschioides* and the rare bentho-pelagic diatom *Nitzschia acicularis*, which did not show any effect. The most important (in terms of biomass) and most abundant dinoflagellates, *Gymnodinium ostenfeldi* and *Heterocapsa rotundata*, showed a significant response to warming as well as to changes in the light regime (Table 2-4). *Coscinodiscus* sp. showed a similar pattern, but it was a rare species. *Dinobryon balticum*, *Tetraselmis* sp. and *Gyrodinium fusiforme* were absent during the bloom time period and they were excluded from Table 2-4.

We calculated the percentage of total biomass for each functional group across the bloom period and found clear responses to warming (Table 2-3, Fig. 2-4). After the bloom, the proportion of diatoms declined rapidly in warmer conditions, whereas in colder tanks, this decrease was much slower (Fig. 2-4).

Table 2-4 (next page). Species-specific response to light intensity and temperature changes (general regression model, best subsets, R^2). See Table 2-3 for full species names. * $p < 0.05$; ** < 0.001.

	Coefficient	SE	*t*	*p*	df	R^2	*F*
C. pelagica							
light	4.516	4.086	1.11	0.30	2	0.58	6.2*
temperature	1.792	0.534	3.36	0.01			
C. curvisetus							
light	-53.891	204.126	-0.26	0.80	2	0.80	17.8**
temperature	159.065	26.667	5.96	< 0.001			
Coscinodiscus sp.							
light	0.141	0.056	2.53	0.03	2	0.87	30.2**
temperature	0.053	0.007	7.35	< 0.001			
P. alata							
light	17.078	7.711	2.21	0.05	2	0.84	30.2**
temperature	-1.672	1.007	-1.66	0.13			
Pseudonitzschia sp.							
light	-6050.781	2812.708	-2.15	0.06	2	0.46	3.8
temperature	-633.583	367.451	-1.72	0.12			
R. setigera							
light	19.844	19.356	1.03	0.33	2	0.84	30.2**
temperature	10.127	2.529	4.00	< 0.001			
T. nitzschioides							
light	-159.219	235.983	-0.67	0.52	2	0.11	0.6
temperature	-25.017	30.829	-0.81	0.44			
T. nordenskioeldi							
light	24.219	104.391	0.23	0.82	2	0.27	1.7
temperature	-24.667	13.638	-1.81	0.10			
T. rotula							
light	505.406	224.804	2.25	0.05	2	0.88	31.8**
temperature	224.590	29.368	7.65	< 0.001			
C. minimum							
light	-273.438	2938.728	-0.09	0.93	2	0.48	4.1
temperature	1105.333	383.914	2.88	0.02			
S. costatum							
light	31088.281	18607.006	1.67	0.13	2	0.67	9.3*
temperature	-9641.250	2430.809	-3.97	< 0.01			
N. acicularis							
light	17.813	30.271	0.59	0.57	2	0.04	0.2
temperature	-0.850	3.955	-0.21	0.83			
Rhodomonas sp.							
light	-653.906	293.489	-2.23	0.05	2	0.57	5.9*
temperature	99.867	38.341	2.60	0.03			
T. amphioxeia							
light	487.766	227.660	2.14	0.06	2	0.78	15.7*
temperature	153.987	29.741	5.18	< 0.01			
C. tripos							
light	0.078	0.035	2.22	0.05	2	0.48	4.1
temperature	-0.008	0.005	-1.81	0.10			
G. ostenfeldi							
light	19.063	5.592	3.41	0.01	2	0.82	20.6**
temperature	3.967	0.731	5.43	< 0.001			
H. rotundata							
light	2791.250	1007.949	2.77	0.02	2	0.65	8.2*
temperature	388.900	131.678	2.95	0.02			
Picoplankton							
light	72881.466	114894.982	0.63	0.54	2	0.35	2.5
temperature	-31936.328	15009.818	-2.13	0.06			

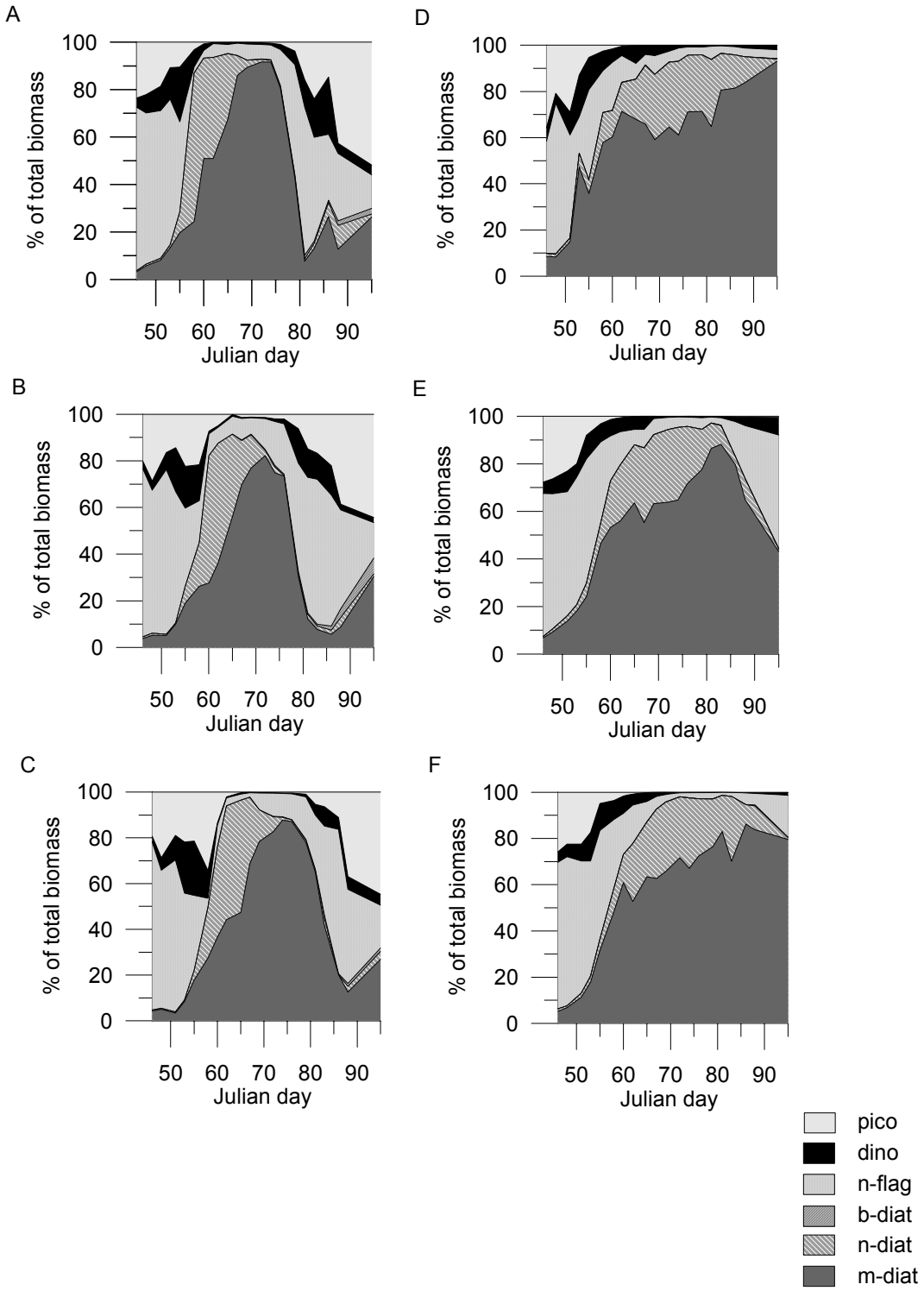


Figure 2-4. Relative phytoplankton biomass (% of total) for the different functional groups (mean of 2 replicates). (A) ΔT = 6ºC and 64% of I_0; (B) ΔT = 6ºC and 48% of I_0; (C) ΔT = 6ºC and 32% of I_0; (D) ΔT = 0ºC and 64% of I_0; (E) ΔT = 0ºC and 48% of I_0; (F) ΔT = 0ºC and 32% of I_0. m-diat: microdiatoms; n-diat: nanodiatoms; b-diat: benthic diatoms; n-flag: nanoflagellates; dino: dinoflagellates; pico: picoplankton.

Light versus temperature effects

The effect of light and temperature on the taxonomic composition of phytoplankton biomass was analyzed by calculating the dissimilarity (Bray-Curtis dissimilarity coefficient) between the different mesocosms and using a subsequent MDS plot. The MDS plot showed a clear separation of mesocosms according to the temperature regimes (462 permutations, global $R = 1$, $p = 0.002$), while the different light regimes did not lead to separation (Fig. 2-5).

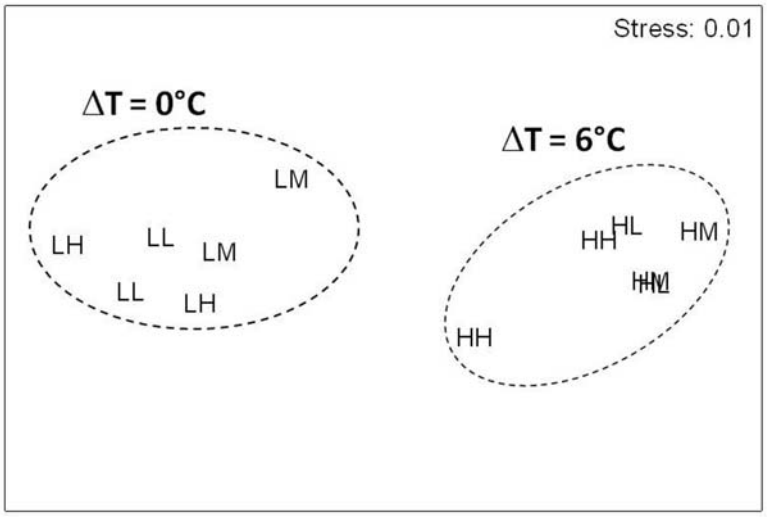


Figure 2-5. Multidimensional scaling plot of variation in assemblages of phytoplankton among treatments. HH: high temperature and highest light intensity (ΔT = 6ºC and 64% of I_0), HM: high temperature and middle light intensity (ΔT = 6ºC and 48% of I_0), HL: high temperature and the lowest light intensity (ΔT = 6°C and 32% of I_0), LH: low temperature and the highest light intensity (ΔT = 0°C and 64% of I_0), LM: low temperature and the middle light intensity (ΔT = 0°C and 48% of I_0), LL: low temperature and the lowest light intensity (ΔT = 0°C and 32% of I_0).

In order to test the potential impact of mesozooplankton grazing on the phytoplankton community, we compared species-specific abundance of copepods at the beginning and end of the experiment. ANOSIM based on the Bray-Curtis dissimilarity coefficient showed no separation at the beginning of the experiment (462 permutations, global $R = 0.232$, $p = 0.091$; Fig. 2-6A) and clear separation according to temperature regime at the end of the experiment (462 permutations, global $R = 1$, $p = 0.02$; Fig. 2-6B).

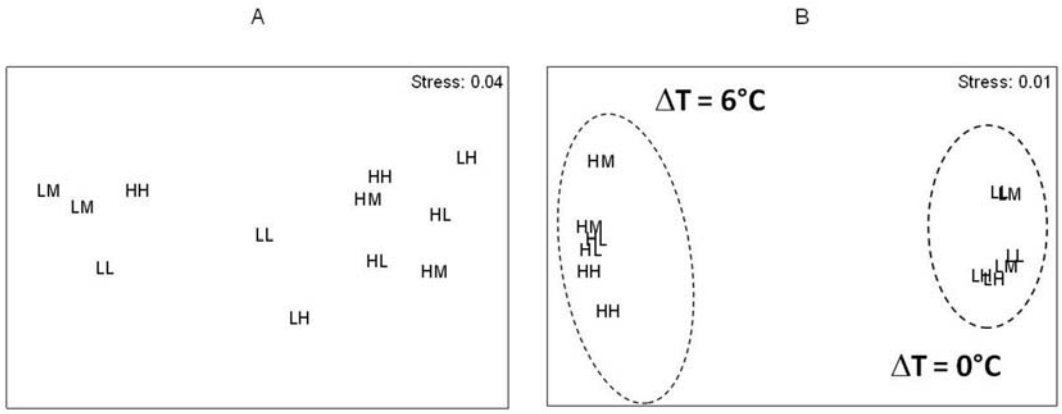


Figure 2-6. Multidimensional scaling plot of variation in assemblages of zooplankton among treatments at (A) the beginning and (B) the end of the experiment. See Fig. 2-5 for temperature – light intensity abbreviations.

DISCUSSION

Direct and indirect effects of temperature and light intensity on phytoplankton

It has been frequently reported that warming should lead to an earlier phytoplankton spring bloom. In most cases, an earlier ice break or an earlier stabilization of the water column was connected with an earlier spring bloom (Edwards and Richardson 2004, Elliott et al. 2006, Hashioka and Yamanaka 2007). These findings suggest that the potentially accelerating factors of both temperature and light could be responsible for the earlier spring bloom.

Monitoring data from the coastal shallow waters of the western Baltic Sea have indicated a shift of the spring phytoplankton bloom of 1 to 2 wk earlier after warm winters (Göbel et al. 2009), which is in agreement with our findings. In contrast, Wiltshire and Manly (2004) reported a retardation of the spring bloom by warming for the shallow German Bight of the North Sea. A later analysis with more years added to the time series found strong interannual variability but no trend related to warming (Wiltshire et al. 2008).

Other authors have suggested that temperature has little direct effect on algal growth, whereas light limitation could be more important as the decisive factor for photosynthesis (Sommer et al. 1986, Moore et al. 1995, Sommer and Lengfellner 2008). A previous study using the same mesocosm system and natural Baltic Sea plankton as inoculums suggests that light should have a stronger effect than the temperature on the

timing of the spring bloom (Sommer and Lengfellner 2008). However, this study did not utilize a factorial combination of the factors light and temperature. Sommer and Lengfellner (2008) performed 3 experiments with 4 temperature levels each, but were able to test only one light level during each experiment. Given the usual interannual differences in natural plankton communities, this means that the factors light and inoculum (phytoplankton and zooplankton) were potentially confounded. Therefore, the parallel responses to temperature found between the different experiments were considered robust, but the conclusions related to light were only tentative.

In the present study, with a factorial combination of light and temperature within the same experiment, phytoplankton community responses to light limitation were related to temperature conditions. Light had a stronger impact on the timing of the phytoplankton maximum in the warmer mesocosms (Table 2-1). Surprisingly, however, we observed only a weak response of phytoplankton to the different light conditions in our experiment. Moreover, most of the phytoplankton species, especially bloom-forming *Skeletonema costatum*, *Rhizosolenia setigera* and *Thalassiosira rotula*, were rather insensitive to the different light treatments (Table 2-4). Admittedly, the range of the irradiance we tested was rather narrow (32 to 64% of I_0), but a ratio of >2:1 between the highest and the lowest light treatment is already quite broad, if we consider interannual differences at the time scale of bloom formation. However, on a day-to-day time scale, much bigger maximum to minimum ratios can be expected.

ANOSIM showed a very clear separation of phytoplankton community composition according to temperature, but no separation according to light (Fig. 2-5). We hypothesize that grazing could have had a stronger impact on phytoplankton community composition than light limitation. For mesozooplankton, we found little change in total abundance of copepods (8 ± 2 ind. l^{-1} at the beginning of our experiment, 7 ± 2 ind. l^{-1} at the end), but remarkable changes in species composition related to warming (Fig. 2-6). Typical overwintering species like *Oithona* sp. and *Pseudocalanus* sp. were replaced in warmer mesocosms by active grazers like *Temora* sp., *Centropages* sp. and *Acartia* sp. (data not shown), which are typically found later in the season in Kiel Bight (Behrends 1996). Because all prominent species in our experiment feed on the same phytoplankton size spectrum (>500 to 1000 μm^3 colony volume, Sommer and Sommer 2006), potentially enhanced grazing rates with warming might lead to a reduction of the preferred

phytoplankton species. A very strong temperature dependence of various activity parameters of Kiel Bight winter zooplankton has been shown by Isla et al. (2008).

Zooplankton food demand and grazing rates respond directly to temperature changes (Schalau et al. 2008). Both the lower total phytoplankton biomass and the shift towards smaller sizes at higher temperature can be interpreted as footprints of more intensive grazing by copepods and ciliates in the warmer mesocosms (Keller et al. 1999). Similarly, the more rapid decrease of biomass at the end of the bloom in warmer tanks could be also caused by a grazing effect (daily phytoplankton biomass decrease: -0.32 ± 0.07 d^{-1} at $\Delta T = 0°C$ and -0.42 ± 0.01 d^{-1} at $\Delta T = 6°C$). This decline was particularly apparent for diatoms, which are the preferred food for herbivorous mesozooplankton (Sommer et al. 1986, Granéli and Turner 2002), but also for winter and early spring ciliates (Aberle et al. 2007). In contrast, there is a feeding preference for nanophytoplankton by summer ciliates (Sommer et al. 2005). We cannot rule out the feeding competition between ciliates and copepods in our experiment. However, higher abundance of picoplankton in warmer mesocosms might suggest that ciliates reduced the abundance of heterotrophic nanoflagellates and thus their feeding impact on picoplankton and bacteria.

Considering only the abiotic factors acting on phytoplankton, one would have hypothesized that the phytoplankton spring succession should be less dependent on temperature than light intensity, because of the relative insensitivity of light-limited production to temperature (Tilzer et al. 1986). However, the comprehensive analysis of phytoplankton species composition showed that the majority of the species present in the community was responsive to temperature changes. The effects of temperature on biomass, size structure and species composition are consistent with the assumption of an indirect temperature effect, acting via enhanced grazing. Enhanced zooplankton grazing at higher temperatures appeared to reverse the importance hierarchy of the factors light and temperature. While it is obvious that the stepwise and prominent light increase at the onset of stratification plays the dominant role in the initiation of the spring bloom in deep waters (Thackeray et al. 2008), the light differences used in our experiment did not play as big a role as was previously suspected (Sommer and Lengfellner 2008).

Changes in phytoplankton community structure and their implication to higher trophic levels

The spring phytoplankton bloom in Kiel Bay, Baltic Sea, is usually dominated by diatoms, in many years exemplified by a high abundance of *Skeletonema costatum* (Tilstone et al. 2000). The same community composition was observed in our experiment, where *S. costatum* was the most abundant species in all treatments and played a major role in forming the phytoplankton bloom in all mesocosms (Table 2-3). In an analysis of a long-term data set of the phytoplankton community in Kiel Bight, Wasmund et al. (2008) presented changes in phytoplankton biomass and species composition similar to those we observed in our mesocosm experiment. Thus, the community structure in the present study was typical and representative of the spring phytoplankton bloom in this region of the Baltic Sea.

Diatom blooms are usually composed of a few co-dominant species (Smayda and Reynolds 2003), as was found in the present study. We found conspicuous, temperature related changes in phytoplankton composition affecting both rare and dominant species like *Thalassiosira rotula* and *Chaetoceros curvisetus* (Table 2-3). The abundance of these species was strongly reduced in the warmer mesocosms, and there was a concomitant decrease in the number of co-dominant species forming the bloom.

Some authors hypothesize a shift to smaller species with an increase in temperature (Hashioka and Yamanaka 2007). In the present study, we also observed higher biomass of picophytoplankton (Table 2-3) and smaller mean cell sizes in warmer conditions (Table 2-2). As mentioned above, the shift to smaller cell sizes with warming might be caused by enhanced grazing on larger phytoplankton species. On the other hand, physiological and metabolic changes related to warming are also possible and might change the outcome of coexistence and competition between different phytoplankton species (Brown et al. 2004).

The observed changes in phytoplankton species composition and the shift to smaller cell sizes with warming could have important consequences for the pelagic food web. Phytoplankton species that are impacted negatively by climate change are reduced, thus permitting increases for other, better adapted organisms. The result of such species shifts is a change in the quality of food available for higher trophic levels, as picophytoplankton and small nanophytoplankton (<500 μm^3 cell volume) species are inedible for copepods (Sommer and Sommer 2006). In such a case, the path of carbon

flow between primary producers and mesozooplankton may become longer through heterotrophic flagellates and ciliates, which can reduce productivity of higher trophic levels, as described by Berglund et al. (2007).

The changes in phytoplankton community structure were mostly caused by temperature. Results of the present study indicate that indirect temperature effects, e.g. enhanced grazing pressure with warming, might strongly modify the size range and composition of the phytoplankton community. Understanding the interactions between direct and indirect effects of warming and the relationships between different species might be essential to predict the consequences of climate change.

ACKNOWLEDGEMENTS

This project was founded by the priority program 1162 “AQUASHIFT” of the Geman Research Fundation (DFG). The authors thank T. Hansen and H. Tomanetz for technical support. C. Meyer and S. Büddicker are acknowledged for help by the sampling and A. Biermann for nutrient data. A. Lewandowska thanks also K. Lengfellner and P. Breithaupt for introduction to the practical work. Jeremy Testa is acknowledged for comments and improving the language.

CHAPTER 3

Temperature induced changes of mesozooplankton affect phytoplankton community structure

ABSTRACT

In order to analyse the combined effects of climate warming and grazing by mesozooplankton on phytoplankton diversity (expressed by richness and evenness), we analysed the results from four mesocosm experiments with Baltic Sea late winter plankton. All experiments contained warming and control treatments, in one of the experiments the factor warming was crossed with the factor grazer density, in one other experiment it was crossed with factor light. We show that warming might lead to a shift in mesozooplankton community composition, which in turn affects phytoplankton diversity. However, the shift in mesozooplankton species composition occurred only in one of the experiments. In general in our study phytoplankton richness and evenness both increased with increasing copepod biomass. The effects of copepods on phytoplankton diversity, however, differed between copepod species. The biomass of *Acartia* sp., *Oithona* sp., and *Temora* sp. increased phytoplankton richness and *Pseudocalanus* sp. and *Centropages* sp. had no significant effect. The positive effect of copepods on phytoplankton evenness was strongly driven by *Pseudocalanus* sp. and *Centropages* sp. biomass and slightly reduced by the biomass of *Temora* sp.. Our study implies that effects on phytoplankton diversity depend on consumer biomass and identity. Thus temperature induced changes in copepod community composition might affect phytoplankton diversity and in turn change the whole food web dynamic.

INTRODUCTION

The first generation of studies on climate change ecology focused on single trophic levels with a predominance of primary producers. More recently, a number of experimental and field studies were performed to examine the impact of increased temperature on trophic cascades and ecosystem functioning (Petchey et al. 1999, McKee et al. 2002, Finke and Denno 2005). Most of the studies predict a shift in community composition (Finke and Denno 2005) and changes in ecosystem productivity and biodiversity with warming (Petchey et al. 1999, McKee et al. 2002), but it is still poorly understood, how the consumer-producer interactions will be affected.

Some authors suggest that the strength of top-down effects in aquatic ecosystems might increase relative to bottom-up control in the future, because warming is suspected to cause an increase of heterotrophic activity (Wiltshire et al. 2008, Barton et al. 2009). In accordance with these predictions O'Connor et al. (2009) found an increasing grazing pressure of mesozooplankton in mesocosms with elevated temperature. The indirect effects of warming via enhanced grazing activity on biomass or phenology of primary producers were reported (Wiltshire et al. 2008, O'Connor et al. 2009, Sommer et al. 2010), however species specific impact of consumers on producers diversity received less attention.

Mesozooplankton grazing might not only reduce the total biomass of primary producers, but also reorganize their community structure with possible secondary impacts on the ecosystem stability (Griffin et al. 2009). Primary producer community structure in turn might determine the strength of top-down and bottom-up effects, because consumers might strongly control edible producers (top-down effect), whereas nutrient limitation more affects inedible plants (bottom-up effect, Thebault and Loreau 2003). Herbivores are suspected to reduce the dominance effect of primary producers in marine ecosystems and tend to reduce a number of species (Hillebrand et al. 2007). This response, however, is strongly related to the producers' community composition and depends on their edibility or inedibility, initial species dominance and environmental factors other than grazing (e. g. nutrient availability).

In this study, we link the zooplankton taxonomic composition with the response of phytoplankton diversity to warming, particularly number of species (richness) and evenness (an opposite of dominance). We hypothesize that 1) temperature increase alters mesozooplankton species composition by promoting omnivorous species with a strong

tendency towards herbivory, which is suggested by field data for the Baltic Sea (Möllmann et al. 2008) and previous analysis of mesocosms (Lewandowska and Sommer 2010), 2) mesozooplankton species composition affects phytoplankton community structure (richness and evenness) in marine environments. To test our hypotheses we performed mesocosm experiments with natural late winter plankton from the Baltic Sea. The copepods dominating Baltic Sea mesozooplankton early in the year (*Acartia* sp., *Centropages* sp., *Oithona* sp., *Pseudocalanus* sp., *Temora* sp.) are omnivores able to feed both on ciliates and diatoms, thus being able to switch between two adjacent trophic levels (Stibor et al. 2004). In previous analyses of the experiments conducted in our mesocosm system, copepods were treated as an aggregate, assuming that because of their behavioural flexibility in the feeding mode, all species would have roughly the same biomass effect on phytoplankton and heterotrophic protists (Sommer and Lewandowska 2010). This tacitly implies that switching between suspension feeding (the more herbivorous feeding mode) and raptorial feeding (the more carnivorous feeding mode, Tiselius and Jonsson 1990) would more depend on food conditions than on intrinsic species properties. In this study, however, we show that different copepods have different effects on phytoplankton diversity and that a shift in copepods species composition with warming reorganizes phytoplankton community, which in turn can lead to changes in food web dynamic.

METHODS

Experimental setup and laboratory techniques. Eight (experiments 2006 and 2007) or twelve (experiments 2008 and 2009) mesocosms (1400 L volume, 1 m depth) were set up in temperature regulated climate rooms. Mesocosms were filled with the natural late winter plankton community (containing phytoplankton, bacteria and protozoa) from the Kiel Fjord, Baltic Sea. Mesozooplankton was added from net catches at appropriate concentrations for each experiment (Tab.3-1). Temperature and light conditions simulated natural daily and seasonal patterns. There were two temperature scenarios (replicated twice) tested in the experiment 2008 and 2009: a baseline corresponding to the decadal mean (1993-2002) of sea surface temperature in Kiel Fjord starting from 15th February ($\Delta T = 0°C$) and a warming scenario where the temperature was elevated 6°C above the baseline ($\Delta T = 6°C$) according to the most drastic warming scenario predicted by the Intergovernmental Panel on Climate Change (IPCC 2007). In

the experiments 2006 and 2007 four temperature regimes: ΔT = 0ºC, ΔT = 2ºC, ΔT = 4ºC and ΔT = 6ºC were tested.

Table 3-1. Experimental design of mesocosm experiments. Tested temperature (ΔT), light (% I_0) regimes and initial copepod densities (ICD).

Experiment	ΔT (°C)	% I0	ICD (ind.L^{-1})	Bloom forming species (%phytoplankton biomass)	References
2009	0, 6	48	1.5, 4, 10	diatoms (93 ± 6% SD)	Sommer & Lewandowska, 2010
2008	0, 6	32, 48, 64	8	diatoms (97 ± 6% SD)	Lewandowska & Sommer, 2010
2007	0, 2, 4, 6	32	4.5	*Dictyocha* (42 ± 38% SD)	Sommer & Lengfellner, 2008
2006	0, 2, 4, 6	64	8.5	diatoms (95 ± 2% SD)	

Phytoplankton was sampled three times per week and counted using the inverted microscope (Utermöhl 1958) and flow cytometry techniques (FACScalibur, Becton Dickinson, Sommer and Lengfellner 2008)). Phytoplankton biomass was defined as carbon content calculated from cell volumes (Menden-Deuer and Lessard 2000) after approximation of cell volumes to geometric standards (Hillebrand et al. 1999). Zooplankton was sampled once a week with a net (12 cm diameter, 64 µm mesh size), fixed with Lugol´s iodine and counted with a binocular microscope. Copepods were specified to the genus level, *Temora* sp. and accidental *Eurytemora* sp., similarly *Pseudocalanus* sp. and rare *Paracalanus* sp. were paired together, because their early copepodid stages are difficult to distinguish. Copepod biomass was estimated as a carbon content using species and stage specific conversion factors (Lengfellner 2008).

Diversity parameters and statistics. The impact of warming on copepod biomass at the sampling date closest to the maximum phytoplankton bloom was calculated using General Linear Model (best subsets, R^2) for the experiments 2009 and 2008 with temperature as a categorical factor and initial copepod density (experiment 2009) or light intensity (experiment 2008) as continuous predictors. For the experiments 2007 and 2006 simple regression analyses were used, because temperature with four treatments was the only factor tested during both experiments. All statistics were made using Statistica 6.0.

Phytoplankton richness (S) was calculated as the total number of species, phytoplankton evenness (J) was calculated according to the equation:

$$J = \frac{H'}{\ln S}$$

where H´ is the Shannon diversity index (Shannon and Weaver 1949), which we based on biomass proportions and S is the phytoplankton richness.

To test effects of warming on phytoplankton diversity (richness and evenness) in the experiments 2008 and 2009 we used General Linear Models (best subsets, R^2) in Statistica 6.0 with temperature as categorical factor and light (experiment 2008) or initial copepod density (experiment 2009) as continuous factors. Simple regression (best subsets, R^2) with temperature as independent variable was used to analyse phytoplankton diversity response in experiments 2006 and 2007.

To calculate the effect size of copepod biomass on phytoplankton richness and evenness at the time of the phytoplankton biomass maximum for each experiment we used Fisher z-transformed correlation coefficients. To test the impact of copepods on phytoplankton diversity across all studies, we calculated an overall effect size, whereby effect sizes for each experiment were weighted by the inverse of variance. 95% confidence intervals were used to test for significant differences from zero. This same procedure was repeated for biomass and relative biomass of each copepod genus separately.

RESULTS

Zooplankton response to warming

Temperature did not affect the total biomass of adult copepods and copepodites at the sampling date closest to the phytoplankton biomass maximum ($P > 0.05$ for the experiments 2007 – 2009, see also Appendix Table A3) except for a decrease of copepod biomass with warming reported for the experiment 2006 (*regression analysis*, $b = -2.25$, $N = 8$, $r^2 = 0.54$, $P = 0.04$) . The copepod composition varied between the experimental years (Fig.1). Warming led to a faster zooplankton development and had a positive impact on the total biomass of nauplii in the experiment 2009 (GLM, $F = 14.02$, $r^2 = 0.76$, $P = 0.002$), whereas no response to temperature was observed in the experiments 2006 – 2008 ($P > 0.05$ for each study). Total microzooplankton biomass was not affected by temperature except for a slight decrease with warming reported for the experiment 2007 (N. Aberle, unpublished data).

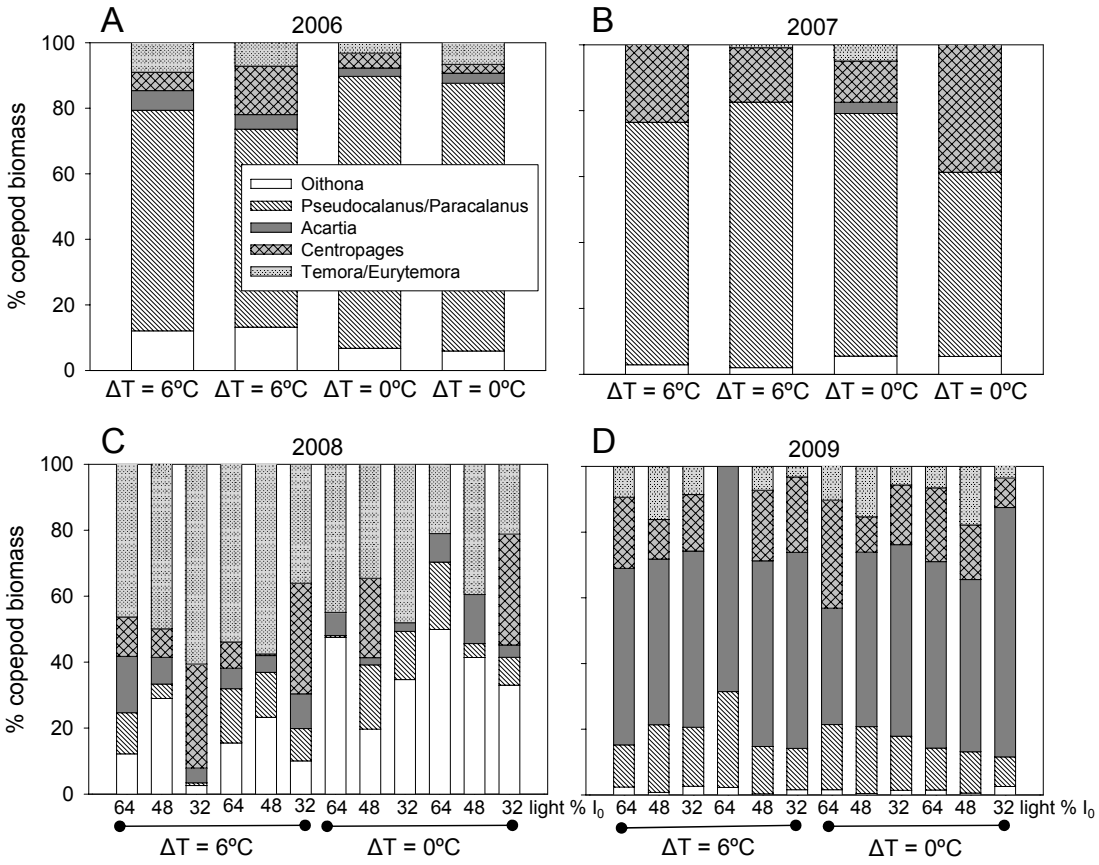


Figure 3-1. Relative biomass of copepods in the experiments: 2006 (A), 2007 (B), 2008 (C), 2009 (D) closest to the maximal phytoplankton biomass.

During the experiment 2008 we observed a shift in the copepod composition from a dominance of *Oithona* sp. to a dominance of *Temora* sp. and *Centropages* sp. in the warmer treatments (Fig.3-2A, see also Appendix Figure A2 for more details). No compositional shift was noticed under ambient temperatures (Fig.3-2B). There was also a slight change in copepod community composition during the experiment 2007 at ΔT = 6ºC. However, this change from a dominance of *Pseudocalanus* sp. and *Oithona* sp. to a dominance of *Centropages* sp. took place only after the phytoplankton bloom (Lengfellner 2008). As a contrast we could not find a similar response to warming during the experiment 2009, where the copepod community was dominated by *Acartia* sp. (57 % ± 13 SD mean total copepod biomass) during the whole experimental period, neither during the experiment 2006, where the copepod community was dominated by *Pseudocalanus* sp..

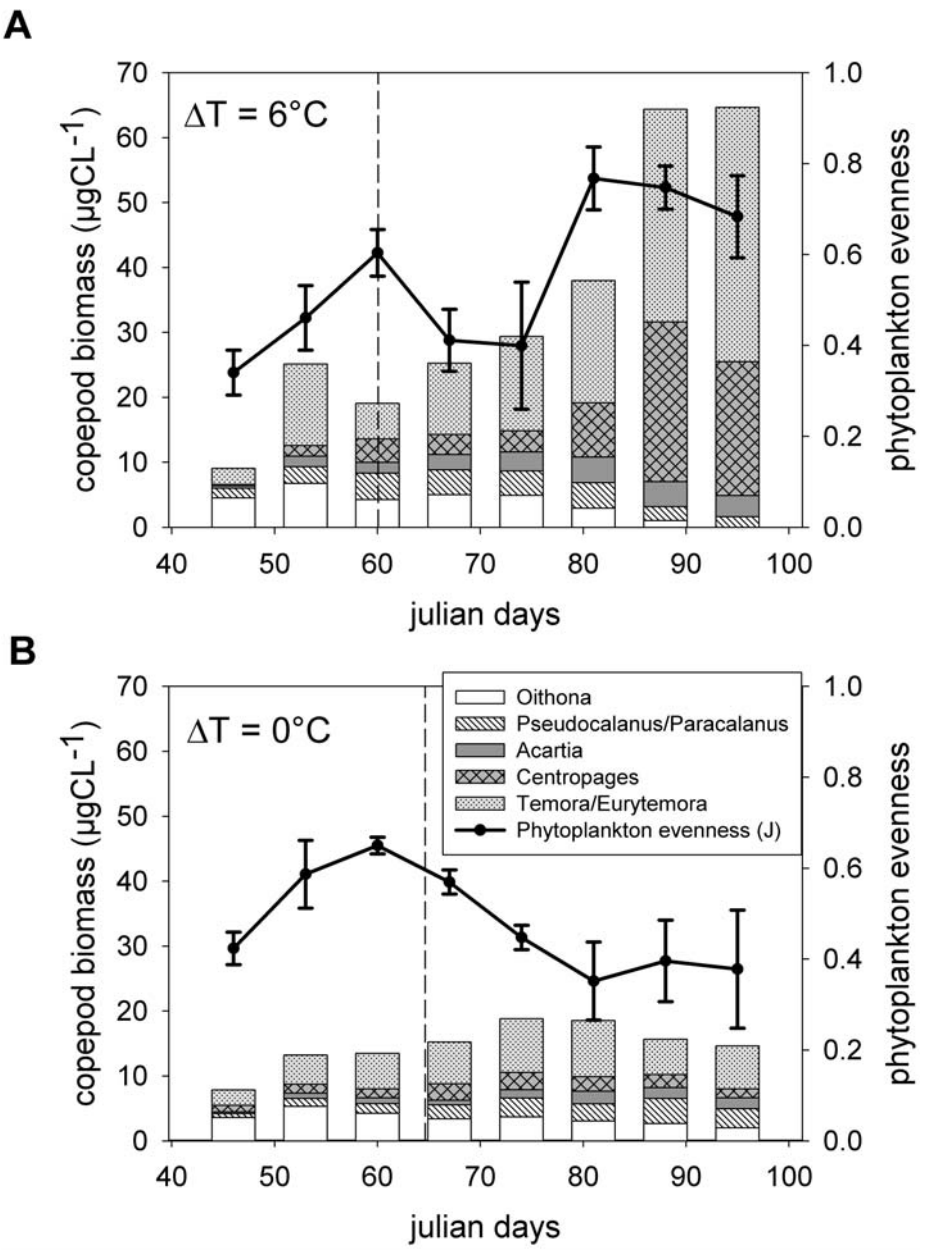


Figure 3-2. Genus specific copepod biomass and the time course of phytoplankton evenness in the experiment 2008. Means of 6 replicates for the warming scenario (A) and ambient temperature (B). Vertical dashed line represent the time of maximal phytoplankton biomass.

There were notable differences in the initial copepod community composition between the experiments. Copepods in the experiments 2006 and 2007 were dominated by *Pseudocalanus* sp. and *Oithona* sp.. In the experiment 2008 we observed an initial dominance of *Oihona* sp., whereas in the experiment 2009 the copepods were dominated by *Acartia* sp..

Phytoplankton dominance and species richness

The response of phytoplankton species richness to warming varied between the studies. A positive response of richness to warming was observed in the experiment 2009 (GLM, F = 16.05, df = 2, $P = 0.001$, $r^2 = 0.78$), while phytoplankton richness responded negatively to warming in the experiment 2008 (GLM, F = 4.50, df = 2, $P = 0.044$, $r^2 = 0.50$), though a previous analysis (experiments 2006 and 2007) showed a negative response (Lengfellner 2008). Relationships between phytoplankton richness and evenness were divergent as well. Richness was positively correlated with evenness in the experiment 2009 ($r = 0.84$, N = 12, $r^2 = 0.70$, $P < 0.001$), but negatively in the experiment 2007 ($r = -0.78$, N = 8, $r^2 = 0.61$, $P = 0.021$) whereas experiments 2006 and 2008 showed no response ($P > 0.05$).

Phytoplankton evenness at the bloom maximum responded positively to temperature and initial copepod density in the 2009 experiment (GLM for the experiment 2009, F = 6.60, df = 2, $P = 0.017$, $r^2 = 0.59$). No significant response to temperature and light intensity was observed at the bloom maximum in the experiment 2008 (GLM, $P > 0.05$). Phytoplankton evenness slightly increased with warming during the experiment 2007 at the point of maximal phytoplankton biomass (*regression analysis*, $b = 0.05$, N = 8, $r^2 = 0.53$, $P = 0.04$) and showed no response during the experiment 2006 (*regression analysis*, $P > 0.05$).

The initial phytoplankton evenness in the experiment 2009 was already very high (0.82 ± 0.03 SD) and remained at this high level during the whole experimental period. A drastic response of the phytoplankton evenness to the temperature changes was observed in the experiment 2008 during the post bloom phase. Phytoplankton evenness increased rapidly after the bloom under enhanced temperature and decreased under ambient conditions (Fig.3-2, see also Appendix Figure A2). Phytoplankton evenness decreased gradually after the bloom in the experiment 2007 over all temperature treatments and increased in the experiment 2006 (Lengfellner 2008).

Linking copepod community composition and phytoplankton diversity

Total copepod biomass had a positive, however not significant, effect on phytoplankton richness when tested across all experiments (overall effect on richness ± 95% confidence interval: 0.35 ± 0.61). The effect size of different copepod species on phytoplankton richness varied however. The biomass of *Temora* sp., *Acartia* sp. and

Oithona sp. had a significantly positive impact on phytoplankton richness. The positive effect was found both when absolute and when relative biomass of these species was used as independent variable. The biomass of *Centropages* sp. and *Pseudocalanus* sp. did not show any significant response and their relative biomass had rather a negative effect on phytoplankton richness (Fig. 3-3A).

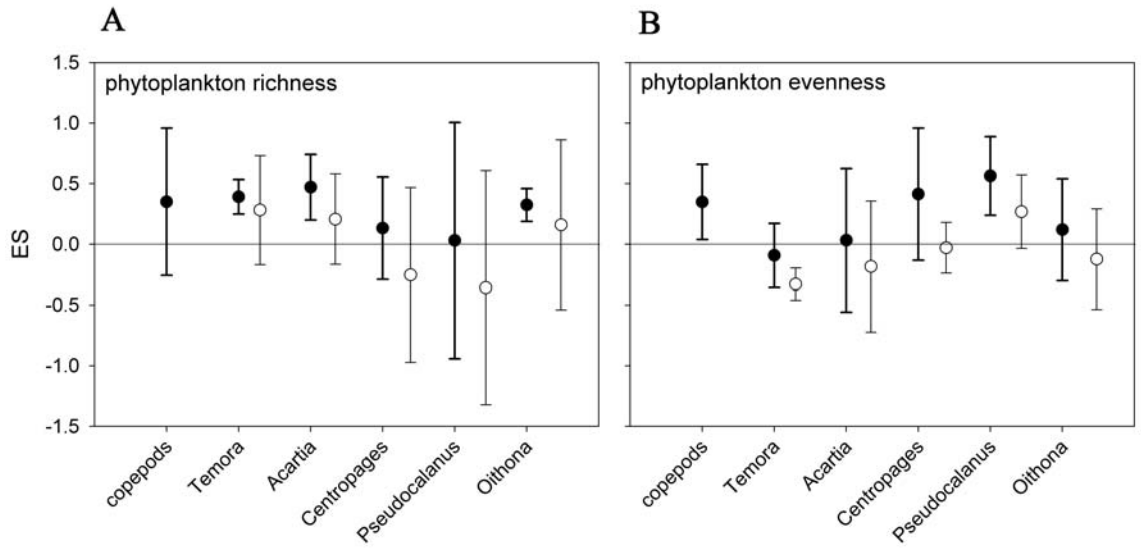


Figure 3-3. Effect sizes ± 95% confidence intervals of the copepod biomass (black circles) and the relative copepod biomass (open circles) on the phytoplankton species richness (A) and evenness (B) closest to the phytoplankton biomass peak.

We observed a significant positive effect of total copepod biomass on phytoplankton evenness (overall effect on evenness ± 95% confidence interval: 0.35 ± 0.31), which seems to be driven mostly by the biomass of *Pseudocalanus* sp. as it was the only species showing significantly positive effect on phytoplankton evenness. As a contrast the relative biomass of *Temora* sp. negatively affected phytoplankton evenness (Fig. 3-3B).

DISCUSSION

We observed a shift in copepods species composition under elevated temperature in the experiment 2008 (Fig.3-2A). However, the causes of the reported shift are not clear and no response of copepods composition to warming at the phytoplankton biomass maximum was found in the experiment 2009 or previous studies (Sommer and Lengfellner 2008). One possible explanation of the observed shift might be availability of ciliates as preferred food for the dominant *Oithona* sp. (Lonsdale et al. 2000). If the

mesozooplankton grazing activity increased with warming, as it has been noticed in other studies (Isla et al. 2008, O'Connor et al. 2009), *Oithona* sp. would reduce the abundance of ciliates very fast under elevated temperature and slower under ambient conditions. Preliminary analysis of protozoa in the experiment 2008 confirm the rapid decline of ciliates in the warm treatments (N. Aberle, unpublished data). The lack of ciliates might promote more herbivorous species like *Temora* sp., which would benefit from the higher diatoms to ciliates ratio and dominate the mesozooplankton community under elevated temperature.

Temora sp. and *Centropages* sp. are usually regarded as summer species in the Baltic Sea (Möllmann et al. 2000) while our experiments were conducted during the winter-spring transition. Thus another explanation of the mesozooplankton community shift with warming in the experiment 2008 might be a higher temperature optimum for *Temora* sp. and *Centropages* sp. than for the typical overwintering species in the Baltic Sea like *Oithona* sp. and *Pseudocalanus* sp. Similar phenological shifts in the zooplankton species composition were already reported for the North Sea and the Baltic Sea (Alheit et al. 2005). However, a shift in mesozooplankton community composition with warming was not observed in the experiments 2006, 2007 and 2009 except for an increased number of *Centropages* sp. reported at the end of the experiment 2007 in the warmest treatments (ΔT = 6ºC, Lengfellner 2008, Sommer and Lengfellner 2008) suggesting that availability of the preferred food might be a major factor affecting the mesozooplankton community composition and dominance structure.

The effects of herbivores on autotroph diversity depend on their relative effects on dominant and subdominant species (Hillebrand et al. 2007). Copepods might feed on numerous coexisting phytoplankton species thereby reducing their number. Thus, the abundance of rare species might fall below the detection limit and reduce apparent richness. Such a mechanism was observed in the experiments 2006 – 2008, where warming, linked with enhanced grazing activity of copepods, decreased phytoplankton richness. However, if copepods feed on the dominant phytoplankton species, they might have a positive effect on phytoplankton richness, because their impact on the dominant competitor is disproportionately greater and species below the limit of detectability might be released from competition and become detectable. We assume, that the positive effect of *Acartia* sp. on apparent richness might be explained this way. A positive impact of warming and enhanced copepod density on phytoplankton richness was observed in the

experiment 2009, in which *Acartia* sp. strongly dominated mesozooplankton community at the peak time and over whole experimental period. Copepods like *Oithona* sp., which prefer feeding on ciliates (Lonsdale 2000), have only a weak direct impact on phytoplankton richness because they foremost actively reduce ciliate abundance. They can, however, have an indirect positive effect on phytoplankton richness by preventing phytoplankton species from ciliate induced exclusion.

A positive response of phytoplankton evenness to increasing copepod biomass observed in our study (Fig. 3-3B) occurs if the dominant phytoplankton species belongs to feeding spectrum of copepods. In such a case the copepods feed mostly on the dominant phytoplankton species reducing their dominance. If the bloom is dominated by inedible phytoplankton (too small or too big species, toxic algae), we would suspect rather a decrease of the phytoplankton evenness with increasing grazing pressure, because copepods would probably feed mostly on the rare edible species increasing phytoplankton dominance. The negative effect of the relative biomass of *Temora* sp. on phytoplankton evenness in our studies might suggest that this copepod had a broader feeding spectrum than other copepod species present in the community and was able to feed on the rare phytoplankton species. It was already reported that *Temora longicornis* is able to feed on very large algae, which are not available for other copepods (Jansen 2008).

Observed effects on the phytoplankton dominance structure can be also confounded with effects on phytoplankton biomass production (Hillebrand et al. 2008). Phytoplankton evenness response could vary between species with different growth rates, especially if they compete for the resources (Polley et al. 2003). This was, however, not the main effect during a build-up phase of phytoplankton bloom in our nutrient rich system. A negative correlation between the phytoplankton evenness and biomass in our studies (Tab.3-2) might be explained as an effect of enhanced consumer activity with warming. It is known that warming and enhanced grazing pressure reduce phytoplankton biomass (Lewandowska and Sommer 2010, Sommer and Lewandowska 2010). If copepods reduce mostly the biomass of dominant species, it is obvious that phytoplankton evenness increases with decreasing producer biomass. Observed positive temperature effects on phytoplankton evenness at the peak time in the experiments 2009 and 2007 might be also driven by the significant negative correlation between phytoplankton evenness and biomass (Tab. 3-2). This confirms our assumption that copepods, which

graze at higher rates in warmer conditions (O'Connor 2009), reduced mostly the biomass of dominant phytoplankton species in the experiments 2009 and 2007.

Table 3-2. Results of Pearson´s correlations between phytoplankton biomass and evenness in the mesocosm experiments.

Experiment	*R*	N	*r2*	*P*
2009	-0.75	12	0.56	0.005
2008	-0.52	12	0.27	0.085
2007	-0.87	8	0.76	0.005
2006	-0.10	8	0.01	0.808

In conclusion our results show that strong top-down control of producers under warmer conditions affects not only the magnitude of phytoplankton biomass, but via selective feeding reorganizes the phytoplankton community structure as it changes producer evenness and richness. Whereas some copepod species might control phytoplankton richness (e.g. *Acartia* sp., *Oithona* sp.), others (e.g. *Pseudocalanus* sp.) appear to be responsible for effects on phytoplankton evenness (Fig. 3-3). Therefore it is highly important to look at the species composition of producers and consumers, which is ignored by most of the recent studies about zooplankton response to warming as they are often restricted to one species. Our results reveal that the zooplankton community composition might be crucial to understand the effect of warming on aquatic ecosystems. Obviously bottom-up processes are also important and nutrient availability might strongly affect producer functions. There is a need of complex ecosystem studies where community interactions could be fully represented.

ACKNOWLEDGEMENTS

This study was founded by DFG (German Research Foundation) within the priority program 1162 ´AQUASHIFT´. T. Hansen, H. Tomanetz and C. Meyer are acknowledged for their technical assistance. We thank N. Aberle for the unpublished microzooplankton data.

GENERAL DISCUSSION

Temperature as an ecological factor for phytoplankton

Overall, the results of the spring bloom experiments conducted within the framework of the DFG-priority program "AQUASHIFT" have provided a balanced picture of the role of temperature as a steering factor for the timing, magnitude and composition of the spring bloom. Indeed, temperature has been shown to be a major factor, which affects spring phytoplankton bloom. Although light intensity and nutrient content have indisputable strong impact on aquatic photosynthesis and algae growth, both light and nutrient availability for phytoplankton in the water column depend on thermal stratification. In deep water bodies, the onset of stratification might act as a light switch, relatively suddenly increasing the light exposure of phytoplankton by an order of magnitude (Sverdrup 1953). This is different in shallow water bodies, like the Kiel Bight of the Baltic Sea, to which our experiments have been tied. Here, temporal variability of the light supply at the start of the spring bloom is primarily dictated by surface irradiance. Short-term and interannual variation of surface irradiance at weekly scales rarely exceeds a factor of 2. Light intensity, nutrient availability and seasonal thermal stratification are coupled in the water column and all together determine the spring phytoplankton bloom. Thus, the impact of warming on phytoplankton succession should be analysed respecting light conditions and nutrient content.

I showed in this study (chapter 2) that changes in light intensity, varying within the natural limits typical for shallow water bodies, had only a weak impact on primary producers, whereas temperature stronger affected phytoplankton, changing their biomass, species composition and community structure. Light, however, affected the response of phytoplankton productivity (PP) to warming (chapter 1). In agreement with Tilzer et al. (1996), I was able to show that temperature had stronger impact on primary productivity under higher light intensity than under light limited conditions. In my studies I did not consider nutrient limitations, because nutrient concentrations in each experiment were high enough to guarantee non-limited growth during most of the ascent phase of the phytoplankton bloom and the processes after the bloom, when nutrient limitation might have been important, were not the main topic of my thesis.

Thackeray et al. (2008), who studied spring phytoplankton bloom phenology in freshwater ecosystems, suggested that light, nutrients and temperature, all are important

for phytoplankton succession, but different factors might alter the growth of different species and their significance changes with bloom development. Similar studies for marine ecosystems could help to understand phytoplankton bloom dynamic in response to predicted climate warming. The evaluation of light and temperature effects on phytoplankton discussed in this thesis (chapters 1 and 2) is the first step to compare different factors affecting spring phytoplankton bloom in marine environment.

Direct and indirect temperature effects

The predicted increase of sea surface temperatures can have a direct and indirect impact on marine phytoplankton communities. The metaanalysis described in chapter 1 confirmed that temperature directly increases specific primary productivity (PP:B), as stated in the metabolic theory of ecology (Brown et al. 2004), which predict an increase of metabolic processes with increasing temperature.

My studies indicate that indirect temperature effects can be even more prominent for phytoplankton growth than direct temperature impacts. It is known that temperature stronger affects heterotrophic than autotrophic processes and that consumer activity increases with warming (O'Connor et al. 2009). Thus, temperature, acting on consumer pressure, can indirectly affect phytoplankton biomass and community structure. Moreover, warming can shift consumer community composition, as described in chapter 3, changing species specific interactions between zooplankton and phytoplankton. In particular, the observed decline of phytoplankton biomass with warming (chapter 2) can be attributed to increased grazing pressure under warmer conditions. Besides a reduction of standing phytoplankton biomass, consumers can change phytoplankton size structure. A shift towards smaller species with warming was reported by Daufresne et al. (2009) and observed in my studies (chapter 2). I hypothesise that higher consumption of large diatoms by copepods in warmer conditions benefited smaller algae species (mainly nanoflagellates), changing size structure of phytoplankton community. Furthermore, warming can directly decrease cell volume (Atkinson et al. 2003).

In the chapter 3, it was illustrated that higher consumer density increased phytoplankton diversity (species richness and evenness). However, it should be kept in mind that all experiments presented in this studies were performed under high nutrient concentrations and nutrient limitation might reverse the sign of consumer-producer diversity relationship, as suggested by Worm (Worm et al. 2002). Furthermore, I found

that phytoplankton diversity depends on consumer identity (chapter 3). Thus, an observed shift in zooplankton species composition with warming might change phytoplankton species richness and dominance structure. Compositional shift of copepods, which are the main consumers of phytoplankton >10 μm, might also affect phytoplankton species composition due to different feeding behaviour and preferences to feed on diatoms or ciliates (Stibor et al. 2004). Some shifts in phytoplankton composition related to warming and copepod density (e.g. reduced biomass of *Thalassiosira* spp.) were already reported for experiments described in this thesis (Sommer and Lewandowska 2010, see also chapter 2).

In conclusion, my work and recent studies on climate warming and aquatic food webs led me to distinguish direct temperature effects on:

- specific primary productivity (chapter 1) and
- phytoplankton cell size (Atkinson et al. 2003),

followed by the strong indirect temperature effects due to consumer pressure, which in response to warming led to:

- decline of phytoplankton biomass and cell size (chapter 2)
- increase of phytoplankton diversity (chapter 3)
- changes in phytoplankton dominance and community composition (chapter 2).

It should be also kept in mind that temperature might indirectly act on phytoplankton due to the other processes like community respiration (Wohlers et al. 2009), aggregation and sinking (Piontek et al. 2009), which were not discussed in my thesis.

Conceptual model of temperature impacts on plankton biotic interactions

Based on the results of my work, I developed a conceptual model of temperature impacts on the biotic relationships in marine pelagic system, which I tested experimentally using indoor mesocosm facility (Fig. 2). I included temperature as the only abiotic factor in this model for better clarity and because I was not able to test other factors (e.g. light, nutrients) in appropriate way to show a complete picture of interactions.

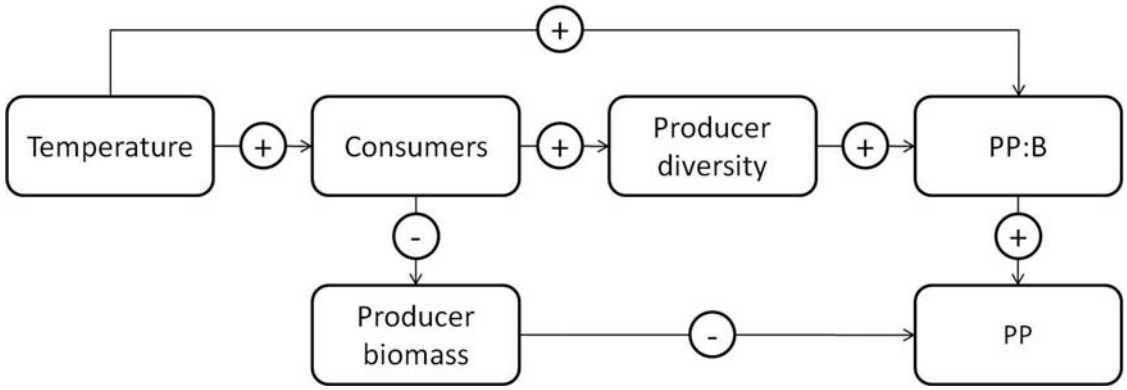


Figure 2. Conceptual model of temperature impacts on biotic interactions in marine plankton. Minus represent a negative and plus – positive relationship, PP is volumetric primary productivity, PP:B is biomass specific primary productivity.

In the proposed model, temperature directly affects species specific primary productivity (PP:B) , as described in chapter 1. Furthermore, temperature has a positive impact on grazing activity and development of consumers, as stated in the metabolic theory of ecology (Brown et al. 2004) and shown empirically by O'Connor et al. (2009) or Isla et al. (2008).

In accordance with the results shown in chapter 3, consumers have a positive impact on producer diversity, based on the assumption that the system is not nutrient limited. Producer diversity, especially species richness, positively affect specific primary productivity, as discussed in chapter 1. Consumers reduce producer biomass, as shown in chapter 2 and reported by Sommer and Lewandowska (2010).

In conclusion, the final effect of warming on volumetric primary productivity (PP) depends on the relative strength between the positive effect of PP:B and negative effect of producer biomass. This proportion depends on two major relationship pathways: 1) balance between direct and indirect temperature impacts and 2) consumer-producer interactions, which lead to decline of producer biomass, but on the other hand consumers increase producer diversity.

Future perspectives

Based on the results of this thesis, several important questions cannot be answered. Thus I suggest three fields of future research, which may help to better understand phytoplankton dynamic in response to climate changes:

1. **Factorial studies on phytoplankton succession.** In the studies discussed here, the factor temperature and light intensity or temperature and consumer density

were combined in two experiments accordingly. It led me to make a first step in the evaluation of different environmental factors, which can drive phytoplankton succession. However, much more can be done in this field of research, especially respecting nutrient limitation, as shown by Thackeray et al. (2008). Experiments with factorial combinations of the factors temperature, nutrient ratios and light intensity might allow to test more realistic scenarios of climate warming and better understand the regional differences in phytoplankton community responses to predicted climate changes. Also indirect temperature effects acting via community respiration and sinking need more attention in the future for better understanding carbon transport in the water column and phytoplankton loss processes, as suggested by Wohlers et al. (2009).

2. **Responses of phytoplankton groups to climate changes.** As reviewed by Boyd et al. (2010) and shown in my studies (chapter 2), different functional groups of phytoplankton might differently response to climate changes. Furthermore, different environmental factors might be important for different phytoplankton groups and determine the competition. As a consequence of climate change, a reorganisation of phytoplankton community might be suspected, which might lead to cascading changes across the whole food web. Thus, understanding species interactions and their main environmental drivers is crucial to predict changes in phytoplankton bloom dynamics in marine ecosystems with climate warming.
3. **Field data and mesocosm studies.** Mesocosm experiments are often criticized for their artificial nature and limitations in space and time. However, mesocosm experiments allow to test mechanisms, which cannot be tested in natural environment, like diversity and nutrient manipulations, temperature gradients etc. Coupling field data analysis with mesocosm experiments would be a complete tool, which could successfully connect environmental changes with ecological patterns and test theoretical approach.

ACKNOWLEDGEMENTS

A number of people participated in the project I was involved in and helped during the time of my stay in Kiel. Thus, I would like to thank some people, without whom my work would not be possible and this thesis could not appear.

I am deeply grateful to my supervisors Ulrich Sommer and Helmut Hillebrand, who always supported me during my work. I thank for giving me a chance to participate in the AQUASHIFT project, sending me worldwide to expand my knowledge, for developing the ideas for my work, for their patience, all discussions and concrete reply to my questions.

Kathrin Lengfellner and Petra Breithaupt are acknowledged for introducing me to the experimental work and laboratory techniques, discussing my scientific problems and a good remark in every moment, when I was lost.

My colleagues Antje Biermann and Markus von Scheibner I want to thank for the all work we made together starting with the car driving and ending with the mesocosm cleaning, for the brainstorms on our data and all fun we had working together.

The best laboratory analyst ever and my office mate Thomas Hansen I want to thank for a solid preparation of all the experiments, solving my technical problems, reviewing the ideas and the best company in the office, which I could imagine.

For further technical support I want to thank Kerstin Nachtigal, Cordula Meyer, Regine Koppe, Horst Tommanetz, Frank Wendler, Thomas Lentfer, Martin Stehn, Uwe Lenz, Sebastian Meyer (the Light Ghost), and the crews of the r/v Polarfuchs and r/v Littorina. Many thanks to my student assistants: Marieta Miteva and Rong Bi. For counting the zooplankton I am indebted to Anja Schibelny, Mona Fuhrmann and Jessica Garzke. Special thanks to Klaus Gocke, who measured primary productivity during my absence and to Hans Peter Hansen, who calculated the total CO_2 concentrations. For statistical advice and help by data analysis I am especially grateful to Juan Carlos Molinero and Monika Winder.

Birte Matthiessen (my hidden supervisor) I would like to thank for all scientific discussions, corrections, comments and suggestions on my research and this thesis. Special thanks to Nicole Aberle-Malzahn for her unpublished ciliates data and motivation

to further work and to Boris Worm, who helped me to find the passion and sense of my research, when I get lost.

My colleagues from the Experimental Ecology Department, especially Andrea Saage, Jamileh Javidpour, Lena Eggers and Erik Mielke, I want to thank for their support, stimulating discussions and nice atmosphere at work and after work. Our secretary Gaby Barth I would like to thank for all administrative work she did to make my life easier.

Grateful acknowledgements are dedicated to Christoph for his patience, motivation and his positive energy, which I needed very much to finish this thesis. I also would like to thank my family and friends, who stayed in Poland, for their encouragement and trust (dzięki za wsparcie!).

REFERENCES

Aberle N, Lengfellner K, Sommer U (2007). "Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming." Oecologia 150(4): 668-681.

Alheit, J., C. Möllmann, J. Dutz, G. Kornilovs, P. Loewe, V. Mohrholz and N. Wasmund (2005). "Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s." Ices Journal of Marine Science 62(7): 1205-1215.

Atkinson, D., B. J. Ciotti and D. J. S. Montagnes (2003). "Protists decrease in size linearly with temperature: ca. 2.5% degree C." Proceedings of the Royal Society 270: 2605-2611.

Barton, B. T., A. P. Beckerman and O. J. Schmitz (2009). "Climate warming strengthens indirect interactions in an old-field food web." Ecology 90(9): 2346-2351.

Beaugrand, G., M. Edwards and L. Legandre (2010). "Marine biodiversity, ecosystem functioning, and carbon cycles." Proceedings of the National Academy of Sciences of the United States of America: 1-5.

Behrends G (1996). "Long-term investigation of seasonal zooplankton dynamics in Kiel Bight, Germany." In: Proceedings of the 13th Symposium of Baltic and Marine Biology, p 93 - 98.

Behrenfeld, M. (2010). "Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms." Ecology 91(4): 977-989.

Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier and E. S. Boss (2006). "Climate-driven trends in contemporary ocean productivity." Nature 444: 752-755.

Berger SA, Diehl S, Stibor H, Trommer G, Ruhenstroth M, Wild A, Weigert A, Jäger CG,Striebel M (2007). "Water temperature and mixing depth affect timing and magnitude of events during spring succesion of the plankton." Oecologia 150: 643-654.

Berglund J, Müren U, Bamstedt U, Andersson A (2007). "Efficiency of a phytoplankton-based and bacteria-based food web in pelagic marine system." Limnology and Oceanography 52(1): 121-131.

Bopp, L., O. Aumont, P. Cadule, S. Alvain and M. Gehlen (2005). "Response of diatoms distribution to global warming and potential implications: A global model study." Geophysical Research Letters 32: 1-4.

Boyce, D. G., M. R. Lewis and B. Worm (2010). "Global phytoplankton decline over the past century." Nature 466: 591-596.

Boyd, P. W., R. Strzepek, F. Fu and D. A. Hutchins (2010). "Environmental control of open-ocean phytoplankton groups: Now and in the future." Limnology and Oceanography 55(3): 1353-1376.

Brock TD (1981). "Calculating solar-radiation for ecological studies." Ecological Modelling 14(1-2): 1-19.

Brown JH, Gillooly JF, Allen AP, Savage VM,West GB (2004). "Toward a metabolic theory of ecology." Ecology 85(7): 1771-1789.

Bruno, J. F., K. E. Boyer, J. E. Duffy, S. C. Lee and J. S. Kertesz (2005). "Effects of macroalgal species identity and richness on primary production in benthic marine communities." Ecology Letters 8: 1165-1174.

Burgmer, T. and H. Hillebrand (in press). "Temperature mean and variance alter phytoplankton biomass and biodiversity in a long-term microcosm experiment." Oikos.

Cardinale, B. J., D. M. Bennett, C. E. Nelson and K. Gross (2009). "Does productivity drive diversity or vice versa? A test of multivariate productivity-diversity hypothesis in streams." Ecology 90(5): 1227-1241.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran and C. Jouseau (2006). "Effects of biodiversity on the functioning of trophic groups and ecosystems." Nature 443: 989-992.

Cushing DH (1990). "Plankton production and year-class strength in fish populations - an update of the match mismatch hypothesis." Advances in Marine Biology 26: 249-293.

Doney, S. C. (2006). "Phytoplankton in a warmer world." Nature 444: 695-696.

Daufresne, M., K. Lengfellner and U. Sommer (2009). "Global warming benefits the small in aquatic ecosystems." Proceedings of the National Academy of Sciences of the United States of America 16: 12788-12793.

Dropp, M. R. (1974). "The nutrients status of algal cells in continuous culture." Journal of the Marine Biological Association of the United Kingdom 54: 825-855

Durant JM, Hjermann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005). "Timing and abundance as key mechanisms affecting trophic interactions in variable environments." Ecology Letters 8: 952-958.

Edwards M, Richardson AJ (2004). "Impact of climate change on marine pelagic phenology and trophic mismatch." Nature 430: 881-884.

Elliott JA, Jones ID, Thackeray SJ (2006). "Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake." Hydrobiologia 559: 401-411.

Falkowski, P. G. and J. A. Raven (2007). Aquatic Photosynthesis, Princeton University Press.

Finke, D. L. and R. F. Denno (2005). "Predator diversity and the funktioning of ecosystems: the role of intraguild predation in dampening trophic cascades." Ecology Letters 8: 1299-1306.

Finkel, Z. V., J. Beardall, K. J. Flynn, A. Quigg, T. A. V. Rees and J. A. Raven (2010). "Phytoplankton in a changing world: cell size and elemental stoichiometry." Journal of Plankton Research 32(1): 119-137.

Gargas E (1975). "A manual for phytoplankton primary production studies in the Baltic." BMB Publ. Horsholm, Danemark, Water Quality Institute. 2.

Göbel J, Lu D, Voss J (2009). "Potential impact of climate change on marine phytoplankton with emphasis on German coastal waters and the East China Sea." Jahresbericht des Landesamtes fuer Natur und Umwelt des Landes Schleswig-Holstein 2007/08: 75 - 82.

Graneli E, Turner JT (2002). "Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study." Marine Ecology-Progress Series 239: 57-68.

Griffin, J. N., E. J. O'Gorman, M. C. Emmerson, S. R. Jenkins, A.-M. Klein, M. Loreau and A. Symstad (2009). "Biodiversity and stability of ecosystem functioning. Biodiversity, ecosystem functioning, & human wellbeing." S. Naeem, D. E. Bunker, A. Hector, M. Loreau and C. Perrings, Oxford University Press.

Hashioka T, Yamanaka Y (2007). "Ecosystem change in the western North Pacific associated with global warming using 3D-NEMURO." Ecological Modelling 2002: 95-104.

Hillebrand, H., D. M. Bennett and M. W. Cadotte (2008). "Consequences of dominance: a review of evenness effects on local and regional ecosystem processes." Ecology 89(6): 1510-1520.

Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin and J. E. Smith (2007). "Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure." Proceedings of the National Academy of Sciences of the United States of America 104(26): 10904-10909.

Hillebrand H, Dürselen C-D, Kirschtel D, Pollingher U, Zohary T (1999). "Biovolume calculation for pelagic and benthic microalgae." Journal of Phycology 35: 403-424.

Huisman J, Sharples J, Stroom JM, Visser PM, Kardinaal WEA, Verspagen JMH,Sommeijer B (2004). "Changes in turbulent mixing shift competition for light between phytoplankton species." Ecology 85(11): 2960-2970.

IPCC (2007). "Climate Change 2007: The Physical Science Basis." IPCC, Geneva.

Isla JA, Lengfellner K,Sommer U (2008). "Physiological response of the copepod *Pseudocalanus* sp in the Baltic Sea at different thermal scenarios." Global Change Biology 14(4): 895-906.

Jansen, S. (2008). "Copepods grazing on Coscinodiscus wailesii: a question of size?" Helgoland Marine Research 62(3): 251-255.

Jassby, A. and T. Platt (1976). "Mathematical formulation of the relationship between photosynthesis and light for phytoplankton." Limnology and Oceanography 21(4).

Ji, R., M. Edwards, D. L. Mackas, J. A. Runge and A. C. Thomas (2010). "Marine plankton phenology and life history in a changing climate: current research and future directions." Journal of Plankton Research 32(10): 1355-1368

Keller AA, Oviatt CA, Walker HA,Hawk JD (1999). "Predicted impacts of elevated temperature on the magnitude of the winter-spring phytoplankton bloom in temerate coastal waters: A mesocosm study." Limnology and Oceanography 44(2): 344-356.

Koeller, P., C. Fuentes-Yaco, T. Platt, S. Sathyendranath, A. Richards, P. Quellet, D. Orr, U. Skuladottir, K. Wieland, L. Savard and M. Aschan (2009). "Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean." Science 324: 791-793

Lassen, M. K., K. D. Nielsen, K. Richardson, K. Garde and L. Schlüter (2010). "The effects of temperature increases on temperate phytoplankton community - A mesocosm climate change scenario." Journal of Experimental Marine Biology and Ecology 383: 79-88.

Lengfellner, K. (2008). "The impact of climate warming on plankton spring succession: a mesocosm study." Christian Albrechts University of Kiel, Kiel. PhD Dissertation: pp 110.

Lewandowska, A. and U. Sommer (2010). "Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton." Marine Ecology Progress Series 405: 101-111.

Litchman, E. and C. A. Klausmeier (2008). "Trait-Based Community Ecology of Phytoplankton." The Annual Review of Ecology, Evolution, and Systematics 39: 615-639.

Litchman, E., C. A. Klausmeier and P. Bossard (2004). "Phytoplankton nutrient competition under dynamic light regimes." Limnology and Oceanography 49(4): 1457-1462.

Lonsdale, D. J., D. A. Caron, M. R. Dennett and R. Schaffner (2000). "Predation by Oithona spp. on protozooplankton in the Ross Sea, Antarctica." Deep-Sea Research Part II - Topical Studies in Oceanography 47: 3273-3283.

MacIntyre, H. L., T. M. Kana, T. Anning and R. J. Geider (2002). "Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria." Journal of Phycology 38: 17-38.

McKee, D., D. Atkinson, S. Collings, J. Eaton, I. Harvey, T. Heyes, K. Hatton, D. Wilson and B. Moss (2002). "Macro-zooplankter responses to simulated climate warming in experimental freshwater microcosms." Freshwater Biology 47: 1557-1570.

Menden-Deuer S,Lessard EJ (2000). "Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton." Limnology and Oceanography 45(3): 569-579.

Menéndez, R., A. G. Megías, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy and C. D. Thomas (2006). "Species richness changes lag behind climate change." Proceedings of the Royal Society 273(1593): 1465-1470.

Moore LR, Goericke R,Chisholm SW (1995). "Comperative physiology of *Synechococcus* and *Prochlorococcus* - influence of light and temperature on growth, pigments, fluorescence and absorptive propoerties." Marine Ecology-Progress Series 116(1-3): 259-275.

Möllmann, C., G. Kornilovs and L. Sidrevics (2000). "Long-term dynamics of main mesozooplankton species in the central Baltic Sea." Journal of Plankton Research 22(11): 2015-2038.

Möllmann, C., B. Müller-Karulis, G. Konrnilovs and M. A. St.John (2008). "Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback coops in a simple ecosystem." ICES Journal of Marine Science 65: 302-310.

Mueter FJ, Broms C, Drinkwater KF, Friedland KD, Hare JA, Hunt GL, Melle W,Taylor M (2009). "Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems." Progress in Oceanography 81(1-4): 93-110.

Mulder, C. P. H., E. Bazeley-White, P. G. Dimitrakopoulos, A. Hector, M. Scherer-Lorenzen and B. Schmid (2004). "Species evenness and productivity in experimental plant communities." Oikos 107: 50-63.

Nixon SW, Fulweiler RW, Buckley BA, Granger SL, Nowicki BL,Henry KM (2009). "The impact of changing climate on phenology, productivity, and benthic-pelagic coupling in Narragansett Bay." Estuarine, Coastal and Shelf Science 82: 1-18.

O'Connor, M. I. (2009). "Warming strengthens an herbivory-plant interaction." Ecology 90(2): 388-398.

O'Connor, M. I., M. F. Piehler, D. M. Leech, A. Anton and J. F. Bruno (2009). "Warming and resource availability shift food web structure and metabolism." PLoS Biology 7(8).

Petchey, O. L., P. T. McPhearson, T. M. Casey and P. J. Morin (1999). "Environmental warming alters food-web structure and ecosystem function." Nature 402: 69-72.

Piontek, J., N. Händel, G. Langer, J. Wohlers, U. Riebesell and A. Engel (2009). "Effects of rising temperature on formation and microbial degradation of marine diatom aggregates." Aquatic Microbial Ecology 54: 305-318.

Polley, H. W., B. J. Wilsey and J. D. Derner (2003). "Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures?" Ecology Letters 6(3): 248-256.

Reynolds C (2006). "Ecology of phytoplankton." New York, Cambridge University Press.

Rose JM, Feng YY, Gobler CJ, Gutierrez R, Hare CE, Leblanc K, Hutchins DA (2009). "Effects of increased pCO(2) and temperature on the North Atlantic spring bloom. II. Microzooplankton abundance and grazing." Marine Ecology-Progress Series 388: 27-40.

Schalau K, Rinke K, Straile D, Peeters F (2008). "Temperature is the key factor explaining interannual variability of Daphnia development in spring: a modelling study." Oecologia 157(3): 531-543.

Shannon, C. E. and W. Weaver (1949). The mathematical theory of communication. Urbana, IL, University of Illinois Press.

Schiermeier Q (2006). "A sea change." Nature 439(7074): 256-260.

Smayda TJ, Reynolds CS (2003). "Strategies of marine dinoflagellate survival and some rules of assembly." Journal of Sea Research 49: 95-106.

Smetacek V,Cloern JE (2008). "On Phytoplankton Trends." Science 319: 1346-1348.

Smith, B. and J. B. Wilson (1996). "A consumer's guide to evenness indices." Oikos 76: 70-82.

Sommer U, Aberle N, Engel A, Hansen T, Lengfellner K, Sandow M, Wohlers J, Zöllner E,Riebesell U (2007). "An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton." Oecologia 150: 655 - 667.

Sommer U, Gliwicz ZM, Lampert W,Duncan A (1986). "The PEG model of seasonal succession of planktonic events in freshwaters." Hydrobiologia 106: 433-471.

Sommer U, Hansen T, Blum O, Holzner N, Vadstein O,Stibor H (2005). "Copepod and microzooplankton grazing in mesocosms fertilised with different Si : N ratios: no overlap between food spectra and Si : N influence on zooplankton trophic level." Oecologia 142(2): 274-283.

Sommer U, Lengfellner K (2008). "Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom." Global Change Biology 14: 1-10.

Sommer, U. and A. Lewandowska (2010). "Climate change and the phytoplankton spring bloom: warming and overwintering zooplankton have similar effects on phytoplankton." Global Change Biology 17(1): 154-162.

Sommer U, Sommer F (2006). "Cladocerans versus copepods: the cause of contrasting top-down controls on freshwater and marine phytoplankton." Oecologia 147(2): 183-194.

Stachowicz, J. J., J. F. Bruno and J. E. Duffy (2007). "Understanding the effects of marine biodiversity on communities and ecosystems." Annual Review of Ecology, Evolution, and Systematics 38: 739-766.

Stibor, H., O. Vadstein, S. Diehl, A. Gelzleichter, T. Hansen, F. Hantzsche, A. Katechakis, B. Lippert, K. Loseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen and Y. Olsen (2004). "Copepods act as a switch between alternative trophic cascades in marine pelagic food webs." Ecology Letters 7: 321-328.

Sverdrup HU (1953). "On conditions for the vernal blooming of phytoplankton." Journal du Conseil International pour l'Exploration de la Mer 18: 287-295.

Thackeray SJ, Jones ID, Maberly SC (2008). "Long-term change in the phenology of spring phytoplankton: species-specyfic responses to nutrient enrichment and climatic change." Journal of Ecology 96: 523-535.

Thebault, E. and M. Loreau (2003). "Food-web constraints on biodiversity-ecosystem functioning relationships." Proceedings of the National Academy of Sciences of the United States of America 100(25): 14949-14954.

Tilstone GH, Miguez BM, Figueiras FG, Fermin EG (2000). "Diatom dynamics in a coastal ecosystem affected by upwelling: coupling between species succession, circulation and biogeochemical processes." Marine Ecology-Progress Series 205: 23-41.

Tilzer MM, Elbrächter M, Gieskes W, Beese B (1986). "Light - temerature interactions in the control of photosynthesis in Antarctic phytoplankton." Polar Biology 5: 105-111.

Tiselius, P. and P. R. Jonsson (1990). "Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis." Marine Ecology Progress Series 66: 23-33.

Tittensor, D. P., C. Mora, W. Jetz, H. K. Lotze, D. Ricard, E. V. Berghe and B. Worm (2010). "Global patterns and predictors of marine biodiversity across taxa." Nature 466: 1-4.

Townsend DW, Cammen LM, Holligan PM, Campbell DE, Pettigrew NR (1994). "Causes and consequences of variability in the timing of spring phytoplankton blooms." Deep-Sea Research Part I-Oceanographic Research Papers 41(5-6): 747-765.

Trenberth, K. E., J. T. Fasullo and J. Kiehl (2009). "Earth's global energy budget." Bulletin of the American Meteorological Society 90(3): 311-323.

Utermöhl H (1958). "Zur Vervollkommung der quantitativen Phytoplankton Methodik." Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 9: 263 - 272.

Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jonsdottir, J. A. Klein, B. Magnusson, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, O. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber and P. A. Wookey (2006). "Plant community responses to experimental warming across the tundra biome." Proceedings of the National Academy of Sciences of the United States of America 103(5): 1342-1346.

Wasmund N, Gobel J, Von Bodungen B (2008). "100-years-changes in the phytoplankton community of Kiel Bight (Baltic Sea)." Journal of Marine Systems 73(3-4): 300-322.

Wilsey, B. J. and C. Potvin (2000). "Biodiversity and ecosystem functioning: importance of species evenness in an old field." Ecology 81(4): 887-892.

Wiltshire KH, Malzahn AM, Wirtz K, Greve W, Janisch S, Mangelsdorf P, Manly BFJ, Boersma M (2008). "Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads." Limnology and Oceanography 53(4): 1294-1302.

Wiltshire KH, Manly BFJ (2004). "The warming trend at Helgoland Roads, North Sea: Phytoplankton response." Helgoland Marine Research 58(4): 269-273.

Winder M, Schindler DE (2004). "Climate change uncouples trophic interactions in an aquatic ecosystem." Ecology 85(8): 2100-2106.

Wohlers, J., A. Engel, E. Zollner, P. Breithaupt, K. Jurgens, H. G. Hoppe, U. Sommer and U. Riebesell (2009). "Chnages in biogenic carbon flow in response to sea surface warming." Proceedings of the National Academy of Sciences of the United States of America 106(17): 7067-7072.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz and R. Watson (2006). "Impacts of biodiversity loss on ocean ecosystem services." Science 314: 787-790.

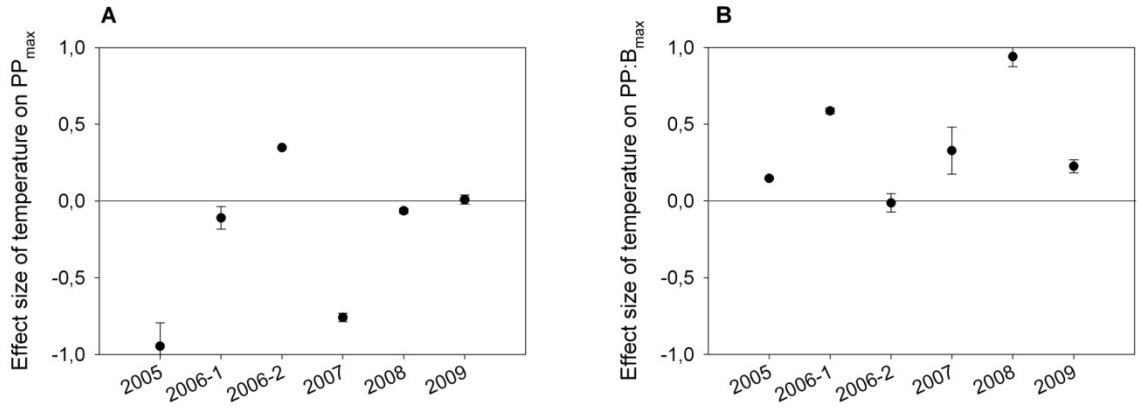
Worm, B. and J. E. Duffy (2003). "Biodiversity, productivity and stability in real food webs." Trends in Ecology and Evolution 18(12): 628-632.

Worm, B., H. K. Lotze, H. Hillebrand and U. Sommer (2002). "Consumer versus resource control of species diversity and ecosystem functioning." Nature 417: 848-851.

APPENDIX

Chapter 1

Appendix Figure A1. Effect sizes (± 95% confidence intervals) of increased temperature on A) maximal primary productivity (PP_{max}) and B) biomass normalized primary productivity ($PP:B_{max}$) for each experiment used in metaanalysis.



Appendix Table A1. Summary results of the effect of increased temperature on the maximal primary productivity (PP_{max}) and biomass normalized primary productivity ($PP:B_{max}$).

	PP_{max}	$PP:B_{max}$
Overall effect	0.04	0.05
Variance	< 0.01	<0.01
Standard deviation	0.49	0.29
+95% confidence interval	0.43	0.28
-95% confidence interval	-0.36	-0.18

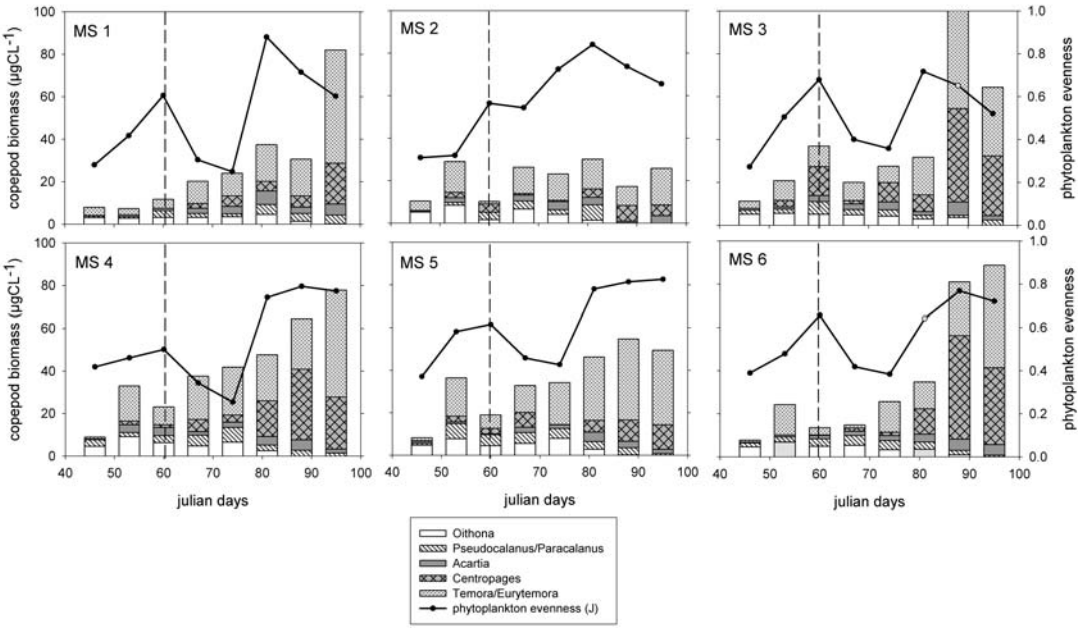
Appendix Table A2. Light intensity and initial grazing density impacts on the effect sizes of increased temperature on PP and PP:B. Regression analysis with (Fac.) and without factorial (N.Fac.) studies.

	y_0	a	b	F	r^2	*P*
Light intensity (PP) - 2nd order polynomial regression						
Fac.	-1.25	0.04	0.0003	9.489	0.79	0.02
N. Fac.	-1.19	0.04	0.0002	3.342	0.77	0.2
Initial copepod density (PP:B) - linear regression						
Fac.	0.62	-0.03	-	3.732	0.38	0.1
N. Fac.	0.80	-0.05	-	2.974	0.50	0.2

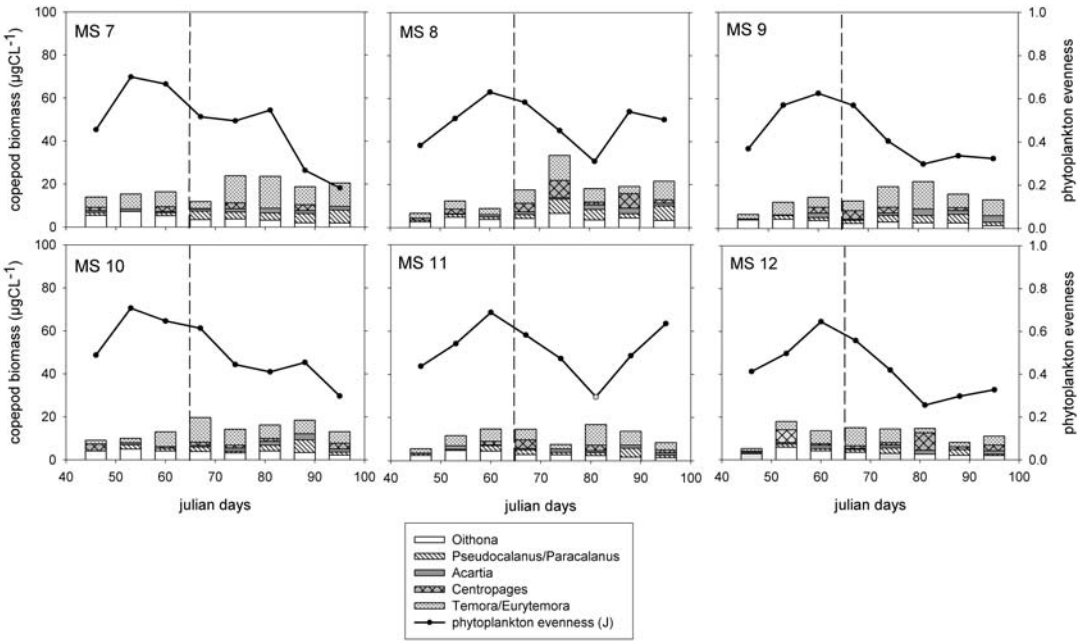
Chapter 3

Appendix Figure A2. Genus specific copepod biomass and the time course of phytoplankton evenness in the experiment 2008 for the warming scenario (A) and ambient temperature (B). MS 1-12: mesocosm numbers. Vertical dashed line represent the time of maximal phytoplankton biomass.

A



B



Appendix Table A3. Copepod biomass (adults and copepodites) response to warming and additional factors (light intensity and initial copepod density, respectively) for each experiment.* $p < 0.05$; ** $p < 0.001$

Experiment	Coefficient	SE	*t*	p	df	R^2	*F*
2009 (*GLM*)							
Temperature	-1.95	0.89	-2.18	0.06	2	0.89	36.78**
copepod dens.	2.08	0.25	8.29	< 0.0001			
2008 (*GLM*)							
Temperature	-1.23	1.34	-0.92	0.38	2	0.09	0.50
Light	0.04	0.10	0.39	0.71			
2007 (*regr.*)							
Temperature	0.96	0.96	1.01	0.35	1	0.14	1.01
2006 (*regr.*)							
Temperature	-2.25	0.84	-2.67	0.04	1	0.54	7.15*

CURRICULUM VITAE

Personal Data

Name:	Aleksandra Magdalena Lewandowska
Date of birth:	08.11.1982
Place of birth:	Warsaw (pol. *Warszawa*), Poland
Nationality:	Polish

Education

2001	Secondary-school final examinations at the XLIV LO im. Antoniego Dobiszewskiego in Warsaw, Poland
2001 - 2006	Studies in Environmental Protection at the University of Life Sciences in Warsaw, Poland
2006	Master thesis at the Institute of Oceanology Polish Academy of Science in Sopot, Poland
2008 - 2011	PhD thesis at the Leibniz Institute of Marine Sciences in Kiel, Germany

Scholarships and professional employments

2004	Institute of Meteorology and Water Management, Department of Oceanography and Baltic Sea Monitoring, Gdynia, Poland
2005	Field course University of Antwerp and Warsaw University of Life Sciences in Biebrza National Park, Poland
2006 - 2007	Institute of Environmental Protection, Lake Protection Laboratory, Warsaw, Poland
2007 - 2008	DBU Scholarship at IFM-GEOMAR, Marine Ecology Research Division, Kiel, Germany
2009	A Summer Colloquium on Ecosystem and Climate, National Centre for Atmospheric Research in Boulder, CO, USA

Publications

Sommer, U., Lewandowska, A. (2010). Climate change and the phytoplankton spring bloom: warming and overwintering zooplankton have similar effects on phytoplankton. Global Change Biology 17(1): 154-162

Lewandowska A., Sommer U. (2010). Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton. Marine Ecology Progress Series 405: 101-111

Soszka, H., Cydzik, D., Golub, M., Kolada, A., Lewandowska, A. (2006) Stan czystości jezior Polski badanych w latach 1999-2004. Inspekcja Ochrony Środowiska, Warszawa.

Description of the individual scientific contribution to the experimental work and publications

The experimental work presented in this thesis was a part of the DFG priority program 1162 "AQASHIFT" coordinated by Prof. Dr. Ulrich Sommer. I worked in cooperation with Antje Biermann supported by Prof. Dr. Ulf Riebesell from the Biogeochemistry Department of the IFM-GEOMAR in Kiel and Marcus von Scheibner supported by Prof. Dr. Klaus Jürgens from the IOW in Rostock. One experiment was conducted in cooperation with Petra Breithaupt supported by Prof. Dr. Hans-Georg Hoppe from the Microbiology Department of the IFM-GEOMAR in Kiel. Aleksandra Lewandowska, Antje Biermann and Marcus von Scheibner equally contributed to the experimental work.

The parts of this thesis are published (chapter 2), submitted to the scientific journal (chapter 3) or ready for submission (chapter 1) with multiple authorship. The list below is a clarification of my personal contribution to the publications.

Chapter 1: Responses of primary productivity to increased temperature and phytoplankton diversity. *Ready for submission*.

Authors: Aleksandra M. Lewandowska, Petra Breithaupt, Helmut Hillebrand, Hans-Georg Hoppe, Klaus Jürgens, Ulrich Sommer

Contributions: US, HH and AL developed the ideas for this study; PB provided the data and conducted the experiments 2005-2007, AL provided the data and conducted the experiments 2008-2009; HGH and KJ supported the work of PB; US and HH supported the work of AL; AL performed data analyses; AL, US and HH discussed the results; AL wrote the manuscript.

Chapter 2: Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton. *Published in 2010: Marine Ecology Progress Series 405: 101-11.*

Authors: Aleksandra Lewandowska, Ulrich Sommer

Contributions: US and AL developed the ideas for this study; AL conducted the experiment; US and AL provided the data; AL performed data analyses; AL and US discussed the results; AL wrote the manuscript.

Chapter 3: Temperature induced changes of mesozooplankton affect phytoplankton community structure. *Submitted.*

Authors: Aleksandra M. Lewandowska, Helmut Hillebrand, Kathrin Lengfellner, Ulrich Sommer

Contributions: US, HH and AL developed the ideas for this study; US provided the data, KL provided the data and conducted the experiments 2006-2007, AL provided the data and conducted the experiments 2008-2009; AL performed data analyses; US, HH and AL discussed the results; AL wrote the manuscript.

Declaration

The content and design of this thesis, apart from the supervisor's guidance, is my own work. The thesis has not been submitted either partially or wholly as a part of a doctoral degree to another examining body and has been prepared respecting the Rules of Good Scientific Practice of the German Research Foundation.

Aleksandra Magdalena Lewandowska