The impact of climate warming on plankton spring succession: a mesocosm study

Dissertation

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Contents

Summary

Our mesocosm studies focused on marine plankton spring succession in Kiel Bight under climate change conditions. Kiel Bight serves as a model for moderately deep water bodies of temperate regions where the plankton bloom can start before the onset of thermal stratification. Plankton spring blooms are critical periods in the seasonal cycle because they form the first food impulse in the year and thus can be linked to reproductive success of many species.

The conducted experiments stand out in their complex nature, monitoring simultaneously plankton food web processes from nutrients up to the copepod level under predicted global warming conditions. In the present thesis, results from phytoplankton, ciliates and copepods were combined and comprehensively examined.

In three subsequent years (Spring seasons 2005 - 2007), indoor mesocosms were stocked with plankton spring communities from Kiel Bight and subjected to temperature regimes warmed by 0°C, 2°C, 4°C and 6°C above the decadal mean in situ temperatures (1992 - 2003) of Kiel Bight. Between the years, we varied mean intensities of the daily light dose for the mixed water column.

Several effects emerged from our studies: At higher temperatures, we observed higher metabolic rates in the key copepod species *Pseudocalanus* sp. as well as increased rates of feeding. At the same time, the overall net growth efficiency in *Pseudocalanus* sp. decreased. Together with increased grazing in ciliates this resulted in stronger top-down control of the phytoplankton at warmer temperatures. Phytoplankton biomass at the bloom peak was diminished at higher temperatures, probably the effect of both, high grazing pressure and reduced growth efficiency in phytoplankton. Further, depending on the level of available food, elevated temperatures decreased reproductive success in *Pseudocalanus* sp. and seemingly prevented younger individuals to develop successfully, which in turn lead to a stronger decline in populations at higher temperatures.

With respect to trophic levels, we demonstrated different temperature sensitivity in autotrophs and heterotrophs: whereas the timing of phytoplankton biomass maxima was rather insensitive towards temperature change and seemingly fixed to a critical mean

daily light dose, ciliate and copepod peaks advanced strongly under global warming conditions. The interplay of light intensity and temperature ultimatively determined whether this differential temperture sensitivity translated into trophic mismatch situations and detrimental effects on copepod offspring and copepod population development. In case of ciliates, temperature increase resulted in a stronger coupling with the phytoplankton bloom and thus likely enhanced energy transfer towards the microbial loop.

Further, higher temperatures partly promoted faster dynamics in species diversity and overall changed population and community size structure in copepods and phytoplankton: during the bloom peak, phytoplankton mean size was shifted towards smaller species; adult copepods showed reductions in prosome length at the end of the experiments. This favouring of small size might emerge as a new rule for how global change affects the biosphere.

Zusammenfassung

Unsere Mesokosmenstudien haben sich mit der Frühjahrssukzession des marinen Planktons der Kieler Bucht unter möglichen Bedingungen künftiger globaler Erwärmung beschäftigt. Die Kieler Bucht diente dabei als Modell für Wasserkörper mittlerer Tiefe in temperierten Breiten, in denen die Frühjahrsblüte bereits vor Beginn der Stratifikation einsetzen kann. Die Frühjahrsblüte gilt als wichtiges saisonales Ereignis, da sie einen ersten Nahrungsimpuls im Jahreszyklus bildet und somit den reproduktiven Erfolg vieler Arten beeinflußt.

Unsere Experimente grenzen sich von anderen Studien durch die komplexe Art und Weise ab, in der das pelagische Nahrungsnetz, angefangen von den Nährstoffen bis hin zur Ebene der Copepoden, im Rahmen prognostizierter Erderwärmunsszenarien untersucht wurde. Die vorliegende Arbeit integriert die Ergebnisse aus Phytoplankton-, Ciliaten- und Copepodendaten.

In drei aufeinanderfolgenden Versuchen (Frühjahre 2005 - 2007) wurden Indoor-Mesokosmenanlagen mit den Frühjahrs-Planktongemeinsschaften besetzt und die Wassertemperaturen um 0°C, 2°C, 4°C und 6°C über den dekadischen Mittel (1993-2002) der *in situ* Wassertemperaturen in der Kieler Bucht angehoben. Zusätzlich wurde zwischen den Jahren die im Mittel eingestrahlte Lichtintensität für die durchmischte Wassersäule variiert.

Die Studien erbrachten folgende Ergebnisse: bei erhöhten Temperaturen wurde ein erhöhter Stoffwechsel in der Copepodenart *Pseudocalanus* sp., der eine Schlüsselrolle im Nahrungsnetz zukommt, registriert, sowie eine gleichzeitige Abnahme der Wachstumseffizienz. Zusammengenommen mit verstärkten Freßaktivitäten der Ciliaten bewirkte dies eine intensivere Top-Down-Kontrolle und somit eine schwächer ausgeprägte Phytoplanktonblüte bei erhöhten Temperaturen - vermutlich zusätzlich verstärkt durch eine reduzierte Wachstumseffizienz im Phytoplankton. Abhängig vom Futterangebot minderten erhöte Temperaturen den Reproduktionserfolg von *Pseudocalanus* sp. und beeinträchtigten offenbar die Entwicklung jüngerer Stadien, was

sich in einer stärkeren Abnahme der Populationen bei höheren Temperaturen widerspiegelte.

Im Hinblick auf die verschiedenen trophischen Ebenen konnten wir eine unterschiedliche Temperaturempfindlichkeit zwischen autotrophen und heterotrophen Organismen zeigen: während der Zeitpunkt der Algenblüte weniger von der Temperatur, sondern stärker von der eingestrahlten Lichtintensität abhing, traten Copepoden- und Ciliatenbiomassemaxima unter wärmeren Bedingungen deutlich früher auf. Das Zusammenspiel von Licht und Temperatur entschied letztendlich darüber, ob der Copepodennachwuchs im passenden, futterreichen Zeitfenster schlüpfen konnte und sich die Population insgesamt positiv entwickeln konnte. Bei den Ciliaten führten höhere Temperaturen zu einer stärkeren Kopplung an die Phytplanktonblüte und damit zu einem erhöhten Energiefluß durch die mikrobielle Schleife.

Zudem konnte gezeigt werden, daß steigende Temperaturen zeitliche Verläufe in Biodiversitätsmustern beschleunigten und die Größenstruktur in Populationen und Gemeinschaften veränderten: zum Zeitpunkt des Blütenmaximums ging der Trend im Phytoplankton hin zu kleineren Arten; Copepoden zeigten am Ende der Experimente eine Reduktion in der Länge des Prosomens. Möglicherweise stellt diese Tendenz zu kleineren Größen eine neue Regel dar, der Organismen im Zuge des Klimawandels unterworfen werden.

Chapter 1 - Introduction

Global warming and marine ecosystems

Oceans cover about 71% of the earth's surface, are major regulators of our climate, home to myriads of species and vital for mankind as a resource for food supply and manifold ecosystem services. Shelf ecosystems are estimated to provide ecosystem services and goods worth approximately US$ 14 trillions, or 43% of the global total product (Costanza *et al.* 1997). However, marine environments are at risk these days: human activities cause habitat destruction, pollution and exploitation, and the increasing amount of anthropogenic carbon dioxide emissions acidifies the oceans and promotes temperature increase on global scales. Rising temperatures in turn have major consequences for the whole biosphere and a growing amount of literature reports on changes, spanning from individual traits to whole community responses in all known ecosystems. But there are still many important questions about how marine environments will react to future conditions. One of them is, whether and how plankton spring bloom could be affected by increasing temperatures. The spring bloom is an essential seasonal event because it can be regarded as the first food impulse on which pelagic as well as benthic organisms depend to start their annual life cycle. Hence this topic clearly merits investigation. In our study we examined climate change impacts on the plankton spring succession in the lower trophic levels of the Baltic Sea community. The following introduction will give brief background information about current knowledge on climate change, induced abiotic and biotic responses, and the framework and aim of the present study.

The warming world

Life on earth has ever since faced changing conditions on our planet. With respect to climate, organisms had to deal with alternating periods of relatively warm and relatively cold temperatures over geological timescales. Observations of the last century indicate

that global temperatures again tend to rise. A recent study by Hansen et al. (2006) shows the increase of global ocean-land temperatures by approximately 0.8°C since the beginning of temperature records in the late 1880s (Fig. 1) and reveals, that global temperatures are already within <1°C near the maximum level of the past million years. Important questions arise: what causes this warming trend? Is it just a temporal phenomenon and emerging from natural short term variability or is it persistent? How does the biosphere respond and what biotic and abiotic responses are to be awaited for the future?

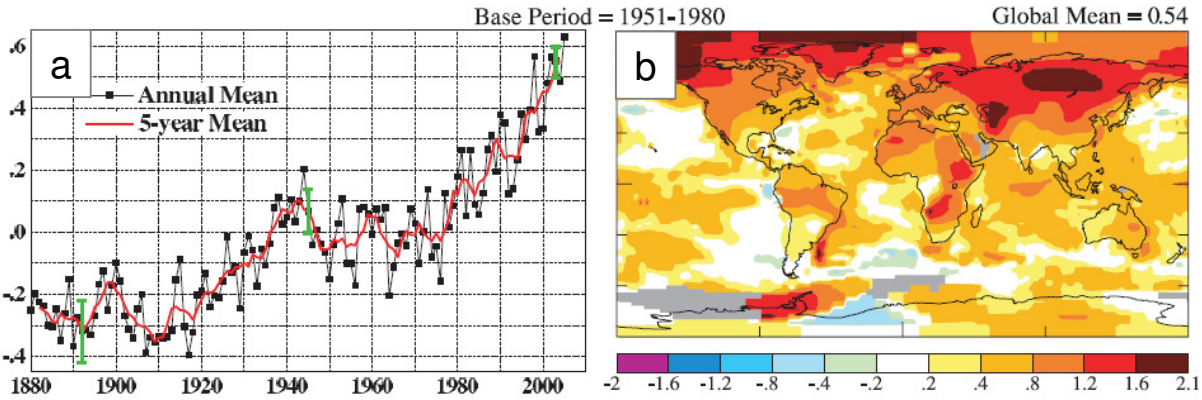

Fig. 1. Surface temperature anomalies relative to 1951–1980 from surface air measurements at meteorological stations and ship and satellite SST measurements. a) Global land-ocean temperature annual mean anomalies (°C). **b)** Mean surface temperature anomaly for the first half decade of the 21st century (200-2005). Hansen et al. (2006).

Causes and trends of global warming

The Intergovernmental Panel on Climate Change (IPCC) published its Fourth Assessment Report in 2007 (IPCC 2007) in order to address these topics and resumed that global temperature increase nowadays is a result of anthropogenic greenhouse gas emissions, such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and halocarbons. Greenhouse gases have constantly increased since the beginning of industrialisation in the 1850s and exceed by far the natural range over the last 650.000 years. Compiled data from ice cores show that for the last ≈450.000 years, global temperature patterns highly correlate with atmospheric composition and CO_2 concentrations (Petit *et al.* 1999) (Fig. 2, curves a and b). Alternative controlling factors for earth's climate are solar activity, variations in earth's orbit and tilt angle (Milankovitch cycles), the arrangement of land

masses on earth's surface, land cover and atmospheric aerosol content. Further more the circulation patterns of the atmosphere itself, ocean currents and the hydrological cycle play important roles. However, advanced climate models show that such natural forcing alone could not explain the observed increase of global temperatures (IPCC 2007).

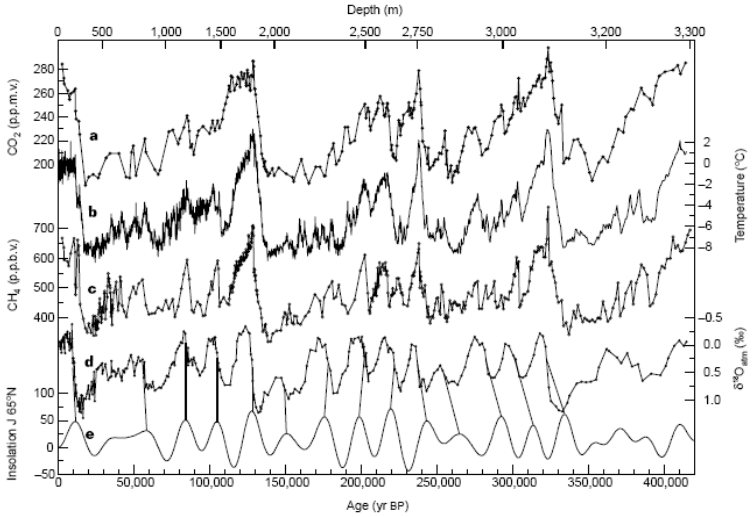

Fig. 2. Vostock ice core data. Time series of **a)** CO_2; **b)** isotopic temperature of the atmosphere; **c)** CH_4; **d)** δ^{18} O_{atm}; **e)** mid-June insolation at 65°N (in Wm^{-2}). For details see Petit et al. 1999

Indeed, it is not, that the planet just constantly warms, the rate of global warming has also increased over the past years: Hansen et al. (2006) show, that just over the past three decades, global temperatures have risen by 0.6°C, compared to 0.8°C over the last hundred years. So presently the warming rate is ≈0.2°C per decade, being higher over land than over ocean and greatest in high latitudes of the Northern Hemisphere. This speed is unprecedented at least during the last 22.000 years (Joos & Spahni 2008).

Predictions on future temperature increase

According to the latest IPCC report (2007) there is "high agreement and much evidence" that global greenhouse gas emissions will continue to grow over the next few decades. Various emission scenarios were constructed and grouped into four families (A1, A2, B1, and B2) which explore alternative development pathways. The models

consider a wide range of demographic, economic, and technological driving forces and resulting greenhouse gas emissions. According to these forecasts, temperature rise for the next century is predicted to range between 1.1 and 6.4°C (Fig. 3), and further global warming is expected for the next centuries, even if spatial greenhouse gas emissions are cut completely from now on. It has to be noted that the atmosphere is a rather chaotic system, hence several uncertainties remain. Especially feedback mechanisms leave open questions, most of all the effects of water vapour, cloud cover and ultraviolet radiation (IPCC 2007). But also biological feedback responses add further complexity to future predictions (Harley *et al.* 2006), for example planktonic productivity and the release of dimethyl sulphide by marine algae.

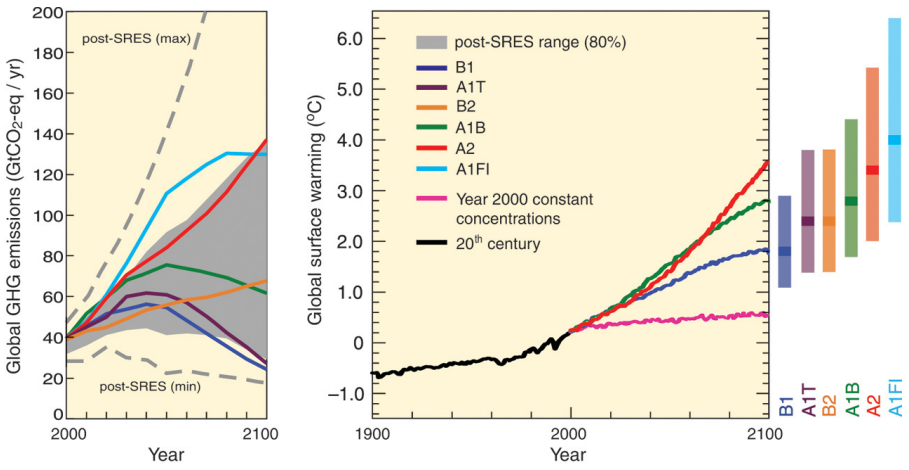

Fig. 3. Global green house gas emission (GHG) scenarios from 2000 to 2100 (in the absence of additional climate policies) and projections of surface temperatures. Left panel: Global GHG emissions (in $GtCO_2$-eq) in the absence of climate policies: six illustrative IPCC Special Report on Emissions (SRES) marker scenarios (coloured lines); grey area: 80th percentile range of recent scenarios published since SRES (post-SRES); dashed lines: full range of post-SRES scenarios. **Right panel**: Solid lines: multi-model global averages of surface warming for scenarios A2, A1B and B1, shown as continuations of the 20th-century simulations. Pink line: simulations where atmospheric concentrations are held constant at year 2000 values. Coloured bars: best estimate (solid line within each bar) and the likely range assessed for the six SRES marker scenarios at 2090-2099. All temperatures are relative to the period 1980-1999. For details see 4th IPCC Asessment Report 2007.

Abiotic responses to climate warming

Up to now a variety of "global changes" have been observed and are attributed to rising concentrations of greenhouse gases and resulting temperature increase: thawing processes extend to permafrost regions and reduce ice and snow covered areas on global scales. Indeed, climate scenarios project an almost ice free Arctic summer even

before the end of the 21st century (IPCC 2007). Furthermore, an increase in ocean heat content has been recorded (Levitus *et al.* 2005), with warming of approximately 0.037°C occurring in the upper most 3000m so far. Resulting thermal expansion and sea ice melt promote sea level rise, which will be amplified when currently warmed water masses from the mixed layers extend to the deep sea layers. Another important impact of global warming is the change of ocean currents, which are core regulators of earth's climate. A slow down of the meridional overturning circulation of the Atlantic, for instance, would have severe consequences on the global scale, such as cooling of the entire Atlantic region, more intense warming in the Southern Hemisphere, amplified sea level rise and a southward shift of the "thermal equator" (WGBU 2006). Simulations for such conditions further predict a collapse of the North Atlantic plankton stocks to less than half of their initial biomass and a decline of globally integrated export production by 20%, both because of nutrient depletion in the upper ocean (Schmittner 2005) which in turn would mean reduced CO_2 uptake (WGBU 2006). Recent projections indeed do forecast a gradual slow down of the meridional overturning circulation for the 21st century (IPCC 2007). With regard to the weather, an increasing frequency of extreme events such as heat waves, droughts, heavy precipitation and floods is expected, and tropical storms are likely to become more intense. Overall, precipitation is projected generally to increase in high latitudes and decrease in subtropical regions which will affect terrestrial-derived nutrient and pollutant inputs by runoff waters as well as coastal salinity and turbidity.

In addition to temperature mediated changes, the growing partial pressure of atmospherical CO_2 leads to another implication, the acidification of the oceans. So far, oceans' pH dropped by 0.1 units in the time period between 1750 and 1994 (Raven *et al.* 2005) and a change of the saturation horizons of aragonite, calcite and other minerals which are essential to calcifying organisms (Kleypas *et al.* 1999; Feely *et al.* 2004). Emission scenarios predict a further acidification between 0.14 and 0.35 units over the 21st century, thus reaching a pH value unprecedented for the past 200-300 million years (Caldeira & Wickett 2003; Orr *et al.* 2005). In summary, the IPPC report (2007) concludes that all observed trends in global change processes will continue and intensify for the next centuries.

Biotic responses to climate warming

A review on all available multi species studies until 2003 revealed, that 41% of the observed species had already responded to climate warming (Parmesan & Yohe 2003). These responses can be roughly grouped into four categories, corresponding to the different levels of ecological organization (Walther *et al.* 2002): temperature impacts on phenology and physiology (individual level), range and distribution of species (population level), composition of and interactions within communities (community level) and structure and dynamics of ecosystems (ecosystem level). The plethora of studies dealing with global warming effects on the biosphere was summarized in several detailed and interesting reviews and reports (e.g. Walther *et al.* 2002; Hays *et al.* 2005; Harley *et al.* 2006; Parmesan 2006; WGBU 2006; IPCC 2007), and for the sake of brevity only a few examples will be given here.

Physiology and phenology

Temperature has a direct impact on physiology, because metabolic rates (e.g. enzyme activities) vary with reaction temperature. Hence, elevated temperatures can shift individual properties, for example increase carbon fixation rates in phytoplankton (Hare *et al.* 2007), but also influence more complex traits such as feeding rates in protists (Rose & Caron 2007) or whole organism body size in general (reviewed in Millien *et al.* 2006). These species-specific, individual reactions can translate into ecologically meaningful shifts concerning the life cycle. In the context of climate warming, the best studied phenomenon so far is phenology, the timing of seasonal activities of animals and plants. For terrestrial systems, climate warming has been reported to result in an overall spring advancement of 2.8 days per decade across the northern hemisphere (Parmesan 2007): higher temperatures, for example, alter the timing of vegetation development (Menzel & Fabian 1999), thereby lengthening the growing season, or shift the egg hatching date of insects (Visser & Holleman 2001). Similarly, but to a lesser extent, changing trends in phenology were reported for aquatic species, e.g. advancing peaks for marine dinoflagellates and meroplankton (Edwards & Richardson 2004) and earlier spawning dates of marine bivalves (Philippart *et al.* 2003).

Range shifts

Global warming also affects the population level, for example in terms of species range shifts, leading to changes in zonation patterns and species invasions in polar, temperate and tropical systems. Most of the species move poleward or upward (in montane regions), thus paralleling the gradual shift of isotherms. From the terrestrial field, examples report on elevations in montane tree lines (Luckman & Kavanagh 2000) or on changing breeding and overwintering ranges in birds (Thomas & Lennon 1999; Austin & Rehfisch 2005). In the marine environment, well known examples include altered latitudinal distributions in zooplankton (Beaugrand *et al.* 2002) and fish species (Southward *et al.* 1995; Southward *et al.* 2005), indicating a shift towards a warmer dynamic equilibrium. A study on North Sea fish demonstrated that species do not only change their latitudinal range but also migrate vertically (Perry *et al.* 2005), comparable to montane species in terrestrial ecosystems. However limitations are set according to species-specific environmental tolerance, dispersal abilities and species interactions. A result can be population declines, for example reported in antarctic penguins (Smith *et al.* 1999; Croxall *et al.* 2002; Ainley *et al.* 2003) as well as in arctic seals and polar bears (e.g. Stirling *et al.* 1999). Climate warming is even linked to population extinctions (e.g. Pounds *et al.* 2006) which are thought to be already widespread and just simply not yet detected because of coarse data resolution (Thomas *et al.* 2006).

Community changes

Individual and population reactions to temperature increase translate into alterations on the next level of ecological hierarchy, the community level. In aquatic systems, data sets reveal transitions of arctic lakes towards more planktonic and warm-water associated communities (Smol *et al.* 2005), shifts of marine algal communities from diatoms towards non-silicified coccolithophores species (Stockwell *et al.* 2001; Noiri *et al.* 2005) and changes in fish communities (Holbrook *et al.* 1997) as a reaction to temperature increase. In grassland communities, altered progressions of flowering and fruiting (Sherry *et al.* 2007) as well as shifts in biodiversity and species dominance can be observed, influencing neighbouring trophic levels and the community pattern on the whole (Suttle *et al.* 2007). Such cascading effects in the food web can be a result of changes in competition strength between species (Bertness & Ewanchuk 2002; Jiang & Morin 2004) or changes in interaction strength (Sanford 1999), originating from direct temperature

effects on physiological properties, or more indirectly, from altered distributional patterns in space and time. With respect to predator-prey relationships, shifts in spatial and temporal distribution and activity can lead to mismatch situations between trophic levels, where food demand by the predator is no longer covered by the food supply, i.e. its prey species (match-mismatch hypothesis, Cushing 1972). Taken all the biotic responses reported so far into account, trophic uncoupling is very likely in the context of climate change, and several studies already report on emerging mismatch situations (see section "Trophic uncoupling").

Ecosystem responses

Expectedly, consequences of global warming can also be detected on whole ecosystem level in terms of productivity, stability and structure. Cleland and colleagues (2007) demonstrate for example, how shifts in plant phenology alter ecosystem productivity and influence carbon cycling on global scales. For marine food webs, Edwards and Richardson (2004) illustrate that decaying synchronization of successive trophic levels induces mismatch situations the North Sea and exacerbates the decline of economically important fish stocks (Beaugrand *et al.* 2003), which are already threatened by human overfishing. More dramatically, changing conditions become evident when ecosystems shift from one stable state to another (known as regime shift), thereby displaying completely new structure and functioning of the subsequent trophic levels. Such regime shifts in aquatic systems have been described for lakes (e.g. Scheffer *et al.* 2001; Scheffer & Carpenter 2003) as well as for marine (e.g. Hare & Mantua 2000; Oviatt 2004; Drinkwater 2006) and brackish water systems (e.g. Möllmann *et al.* 2003b; Alheit *et al.* 2005; Möllmann *et al.* 2008), where for the new state, conditions seem to have swung into a warm water equilibrium. Altered regimes can be fatal for the involved organisms. This is clearly depicted in a study by Bakun and Weeks (2004): they show how intensification of near-shore upwelling can lead to displacement of herbivorous grazers and thus deposition and decomposition of surplus phytoplankton biomass which in turn promotes hypoxia and thus extinction in near-shore organisms. From the human point of view regime shifts in marine ecosystems are detrimental because they are usually accompanied by severe declines if not depletions in economically exploited fish stocks (Möllmann *et al.* 2008). Nevertheless it is exactly human activities (e.g. the removal of top predators) that often trigger and amplify those sudden ecosystem transitions and

degradations (Frank *et al.* 2005; Daskalov *et al.* 2007; Österblom *et al.* 2007). In concert with additional stress through global change, unexpected and disadvantageous changes in nature are guaranteed and likely to happen more frequently.

Trophic uncoupling

Organisms can use different environmental cues to coordinate their life cycle: the seasonal onset of production and reproduction can be regulated for example via photoperiodicity, temperature or other factors. The right timing of events is vital to maximize the synchronization with resources and thus reproductive success. Consequently, species-specific shifts in phenology can result in so called mismatch situations, where predator and prey are temporally (or spatially) out of synchrony (Cushing 1972).

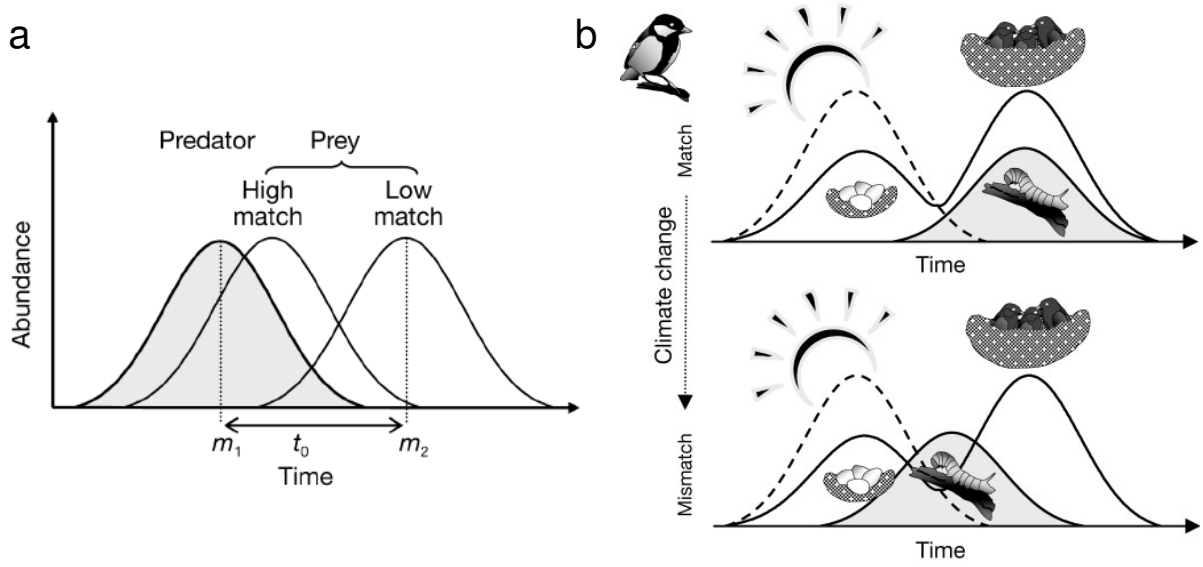

Fig. 4. Match-mismatch hypothesis (MMH). a) Scheme of MMH. Optimal temporal overlap between predator and prey when predator population peaks at time point m_1 (i.e. match situation). A shift of the predator population peak to a later time point m_2 leads to a low temporal match (i.e. mismatch situation). Durant et al. (2007), adapted from Cushing 1990. **b)** Mismatch in the Great Tit (*Parus major*). The environmental cues (dashed line), triggering onset of egg laying, change in asynchrony to the environmental conditions prevailing when chicks are reared and when birds' energetic demands are highest, as shown for the great tit. Food supply is represented by the caterpillar abundance. Durant et al. 2007, adapted from Visser et al. (1998) and corrected from Stenseth & Mysterud (2002).

Figure 4a shows schematically how a mismatch situation can emerge when timing of the prey species is temporally shifted from a synchronized timing with the predator (time

point m_1) to later occurrance resulting in low temporal overlap (time point m_2). Fig. 4b illustrates climate change induced mismatch already observed in birds (Visser *et al.* 1998): egg laying in great tits (*Parus major*) is initiated by environmental cues in a way that the energetically expensive period of feeding afterwards coincides with food availability (shown as caterpillars). Climate change has been shown to alter these environmental clues so that offspring requirements no longer meet favourable conditions and mismatch arises between food demand and supply.

Global temperature increase has already been proven to induce such mismatch situations frequently in terrestrial (e.g. Inouye *et al.* 2000; Visser & Holleman 2001; Barbraud & Weimerskirch 2006) and aquatic (e.g. Beaugrand *et al.* 2003; Edwards & Richardson 2004; Winder & Schindler 2004) ecosystems. In Lake Washington, for example, spring peaks of the keystone herbivore *Daphnia* have been advancing markedly slower than the peak timing of their main food resource (diatoms) for the last 40 years (1962-2002). As a consequence, *Daphnia* populations declined (Winder & Schindler 2004). Another example, given by Philippart et al. (2003) which shows a mismatch of bivalve larvae occurrence and phytoplankton bloom timing in the European Wadden Sea: due to increasing water temperatures, bivalves have begun to spawn earlier in the year for the last three decades, and therefore no longer match the timing of maximum food supply by phytoplankton.

In general, trophic uncoupling leads to reductions in energy flow and can thus have cascading effects through the food web. Expectedly, evolving mismatch situations are likely to influence food web structure and ultimately ecosystem stability and functioning.

The need for experimental studies

The current state of knowledge clearly shows how important it is to investigate and understand climate impacts on ecosystems at all levels of ecological organization. In our study, we have chosen an experimental approach to do so. In contrast to the collection of field data, experiments have the advantage to consist of a reduced, manageable subset of responding variables and to be conformed under clearly defined conditions of interest. Of course, conclusions have to be drawn with caution, because due to their artificial nature, experiments do not represent natural intricacy and therefore can miss

important factors which may influence the studied system under real conditions. But apart from that, experimental work a vital tool to study and explain structures and processes in a mechanistic, causal way. Furthermore, only few experimental data exist so far for marine communities with respect to global warming and trophic uncoupling (e.g. Keller *et al.* 1999), and specifically, the important question of how plankton spring phenology could be altered is not well understood yet.

Aim of this thesis

The present work investigates global warming impacts on spring plankton communities in moderately deep, well mixed water bodies such as Kiel Bight, where the phytoplankton bloom can start before the onset of thermal stratification. A set of mesocosms was established and stocked with the plankton spring community from Kiel Bight in subsequent years (2005 - 2007). Communities were exposed to different spring temperature scenarios (ambient and elevated temperatures) under natural light conditions, which varied between the years (for details of the set up see Material and Methods). We chose mesocosms as they can be seen as a bridgeover on spatial scales between field studies and culture experiments in the laboratory. Mesocosms can host whole populations or communities of small organisms and thus combine high complexity with the opportunity of experimental manipulation. Our study thus provided an insight into climate change impacts on the different levels of ecological hierarchy and allowed to capture possible responses at different scales of the marine ecosystem in a comprehensive way. It can be regarded as innovative as for the first time a complete subset of the plankton community (up to the copepod level) was exposed to controlled climate scenarios projected by the Intergovernmental Panel on Climate Change (IPCC 2001, 2007). Besides, experimental temperature and light regimes were optimized to a highly lifelike standard.

First, this thesis investigates temperature effects at the population level, focusing on the copepod *Pseudocalanus* sp. This animal can be seen as a key species in the Baltic Sea and many temperate marine ecosystems as it is abundant in northern oceans around the globe and forms a major food web link to higher trophic levels. Population dynamics and

stage structure, nutritional status, body size, as well as rates of mortality and egg production were investigated (Chapter 3). The next chapter scales up to different trophic levels and encompasses observations on functional groups in phytoplankton, ciliates and copepods. It describes biomass dynamics, timing and magnitude of biomass peaks as well as functional group compositions and investigates possible implications of trophic mismatch and altered energy flux through the food web (Chapter 4). The fith chapter steps up to the community level and analyses temperature effects on two central characteristics, biodiversity and body size (Chapter 5). The last chapter sums up conclusions and outlines further implications of our work in the context of current literature on global change (Chapter 6).

Drawbacks of the experimental design

Our set up imitated the natural temporal development of spring temperatures in Kiel Bight and the appropriate day lengths and light intensity curves. Nevertheless, it has to be noted that actual water temperatures in mesocosms of the same temperature treatment did not exactly match desired values due to an inherent variance in the applied cooling system. Additionally, inertia of the water bodies and changing ambient water temperatures at the beginning of each study slightly delayed the time point, where the mesocosms reached their specified temperature. The initial cooling (or respective heating) problem is probably negligible, as it concerned only the very first days of each study. Divergence in mesocosm temperatures of the same thermal treatment were monitored and thus did not have any negative effect on the resulting data quality as corrections were possible though usually not necessary because temperature trends clearly emerged.

Another drawback of the applied design is the problem of wall growth: depending on light intensity and duration of the experiment, a biofilm of benthic organisms grew on the mesocosm walls. Algae from this benthic community exploited the nutrient pool in the water column, hence competing with pelagic species for the present resources. Biofilms became visible very late in the experiments and though admittedly they probably enhanced nutrient limitation during the build up phase of the phytoplankton bloom, nutrients bound in benthic algae are qualitatively similar to nutrient losses due to

sedimentation. Benthic algae with a bentho-pelagic life style some times detached from the wall and further dwelled in the water column. However, such species were not important contributors to phytoplankton biomass, at least not before the onset of the bloom. Analysis thus focus on the phytoplankton bloom peak when considering aspects of peak timing and magnitude (Sommer & Lengfellner 2008).

Due to limited space and in order to keep the set up manageable, the mesocosms were restricted to a volume of 1300L (maximal filling to 1500L). For larger organisms, such as copepods, this implicates small sample size and thus larger errors in estimation - an inevitable trade off. Additionally it should be mentioned that the lack of a benthic component (in 2006 and 2007) means that benthopelagic coupling processes could not be taken into account, e.g. the supply of species germinating from resting eggs (such as *Acartia* or *Centropages*) or those being continuously released over the spring period.

Data contributions

This thesis comprises (in parts unpublished) data on phytoplankton, ciliates and copepods, collected and supplied (as raw data) by the following persons:

Kathrin Lengfellner	Mesozooplankton, metazoan microplankton, nano- and picophytoplankton (flowcytometer)
Dr. Nicole Aberle-Malzahn	Ciliates (Utermöhl microscopy)
Prof. Dr. Ulrich Sommer	Phytoplankton; all size classes (Utermöhl microscopy)

Chapter 2 - Materials and Methods

Donor site

Kiel Bight is part of the Belt Sea, one of a series of basins and swells connecting the brackish Baltic Sea with the North Sea (Fig. 5). The Bight has an average depth of 17m and is characterized by influx of low salinity surface water (maximum in May) from the Fehmarn Belt and high salinity bottom water (maximum in fall and winter) through a system of channels from the Great Belt. On average, salinity ranges between 14 to 24 PSU. From December to mid-February the water column contains little biomass (<50 mg C m^{-3}) and is rich in nutrients, usually around 1.1 mmol phosphate m^{-3} and 12.1 mmol nitrogen m^{-3}. Phytoplankton abundance during this period is low and small numbers of all the important copepod species can be found, which spent the winter in Kiel Bight (Smetacek 1985 and references therein).

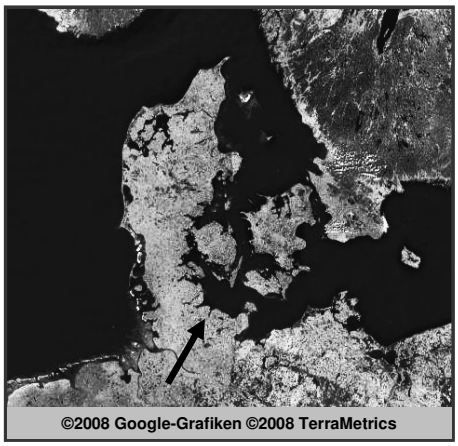

Fig. 5. **Baltic Sea Region**. Map of the western Baltic Sea region including Skagerrak, Kategat and the Belt Sea. The location of Kiel Bight is marked by the arrow. Copyright by Google (2008).

Kiel mesocosm facility

Our experiments were conducted in four climate chambers of the Leibniz Institute for Marine Sciences, Kiel, Germany. Each chamber was equipped with two 1500L mesocosms (parallel treatments), made of food safe polyethylene. This material minimized the risk of unknown substances leaking out and affecting the outcome of the studies. In the spring experiment of 2005, we had additional 300L chambers (so called benthos chambers), one connected to each 1500L mesocosm by a connecting pipe (8cm diameter) and an extra spiral pump to enable water exchange between the two mesocosms. At the bottom, the benthos chambers contained a layer of approximately 5cm sandy sediment from Kiel Bight. This layer should serve as a seed bank for organisms which hatch and develop from resting stages. Moreover, we placed 20 blue

mussels (*Mytilus edulis*) on top of the sediment layer. *Mytilus* is a common and very abundant filter feeder in the Baltic Sea and releases it's larvae during spring time (Fig. 6).

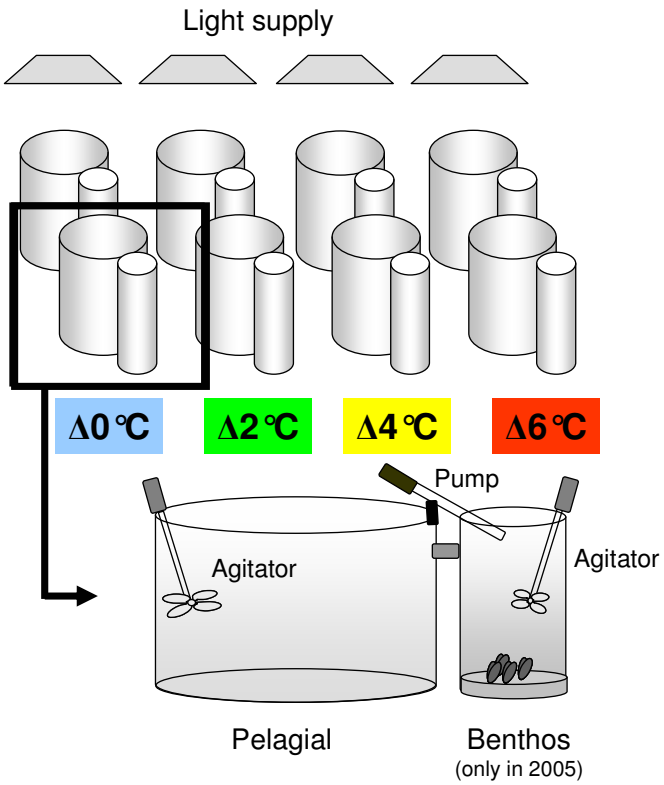

Fig. 6. Mesocosm set up. Climate chambers were run at ΔT=0°C, ΔT=2°C, ΔT=4°C and ΔT=6°C above the decadal mean of Kiel Bight spring temperatures. Each chamber was equipped with two mesocosm systems, consisting of a 1500L pelagic unit where the water column was gently stirred. Light was supplied from installed light systems above, following triangular daily light curves. In the study of 2005 an additional 300L benthic unit with a layer of sandy sediment at the bottom and filter feeding blue mussels was coupled to the pelagic unit.

Stocking procedure

At the beginning of each experiment, the mesocosms were filled with water from Kiel Bight: sea water was pumped in from the institute's pier (from 6m depth), filled into an intercepting tank and further evenly distributed to the mesocosms by hosepipes. Hence we were able to fill all mesocosms simultaneously and guarantee identical starting conditions. Damage by the pumping procedure was tolerable for algae and ciliates, but mesozooplankton organisms did not survive this kind of transfer. Thus we added mesozooplankton from net catches, gathering the organisms by vertical hauls with a 200µm WP2 net (Hydrobios, Kiel, Germany) at several stations in Kiel Bight. The catches were kept for at least 24 hours at cool conditions so that sunken dead organisms and chain forming microdiatoms could be removed before transfer into the mesocosms. We tried to keep mesozooplankton densities at natural levels and thus stocked our setup with the commensurate number of copepods, varying between approx. 12 and 20 N L^{-1} in 2005, and 7 and 10 N L^{-1} in 2006. In 2007 however, copepod abundance in Kiel Fjord

was extremely low, so we started our studies with only approx. 3 to 6 N L^{-1}. After the filling procedure, the water column in all mesocosms was stirred moderately with agitators. Stirring speed was slow enough to ensure that mesozooplankton was not harmed.

Temperature regime

For the baseline treatment (so called ΔT=0°C) we chose the decadal mean (1993-2002) of daily *in situ* temperatures from Kiel Bight. Global warming scenarios were created by adding 2°C, 4°C and 6°C upon these temperatures (so called ΔT=2°C, ΔT=4°C and ΔT=6°C treatments) during the first period in February. From March on, the temperature difference decreased by 0.25°C per month, because global warming is predicted to be stronger during wintertime on the Northern hemisphere (IPCC 2001, 2007) (Fig. 7). Each experiment started with conditions set for the 4th of February, so values for starting temperatures were 2.4°C, 4.4°C, 6.4°C and 8.4°C. It has to be mentioned that due to the big volumes it took the mesocosms a few days after the experimental start until the water reached the desired values.

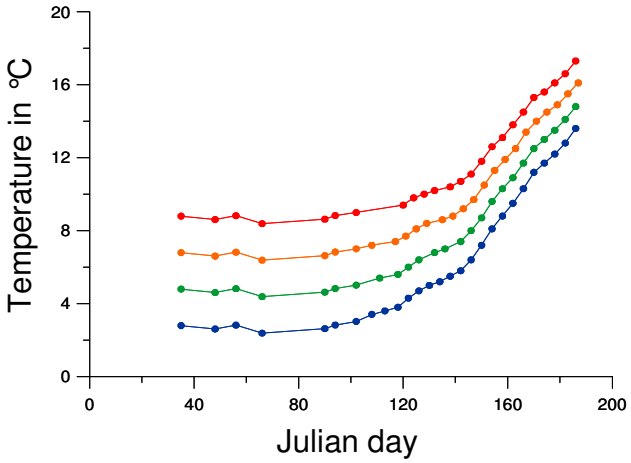

Fig. 7. Spring temperature model. Model spring temperature regimes (°C) shown for climate warming conditions within the predicted range from the IPCC. The „baseline" temperature scenario corresponds to the decadal mean of Kiel Bight water temperatures between 1993 and 2002 (blue: ΔT=0°C treatment). Climate warming regimes were elevated by +2, +4 and +6°C above the baseline (green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C treatments).

Light regime

Above each mesocosm we installed light units, containing an assemblage of fluorescent tubes (5 x T5 "Solar Tropic" tubes, and 1 x T5 "Solar Nature" tube; JBL, Neuhofen, Germany) with different spectra, in order to mimic solar irradiance as good as possible. The 1500L mesocosms were supplied by two light units (equipped with 80W tubes) whereas only one light unit (equipped with 56W tubes) was fitted to the smaller 300L chambers. Light units of each mesocosm setup were connected to computers (Profilux II,

GHL Groß Hard- and Software Logistics, Kaiserslautern, Germany) which in turn received instructions for brightening and dimming from an external control computer (data-based control program "Prometheus", GHL; modified and adjusted by MiVo-Tech, Kiel, Germany).

Daily light cycles (i.e. sunrise and sunset) corresponded to the natural conditions in Kiel Bight and were transformed to triangular light curves with integrated daily intensities, which varied between the subsequent years: in 2005 we applied 16% of the natural intensity I_0 (I_0 above cloud level, calculated according to the geographical position of Kiel after the model of Brock 1981), 64% I_0 in 2006 and 32% I_0 in 2007. All experiments started with the natural day length of the 4th of February.

Sampling procedure

Unfiltered water samples for phytoplankton and ciliates were taken thrice a week, filled into brown glass bottles and preserved with Lugol's iodine solution. Mesozooplankton was sampled by taking three vertical hauls per mesocosm with a special mini-net (Apstein type with 64µm mesh size, 12cm diameter; Eydam, Kiel, Germany). The samples were fixed with industrial alcohol (experiment in 2005) or immediately frozen with liquid nitrogen (experiments in 2006 and 2007) and later on counted separately under the binocular. On workdays, in vivo fluorescence was detected with a fluorometer (10 AU Turner Fluorometer, Turner Designs, Sunnyvale, CA, USA), and salinity as well as temperature and pH data (pH-detector by WTW, Weilheim, Germany) were collected. Colleagues from other working groups gathered further data for microbial abundance, community structure and activity (Katja Walther, Petra Breithaupt, Stefan Bleck, Regine Koppe), as well as for biogeochemical parameters and nutrient dynamics (Julia Wohlers, Andrea Ludwig, Eckart Zöllner).

Microscopic routine counts of organisms

To calculate species and genus abundances for phytoplankton and microzooplankton, fixed samples were counted according to the Utermöhl (1958) technique under the inverted microscope (DMIRB, Leica, Wetzlar, Germany and Axiovert 200, Zeiss, Ulm, Germany). For technical details see Aberle et al. (2007) and Sommer et al. (Sommer *et al.* 2007). Phytoplankton and microzooplankton (i.e. ciliates) were determined on species and genus level, copepods were resolved at the genus level. Mesozooplankton

was specified to genus level (copepods) or larval type (rest of the mesozooplankton). For the copepod genera *Pseudocalanus sp*. and *Paracalanus sp*., copepodid stages were lumped together to mixed-genus stage groups for stages C1, C2 and C3, because these genera are optically almost indistinguishable during those first stages. As only a very small amount of adult *Paracalanus sp*. appeared irregularly throughout all experiments and almost no eggs except those from *Pseudocalanus sp*., *Centropages* and *Oithona* were found, *Pseudocalanus* sp. and *Paracalanus* sp. were merged and copepodids regarded as offspring from *Pseudocalanus sp*..

Flow cytometer analysis

In order to enumerate phytoplankton cells smaller than 22µm as well as bacteria, we performed flow cytometer measurements. To adjust front scatter value and actual cell size, the instrument (FACScalibur, Becton Dickinson, New Jersey, USA) had been calibrated beforehand with different types of culture algae (*Dunaliella tertiolecta*, *Emiliana huxley*, *Isochrysis galbana*, *Merismopedia* sp., *Prorocentrum minimum*, *Rhodomonas* sp. *and Thalassiosira weißflogii*). Throughout the experiments, we calibrated both cytometer lasers (480nm and 633nm) with fluorescent latex beads (MobiTech GmbH, Göttingen, Germany) to ensure high detection quality. For analysis, mesocosm water was prefiltered by a 64µm net in order to exclude big particles that might clog the cytometer. Part of the water was fixed with formalin (final concentration 2%) and stained with SYBR Green I (Sigma-Aldrich, St. Louis, USA). Numbers and cell size of chlorophyll a, phycoerythrin and allophycocyanin containing particles (i.e. small phytoplankton) in the range of 1 to 22µm were measured from the unfixed samples. Fixed and stained samples were processed likewise for bacterial abundances with appropriate instrument settings. Where numbers and pigment contents matched between Utermöhl and cytometer counting we used data from the flow cytometer because of higher accuracy.

Body size estimation and carbon conversion

Cell size of phytoplankton and ciliates was determined under the inverted microscope by using an optical micrometer. Phytoplankton carbon content was calculated according to Menden-Deuer and Lessard (2000). For ciliate biovolume, geometric proxies were used according to Hillebrand et al. (1999) and ciliate carbon biomass was calculated

using the conversion factors given in Putt and Stoecker (1989). In addition, ciliates were grouped into size categories (small: <25 µm, medium: 25-50 µm, large: >50 µm). Copepod body size was determined for adult *Pseudocalanus sp.*: individuals were placed under a binocular (SteREO Discovery. V8, Zeiss, Ulm, Germany) and photographed (Coolpix 5000, Nikon GmbH, Germany). The pictures were digitally analyzed (Image-Pro Plus 4.5, Media Cybernetics, Maryland, USA) to estimate prosome lengths. Copepod carbon content of all genera was calculated according to literature values whereby copepodid stages C1-3 and C4-6 were lumped together. In 2005, no stage resolution of copepodids was possible and copepodid carbon was calculated by using carbon contents of adult forms only. A list of carbon conversion factors is given in the Appendix.

Elemental analysis

Adult *Pseudocalanus sp.* (5 to 15 individuals) were picked out from mesozooplankton samples, transferred into tin capsules (5 x 9mm, Hekatech, Wegberg, Germany) which were preloaded with 50 to 100µl of distilled water. Samples were dried overnight at 60°C (Memert, Schwabach, Germany). The samples were stored in a desiccator until further processing. Elemental and stable isotope analysis was performed with the HSEA-IRMS (high sensitivity elemental analyzer-isotope ratio mass spectrometer) method after Hansen and Sommer (2007).

Population growth

Under ideal conditions, populations grow according to the exponential growth model which follows the equation:

$$N(t) = N_0 \, e^{rt}$$

Usually, resources such as food or space are limited and therefore populations show logistic growth, which is characterized by a so called lag-phase at the beginning, an exponential phase (log-phase) and the final phase, where the growth rate approaches zero and the carrying capacity of the system is reached. For the exponential phase, the growth rate (r) can be calculated from the exponential equation:

$$r = \frac{\ln \frac{N_2}{N_1}}{t_2 - t_1} .$$

Egg production rate

Egg production rate (EPR) was calculated according to the egg ratio method of Edmonson (1971) following the equation

$$EPR = \frac{ER}{D} \quad [\text{eggs female}^{-1}\ \text{day}^{-1}]$$

where ER is the egg ratio (eggs female^{-1}), calculated by dividing the number of eggs per sample by the number of adult females, and D is the embryonic duration. D was estimated according to the Bělehrádek function $D = a(T-\alpha)^b$ with the parameters a, α and b given for *Pseudocalanus* and other species by Eiane and Ohman (2004).

Instantaneous mortality rates

The instantaneous the mortality rate (m_i, in day^{-1}) was calculated according to the model from Aksnes and Ohman (1996). For nauplii and copepodid stages C1 to C4, m_i is the numerical solution of the following transcendent equation:

$$\frac{A_i}{A_{i+1}} = \frac{e^{mi^*\ Di} - 1}{1 - e^{-mi\ (Di\ +\ 1)}}$$

where A_i and A_{i+1} are the abundances of stage A_i and the next stage A_{i+1} at a certain time point, m_i is the instantaneous mortality rate of stage A_i, and D_i and D_{i+1} are stage durations of stages A_i and A_{i+1}. Stage durations of each stage for each week were calculated according to the Bělehrádek function $D = a(T+\alpha)^b$, where D is stage duration time in days and T is temperature in °C. T was daily measured in each mesocosm, the parameters a, b and α for *Pseudocalanus* can be found in the literature (Eiane & Ohman 2004). As adult copepods have infinite stage duration, the mortality rate for copepodid stage C5 was calculated with a slightly simplified equation:

$$m_5 = \frac{\ln\left(\frac{A_5}{A_{adult}}\right) + 1}{D_5}$$

where D_5 is the stage duration of copepodid stage C5 and A_5 and A_{adult} are the abundances of C5 and adult *Pseudocalanus* at the time of interest. Calculations of m_i were performed on data points where at least 14 individuals of successive stages were found. Only positive values were taken into account (see Aksnes & Ohman 1996; Thor *et al.* 2008). For each mesocosm, m_i calculations for a specific stage were averaged over the whole experiment.

Encounter rates

Encounter rates (E) for *Pseudocalanus* were calculated according to the model of Kiørboe and Bagøien (2005):

$$E = ß\ C_M\ C_F \qquad [day^{-1}]$$

whereby E is the encounter rate of the entire population, ß (in m^{-3} day^{-1}) is the search volume rate of males and C_M and C_F (in N m^{-3}) are the concentrations of males and females. Female encounter rates (E_F) are the product of ß and C_M. ß has been derived from experiments and is given for *Pseudocalanus* as ß = 0.094m^{-3} day^{-1}.

Richness, evenness and diversity

Species or genus richness (R_S or R_G) gives the number of different species or genera of a certain group at a certain time point. Diversity (H') was calculated after Shannon and Weaver (1963):

$$H' = -\sum_{i=1}^{S} p_i \log(p_i)$$

p_i is the relative abundance of a species or genus i from the sum of individuals of the focal species or genus pool (S), e.g. phytoplankton, ciliates or copepods.

Species or genus evenness (E_S or E_G) is calculated according to the following equation:

$$E = \frac{H'}{H_{max}}$$

H_{max} is the maximum diversity calculated as $H_{max} = -\log(p_i^{-1})$.

Level of significance

Generally, regressions, correlations and any other statistical calculations were considered to be significant if the p-value was $p \leq 0.05$.

Software

Zooplankton pictures were digitally analyzed with Image-Pro Plus 4.5 (Media Cybernetics, Maryland, USA). Basic calculations were performed with Microsoft Excel (Microsoft Corporation, Washington, USA), statistical analysis were made with

STATISTICA 8.0 (Statsoft Inc., Oklahoma, USA), and plots were drawn with Grapher 5.03 (Golden Software Inc., Colorado, USA) or SigmaPlot 10.0 (Systat Software Inc., California, USA). Data from the flowcytometer were analyzed with CellQuestPro (Becton & Dickinson, New Jersey, USA). Numerical solutions for mortality rate calculations were generated with Maple 12.0 (Maplesoft, Waterloo Maple Inc., Ontario, Canada).

Chapter 3 - Population dynamics and physiological responses of *Pseudocalanus* sp.

Introduction

Copepods

A special focus of this thesis lies on the copepod fraction, which formed the highest trophic level in our experimental plankton community. Copepods can be generally regarded as key components in marine food webs and many aquatic ecosystems because of several reasons: on the one hand, they are globally distributed across all oceans, marginal seas and brackish water environments and supposed to be the most numerous metazoans worldwide (Mauchline *et al.* 1998). On the other hand copepods are important grazers of phytoplankton and microzooplankton and form the dominant link between primary production, the microbial loop and higher trophic levels (Atkinson 1996). Therefore, copepods play a fundamental role in the upper ocean, exporting, redistributing and repackaging carbon and nutrients (Banse 1995).

The model species *Pseudocalanus* sp.

In our study, we put special emphasis on the investigation of the copepod genus *Pseudocalanus*. As we did not perform any genetic analysis, we refer in our experiments simply to the genus level. *Pseudocalanus* is one of the dominant copepods in the northern hemisphere - widespread in the northern seas round the globe (North Atlantic, North Pacific, parts of the Mediterranean and the Black Sea), virtually found in all sampled areas and often numerically the most abundant group per sample (Corkett & McLaren 1978). In many temperate food webs *Pseudocalanus* is seen as a key species of the pelagic zone because it serves as a major food organism for larval as well as for adult pelagic planktivorous fish (Cardinale *et al.* 2002; Möllmann *et al.* 2003b; Rönkkönen *et al.* 2004). In the Central Baltic Sea for example, it plays a key role in the stock dynamics of herring, sprat and cod (Hinrichsen *et al.* 2003; Möllmann *et al.* 2003a).

Pseudocalanus populations in the Baltic Sea are probably comprised mainly by specimens of *Pseudocalanus ascuspes* (Frost 1989), a species that mainly inhabits high latitudes and is considered to be a glacial relict species originating from North Atlantic habitats of the Arctic and Norwegian Sea (Renz *et al.* 2007). This explains its affinity to cold and high saline waters (Renz & Hirche 2006) in the Baltic Sea, where temperature and salinity conditions pose a physiological limit to *P. ascuspes*.

Because of its importance in trophodynamics, the genus *Pseudocalanus* has become a very well studied model organism. A fundamental, detailed work comprising the available literature until the mid seventies, is given by Corkett and McLaren (1978). Since then, an avalanche of information came up on geographic distribution (e.g. Barnard *et al.* 2004) and important physiological aspects such as reproduction (e.g. Irigoien *et al.* 2005; Napp *et al.* 2005; Renz *et al.* 2007; Renz *et al.* 2008), mortality (e.g. Hirst & Kiorboe 2002; Eiane & Ohman 2004), grazing (e.g. Leising *et al.* 2005; Fileman *et al.* 2007), growth and development with regard to temperature (e.g. Hirst & Bunker 2003; Dzierzbicka-Glowacka 2004a, b; 2005) and food quantity (e.g. Vidal 1980a; Breteler *et al.* 1995; Hirst & Bunker 2003) as well as food quality (e.g. Koski *et al.* 1998). Most of these studies are based on field data or experiments with copepod monocultures and a small variety of specific food items – often only one or two algae species. In contrast to this, our experimental setup was designed to reveal temperature effects on *Pseudocalanus* physiology and population dynamics within an complex subset of the Baltic Sea pelagic food web up to the trophic level of mesozooplankton. Our natural spring plankton assembly offers a variety of food resources as well as competitors for *Pseudocalanus*. Therefore, our study reflects a more realistic picture of the whole plankton community confronted with climate induced water warming. The response of *Pseudocalanus* to temperature change in this context is described in the following chapter. Experimental results from the studies in 2006 and 2007 will be given, depicting overall population dynamics, sex ratios, egg production rates, nutritional status and body size. These data should outline possible impacts of climate change on the population level of ecological hierarchy.

Results

Population dynamics

The development of the *Pseudocalanus* population (nauplii and copepodid stages) in the year 2006 was characterized by initial, rather short growth phases in all temperature treatments and declining abundances thereafter (Fig. 8a). Growth and decline phase had different temporal patterns in the different temperature treatments: abundances increased and then dropped first in the warmest mesocosms and successively later in the colder treatments. Population growth rates were positively correlated to temperature treatment: in the warmer treatments, at ΔT=6°C, the *Pseudocalanus* populations had higher exponential growth rates (r = 0.08 day^{-1}, growth rate significant only for one mesocosm) than those in the coldest mesocosms at ΔT=0°C (r = 0.04 day^{-1} for both mesocosms). Across the gradient of applied temperature treatments, the growth rate increased by 0.008 per °C (Tab. 1). Rates of population decline after the maximum could only be calculated for the treatments ΔT=2°C, ΔT=4°C and ΔT=6°C because there were not enough data points at ΔT=0°C to estimate population decline correctly. No significant trend was found (Tab.1).

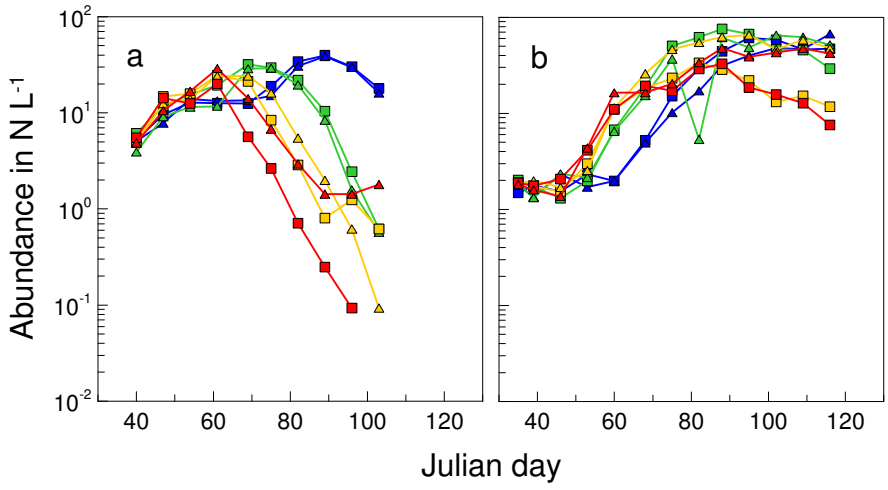

Fig. 8. *Pseudocalanus* population dynamic. Time series of *Pseudocalanus* abundance (N L^{-1}) in **a)** 2006 and **b)** 2007 shown for the different temperature treatments. Note the logarithm scale on the y-axis. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

A similar temperature effect on population dynamics was found in 2007, where abundances increased earlier in the warmer treatments and later the coldest ones (Fig.

8b). Around Julian day 75, the temperature effect was blurred because of unequal development between the parallel mesocosms at ΔT=6°C and ΔT=4°C: one mesocosm showed rising copepod numbers and the other a decline of the *Pseudocalanus* population. At ΔT=0°C and ΔT=2°C numbers still increased after Julian Day 75 and began to slightly decrease from Julian Day 88 onwards. Thus, no temperature dependent trend could be found for population growth rates (Tab. 1). The highest growth rates occurred in the intermediate temperature treatments at ΔT=2°C (0.13 day^{-1} in one mesocosm) and ΔT=4°C (0.12 day^{-1} in one mesocosm). Neither linear nor cubic models gave significant fits for temperature dependance of growth rates because parallel mesocosms differed too much from each other. Rates of decline could not be calculated because only three out of eight mesocosms showed clearly declining abundances.

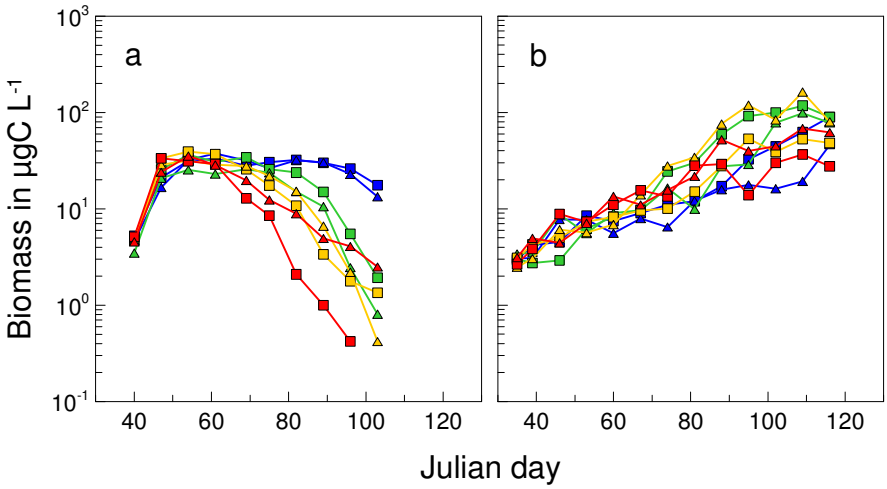

Fig. 9. *Pseudocalanus* biomass dynamic. Time series of *Pseudocalanus* biomass (µg C L^{-1}) in **a)** 2006 and **b)** 2007 shown for the different temperature treatments. Note the logarithm scale on the y-axis. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

Conversion of *Pseudocalanus* abundance data into biomass (i.e. carbon content) gave similar dynamics for the populations in 2006 (Fig. 9a): in 2006, biomass declined earlier and earlier in the warmer treatments whereas in 2007 (Fig. 9b) no temperature related trend emerged.

Table 1. *Pseudocalanus* population growth (r_G, in day^{-1}) and decline (r_D, in day^{-1}) rates during the exponential phase. r_G, r_D according to the model: $r = y_0 + a(\ln x)$.

ΔT	0	0	2	2	4	4	6	6
r_G 2006	0.037	0.036	0.053	0.059	ns	0.071	ns	0.083
r_D 2006	ns	ns	-0.104	-0.122	-0.104	-0.130	-0.136	-0.068
r_G 2007	0.101	0.097	0.121	0.093	0.087	0.122	0.064	0.075
r_D 2007	n.s.	n.s.	-0.036	n.s.	-0.031	n.s.	-0.042	n.s.
Dependence of r_G, r_D on temperature elevation ΔT according to the regression model: $f(x) = y_0 + a\,\Delta T$								
	y_0	a	p					
r_G 2006	0.038	0.0079	***					
r_D 2006	n.s.	n.s.	n.s.					
r_G 2007	n.s.	n.s.	n.s.					
r_D 2007	n.s.	n.s.	n.s.					

n.s. = not significant; **** = p≤0.0001; *** = p≤0.001; ** = p≤0.01

Stage structure

Figure 10 and Figure 11 give the abundances of nauplii (all stages as one bulk group) and copepodid stages in 2006 and 2007. Copepodid stages were counted separately, except in 2006, where stage C4 and C5 were lumped together to a mixed group (C4+5).

The stage structure in 2006 showed very similar patterns in all treatments (Fig. 10): at the beginning of the study, nauplii abundances were low and the population was dominated by stages C1 to C3. Numbers of these younger stages declined until Julian Day 61 in the coldest treatment and around Julian Day 54 in the warmer treatments, and the abundance of older stages increased instead. Until the nauplii maximum, stage group C4+5 also decreased so that apart from the nauplii, adult *Pseudocalanus* individuals were the dominating age class. An increase of C1 could be observed in all treatments with a peak around Julian Day 61 at ΔT=6°C and ΔT=4°C and a week or two later at ΔT=2°C and ΔT=0°C. At the same time, or soon after, there was also a slight increase in stages C2 and C3. After the nauplii maximum, nauplii and adult forms continued to dominate the stage distribution, whereby both decreased in their abundances until the end of the experiment. Overall, the stage structure showed a rather similar pattern across all temperature treatments, and differences between the treatments arose mainly with respect to the abundance of nauplii: highest numbers were found in the colder treatments, lower numbers in the warmer treatments. In addition, there was a temperature related reappearance of stage C1: on average its peak appeared 3.6 days $°C^{-1}$ later at colder temperatures (linear regression model: $f(x) = 77.15 - 3.55\Delta T$; $p = 0.0005$).

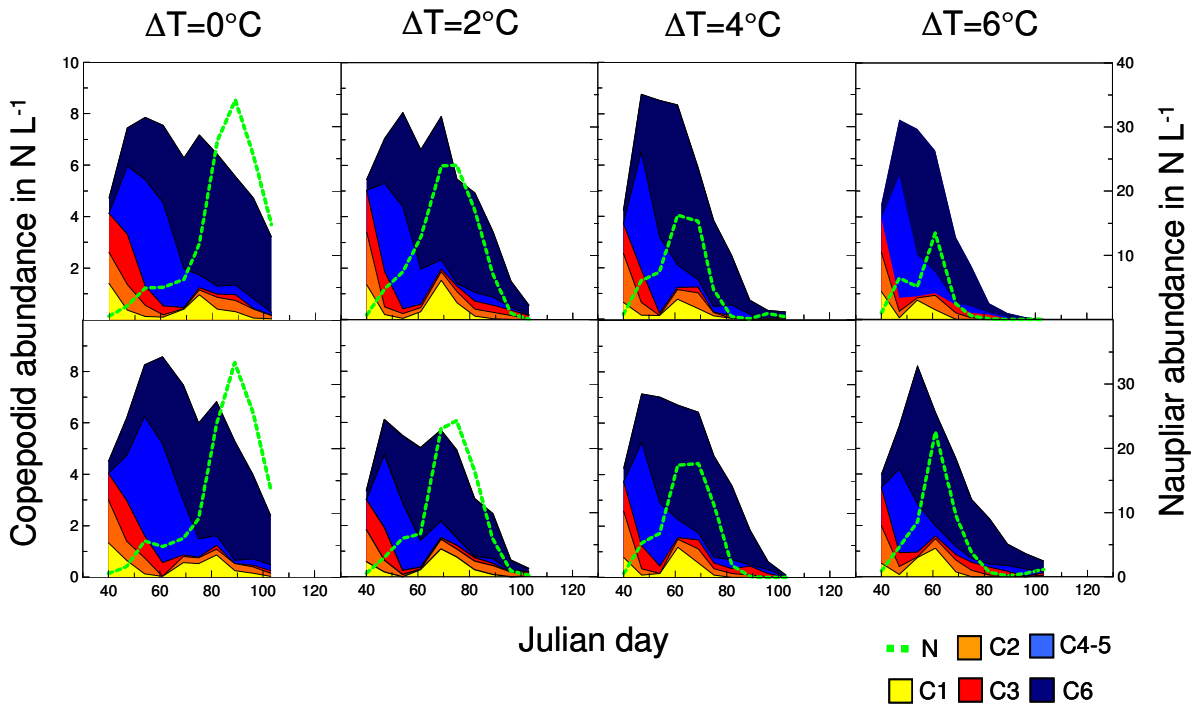

Fig. 10. Pseudocalanus stage structure 2006. Time series of *Pseudocalanus* naupliar and copepodid stage abundances (N L^{-1}) shown for the different temperature treatments. Abundances of copepodid stages scale to the left y-axis, nauplii scale to the right y-axis. Dotted green line (N): sum of all naupliar stages; area plots: copepodid stages: yellow (C1): first stage; orange (C2): second stage; red (C3): third stage; bright blue (C4-5): fourth and fith stage; dark blue (C6): adult forms

Compared to 2006, stage distribution in 2007 revealed a contrary pattern (Fig. 11): in this experiment, copepodid stages fluctuated at very low numbers at the beginning and gained relative abundance only shortly before the nauplii peak. At the timing of the nauplii peak and thereafter, all copepodid stages could be found in all temperature treatments, some depicting a succession of stages: plot area and peak of the older stage was skewed to the right side of younger stage's plot. No trend in stage distribution could be found with respect to temperature treatment except that at ΔT=0°C and ΔT=2°C on average a higher recruitment of stages C1 to C5 occurred.

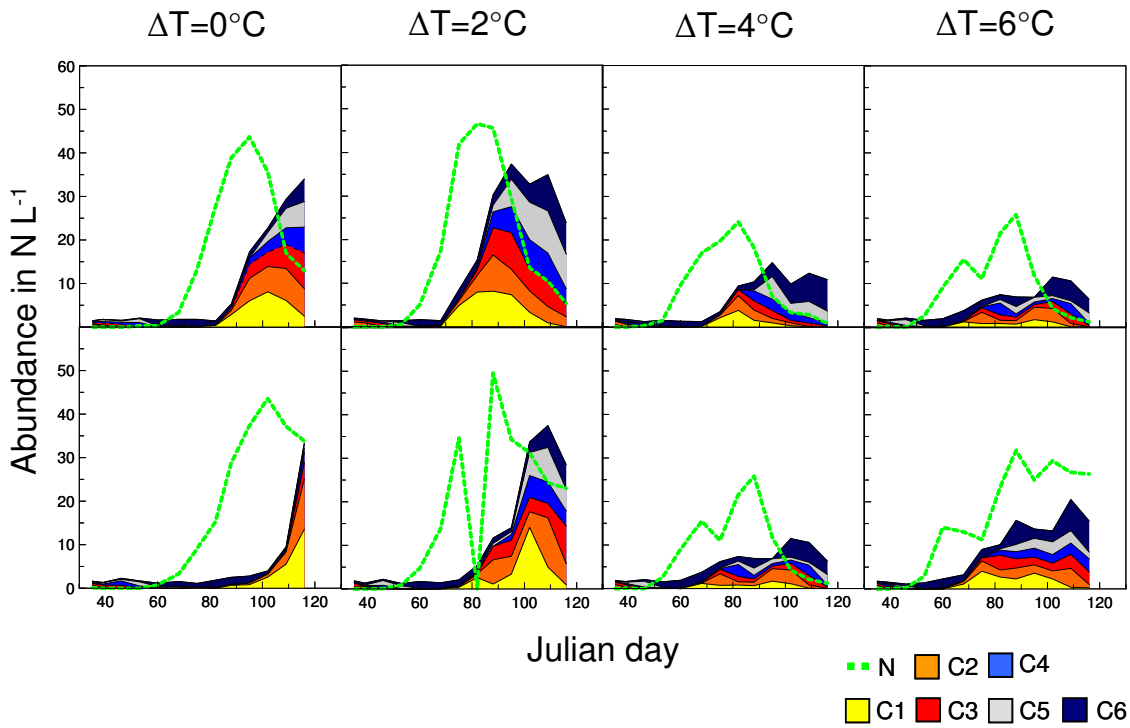

Fig. 11. Pseudocalanus stage structure 2007. Time series of *Pseudocalanus* naupliar and copepodid stage abundances (N L^{-1}) shown for the different temperature treatments. Dotted green line (N): sum of all naupliar stages; area plots: copepodid stages: yellow (C1): first stage; orange (C2): second stage; red (C3): third stage; bright blue (C4): fourth stage; grey (C5): fith stage; dark blue (C6): adult forms.

Instantaneous mortality rate

On basis of the stage structure, instantaneous mortality rates (m_i) were calculated according to the vertical life table method (Aksnes & Ohman 1996, see Materials and Methods) and estimates averaged over the experimental period. In 2006, it was only possible to calculate m_i for naupliar stages (all stages in one group). Values for m_i ranged between 0.06 day^{-1} and 0.12 day^{-1} without any temperature dependency (Fig. 12a). In 2007, m_i could be calculated for nauplii (all stages in one group) and copepodid stages C4 and C5. Values for m_i in nauplii ranged from 0.02 day^{-1} to 0.12 day^{-1} without temperature dependency, but with a clear difference between m_i in the coldest mesocosms at ΔT=0°C (m_i = 0.04 day^{-1} and 0.03 day^{-1}) and m_i in one of the warmest mesocosms at ΔT=6°C (m_i = 0.12 day^{-1}). Data from the other mesocosm at ΔT=6°C rendered only one single calculation possible and may thus not be very reliable (Fig. 12b). For the C4 stages in 2007, m_i ranged from 0.05 day^{-1} to 0.14 day^{-1} and seemed to show a weak temperature dependency with increasing mortality at higher temperatures. However, the trend was not significant (Fig. 12c). In the C5 stages of 2007, m_i ranged

from 0.12 day^{-1} to 0.19 day^{-1} and the trend appeared reversed, with m_i being on average lower at ΔT=4°C and ΔT=6°C, compared to ΔT=0°C and ΔT=2°C. Again, the trend was not significant (Fig. 12d). Generally, in all temperature treatments there was a tendency of increasing mortality with older stages, as the stages could be ordered according to thier m_i-values as follows: nauplii < C4 < C5. The only exception to this was one mesocosm at ΔT=2°C, where the order was: nauplii and C4 < C5.

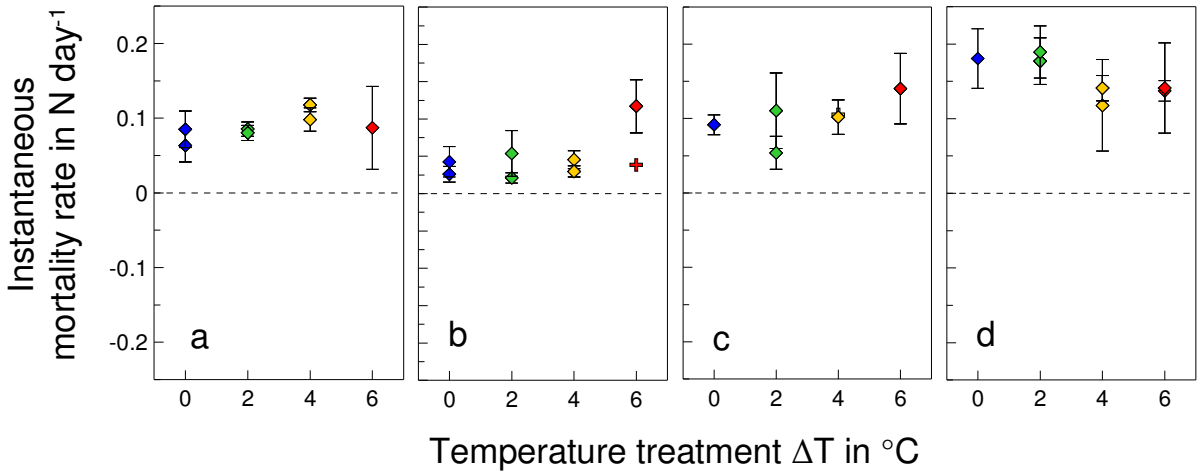

Fig. 12. Instantaneous mortality rates of *Pseudocalanus*. Mean instantanous mortality rates (m_i, day^{-1}) for *Pseudocalanus* stages shown for the different temperature treatments. m_i for **a)** nauplii in 2006, **b)** nauplii in 2007, **c)** copepodid stage C4 in 2007 and **d)** copepodid stage C5 in 2007. Crosses mark single calculations; squares show multiple calculations (only positive values acc. Thor et al. (2008)) where N = 2 to 6; error bars indicate ±1 SE.

Male and female dynamics, sex ratio and female encounter rates

Figure 13 and Figure 14 show the abundance data of female and male *Pseudocalanus* and resulting sex ratios from the studies of 2006 and 2007. On basis of male abundance data, female encounter rates (E_F) were calculated according to the model presented by Kiørboe and Bagøien (2005) (see Materials and Methods).

In 2006, the abundance of male and female *Pseudocalanus* displayed similar dynamics (Fig. 13a, b): on the first sampling day in 2006, neither adult male nor adult female individuals were found. From Julian Day 47 on, male and female abundance increased at the beginning and then decreased in a temperature dependent way: increase, peak and decline happened earlier in the warmer mesocosms compared to the colder ones. Peaks in male abundance advanced with 5.1 days °C^{-1} (linear regression model: f(x) = 80.8 - 5.1ΔT; p = 0.002) and female peaks with 3.9 days °C^{-1} (linear regression model: f(x) = 80 + 3.88ΔT; p = 0.0007). On the last sampling day, no females were found in one of the

warmest mesocosms at ΔT=6°C. Sex-ratios overall declined from the beginning on and there was a tendency towards faster decline at higher temperatures. However, this trend was not significant. Increasing ratios at ΔT=4°C and ΔT=6°C at the end of the experiment are due to a slight increase in male numbers. From Julian Day 60 on, females dominated the adult population and sex-ratios were below 1.0 in all treatments (except for the last date in one mesocosm at ΔT=4°C) (Fig. 13c). Encounter rates basically reflected the pattern of male abundances due to the calculation method. It can be noticed, that males reached the detection limit in one of the warmest mesocosms at ΔT=6°C on Julian Day 89 and in one mesocosm at ΔT=2°C on Julian Day 96. This translated into a minimal encounter rate of E_F = 1.5 day^{-1} per female. In the coldest treatment at ΔT=0°C, encounter rates for females were still very high at the end of the study with values of E_F = 43.8 day^{-1} and 56.9 day^{-1} (Fig. 13d).

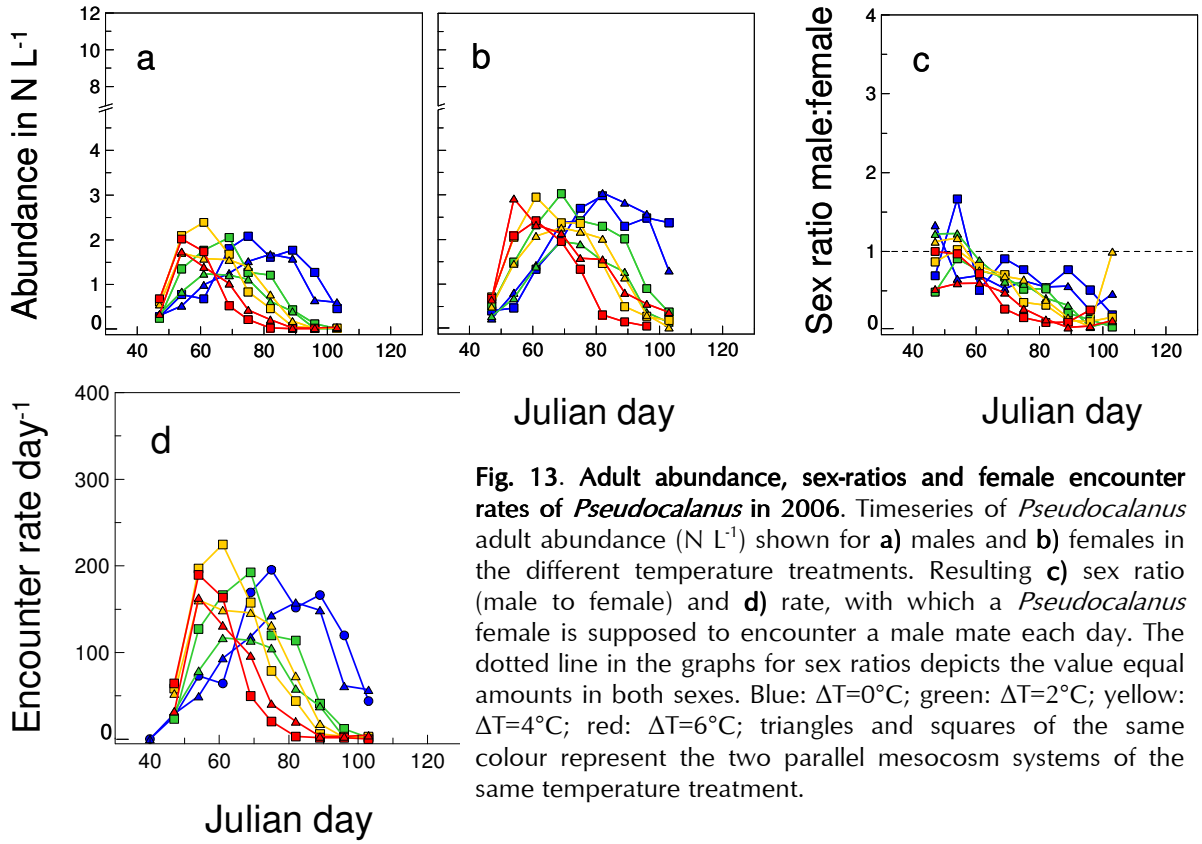

Fig. 13. Adult abundance, sex-ratios and female encounter rates of *Pseudocalanus* in 2006. Timeseries of *Pseudocalanus* adult abundance (N L^{-1}) shown for **a)** males and **b)** females in the different temperature treatments. Resulting **c)** sex ratio (male to female) and **d)** rate, with which a *Pseudocalanus* female is supposed to encounter a male mate each day. The dotted line in the graphs for sex ratios depicts the value equal amounts in both sexes. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

In 2007, no adult females were found within the first 2 to 3 weeks, except for one mesocosm at ΔT=2°C. Adult males appeared first between Julian Day 35 and 46 at ΔT=6°C and ΔT=4°C, and successively later in the colder mesocosms (Julian Day 53 at ΔT=2°C and Julian Day 60 at ΔT=0°C). Over the whole experimental period, abundances

of both sexes continuously increased in a fluctuating manner. In the coldest mesocosms at ΔT=0°C, dynamics of both sexes timely lagged behind those in the warmer treatments at ΔT=2°C, 4°C and 6°C (Fig. 14a, b). Sex ratios fluctuated during most of the experimental period below 1.0 without any obvious temperature related trend. In the first part of the study, males sometimes dominated, resulting in peak sex-ratios above 1.0. Zero values were reached in one of the coldest mesocosms at ΔT=0°C at the end of the experiment because no males were found in the samples (Fig. 14c).

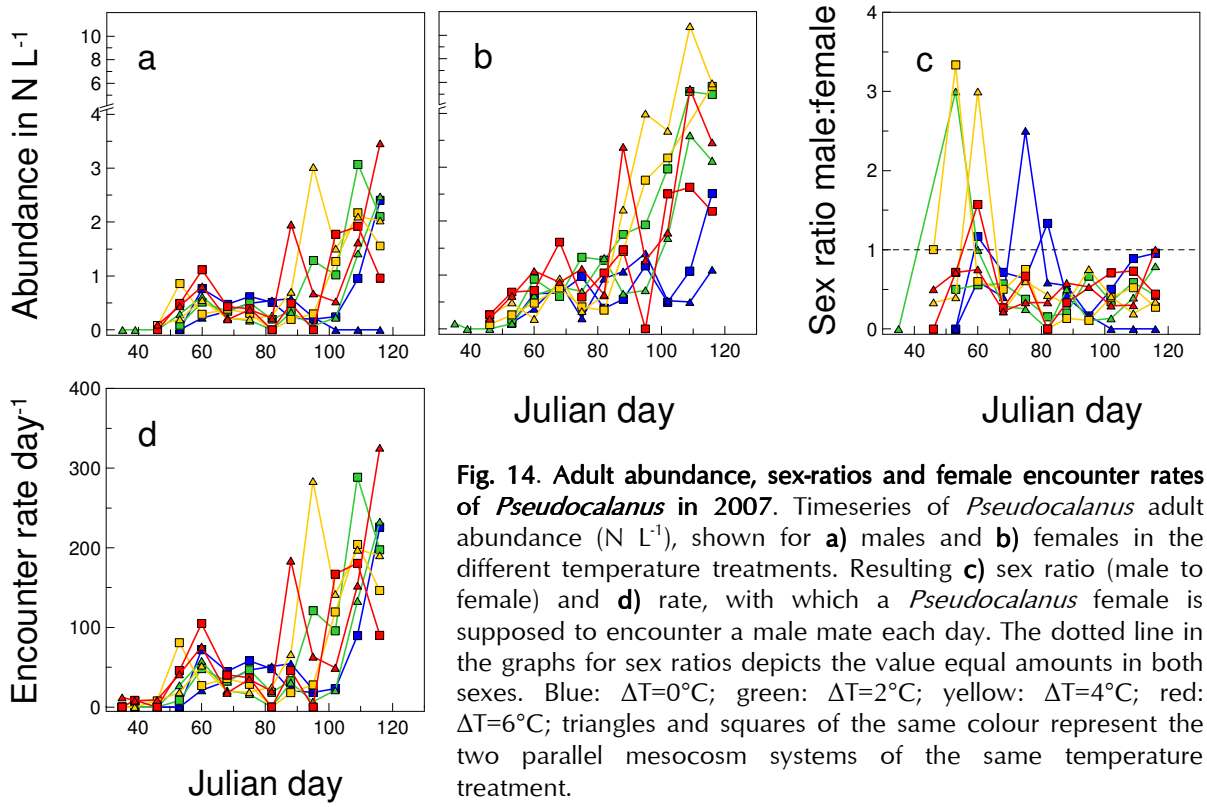

Fig. 14. Adult abundance, sex-ratios and female encounter rates of *Pseudocalanus* in 2007. Timeseries of *Pseudocalanus* adult abundance (N L^{-1}), shown for **a)** males and **b)** females in the different temperature treatments. Resulting **c)** sex ratio (male to female) and **d)** rate, with which a *Pseudocalanus* female is supposed to encounter a male mate each day. The dotted line in the graphs for sex ratios depicts the value equal amounts in both sexes. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

Encounter rates started with values of E_F = 7.7 day^{-1} and higher at the time when the first males were detected. In the warmer treatments at ΔT=2°C, 4°C and 6°C, the general trend of E_F was characterized by a first peak between Julian Day 50 and 60, a minimum around Julian Day 80 and increase thereafter. In the coldest treatment at ΔT=0°C, the intermediate peak was broad and located between Julian Day 60 and 80. Minimum values for E_F were found around Julian Day 95 and thereafter E_F increased towards the end of the study. An exception to this was one mesocosm at ΔT=2°C, where E_F dropped intermediately to E_F = 6.7 day^{-1} on Julian Day 95. In one of the coldest mesocosms at ΔT=0°C, the encounter rate for females was zero because male abundances fell below the detection limit (Fig. 14d).

Egg production

Egg production rate (EPR) was calculated according to the egg ratio method of Edmonson (1971) and timeseries for egg ratio (ER) and EPR are shown for each temperature treatment in Figure 15. To investigate the relation of egg production and food supply, ER was regressed versus phytoplankton carbon content (Fig. 16). Table 2 shows the regressions for maximal EPR and maximal ER versus temperature treatment.

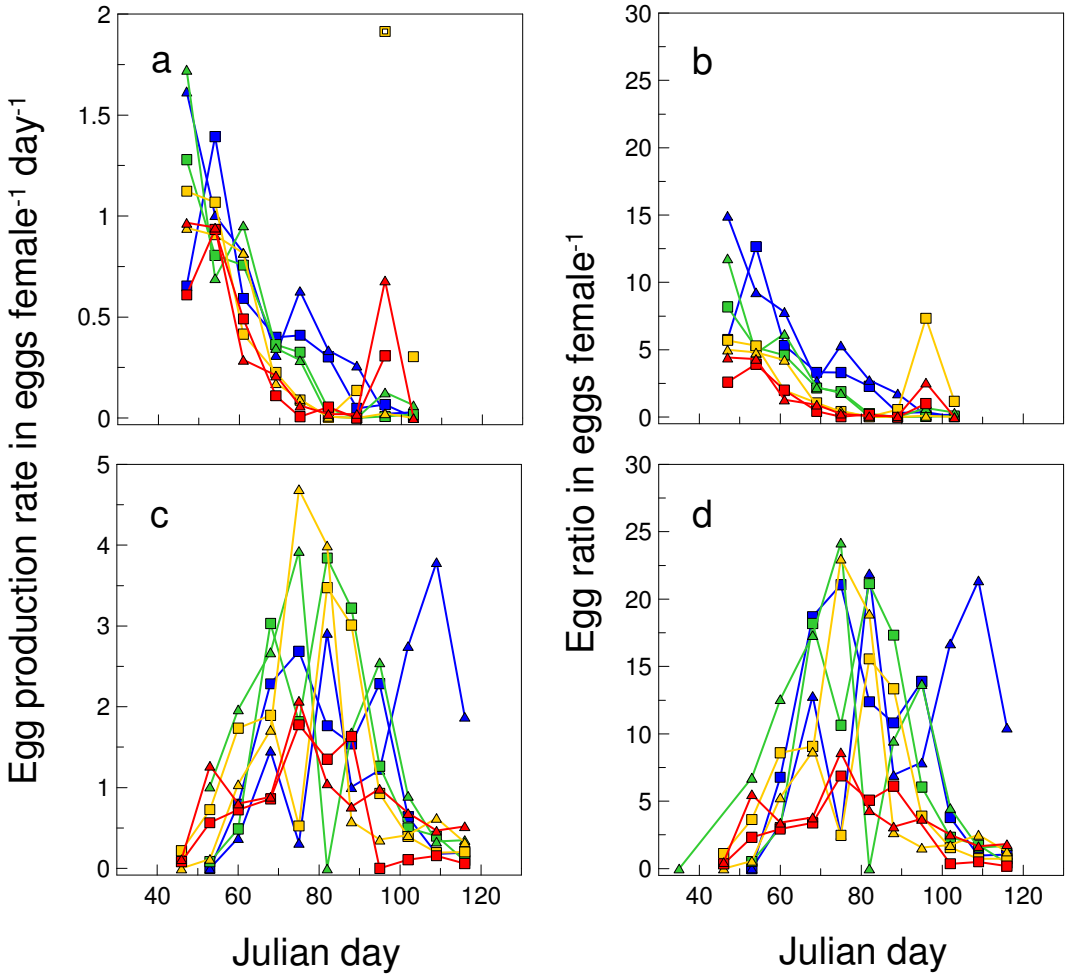

Fig. 15. Egg production rates and egg ratios in *Pseudocalanus*. Egg production rates (eggs female^{-1} day^{-1}) of *Pseudocalanus* females shown for the different temperature treatments in **a)** 2006 and **c)** 2007. Note the different scale on the y-axis. The underlying egg ratios (eggs female^{-1}) are given in **b)** for 2006 and **d)** for 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

In 2006, EPR generally declined more or less continuously from the beginning of the experiment onwards in all treatments. Maximal EPR at the start showed a significant negative correlation with temperature (Tab. 2): rates were higher in the colder mesocosms at ΔT=0°C (1.4 and 1.6 eggs female^{-1} day^{-1}) and ΔT=2°C (1.3 and 1.7 eggs female^{-1} day^{-1}), and lower in the warmer treatments at ΔT=4°C (0.9 and 1.1 eggs female^{-1} day^{-1}) and ΔT=6°C (0.9 and 1.0 eggs female^{-1} day^{-1}) (Fig. 15a). The same significant trend could be seen in the egg ratios which ranged from 3.9 and 4.4 eggs female^{-1} in the warmest mesocosms, up to 12.7 and 14.9 eggs female^{-1} in the coldest ones (Tab. 2). ER dynamics were similar to those of EPR. No statistically significant temperature effect on the decline rates of both, EPR and ER, were found (Fig. 15b). A different dynamic could be observed in 2007, where egg production started almost at zero in all temperature treatments, then increased to peak values between Julian Day 75 and 82 and declined thereafter to minimum values at the end of the experiment. An exception to this was one of the coldest mesocosms at ΔT=0°C, where the egg production reached a second maximum (Fig. 15b). No temperature related trends could be found for EPR growth or decline rates. Maximum EPR ranged from 1.8 to 4.7 eggs female^{-1} day^{-1} and did not show any temperature related pattern. Egg ratios of 2007 were very high in the colder treatments at ΔT=0°C and ΔT=2°C, with more than 21 eggs female^{-1}. At ΔT=4°C, 15.6 and 23.0 eggs female^{-1} were found at maximum and only 6.9 to 8.6 eggs female^{-1} at ΔT=6°C. This resulted in a significant positive correlation of temperature an egg ratio (Tab. 2), however seemingly driven by the comparably low egg ratios in the warmest treatment.

Table 2. Maximum egg ratio (ER_{MAX}, in eggs female^{-1}) and egg production rate (EPR_{MAX}, in eggs female^{-1} day^{-1}) of *Pseudocalanus*.

ΔT	0	0	2	2	4	4	6	6
ER_{MAX} 2006	12.7	14.9	8.2	6.2	5.7	4.8	3.9	4.4
ER_{MAX} 2007	21.1	21.9	21.1	24.2	15.6	23.0	6.9	8.6
EPR_{MAX} 2006	1.39	1.62	1.28	1.72	1.12	0.94	0.93	0.97
EPR_{MAX} 2007	2.69	3.79	3.84	3.93	3.47	4.69	1.78	2.07
Dependence of ER_{MAX}, EPR_{MAX} on temperature elevation ΔT according to the regression model: $f(x) = y_0 + a\,\Delta T$								
	y_0	a	p					
ER_{MAX} 2006	12.22	-1.54	**					
ER_{MAX} 2007	24.48	-2.23	0.02					
EPR_{MAX} 2006	2.96	-0.46	***					
EPR_{MAX} 2007	n.s.	n.s	n.s.					

n.s. = not significant; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

With respect to food resources (phytoplankton carbon content, PC), both years revealed a positive correlation between overall ER and phytoplankton carbon content (whole data sets across all temperatures, log-transformed) whereby the four thermal regimes apparently did not differ from each other (single exponential models: $ER_{2006} = 9.51(1 - e^{-0.0067 \log PC})$; $p < 0.0001$ and $ER_{2007} = 13.22\ (1 - e^{-0.0183 \log PC}$; $p < 0.0001$) (Fig. 16).

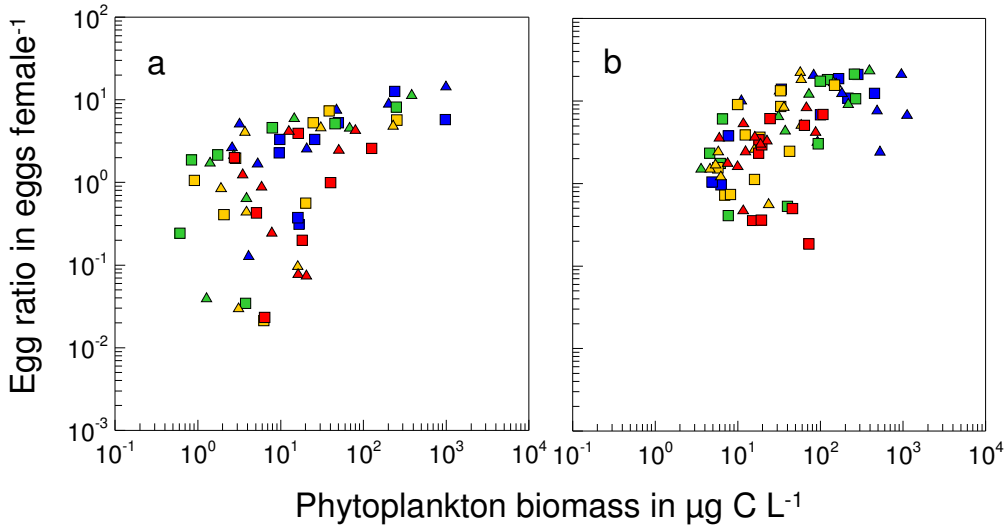

Fig. 16. Egg ratios of *Pseudocalanus* versus phytoplankton biomass. The number of eggs produced per female *Pseudocalanus* shown in relation to the amount of available food in terms of phytoplankton biomass (µg C L^{-1}) in **a)** 2006 and **b)** 2007. Note the logarithm scale on both axis. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C; triangles and squares of the same colour represent the two parallel mesocosm systems of the same temperature treatment.

Body size

Female mean prosome length at the end of the study period in 2006 ranged from 1008µm to 1098µm (Fig. 17a). In 2007, female prosome length varied between 984µm and 1082µm whereas male individuals were much smaller with prosome lengths between 824µm and 906µm (Fig. 17b). Generally, body size for both sexes was negatively correlated to temperature treatment: at higher temperatures, final prosome length was smaller (Tab. 3). Over a temperature gradient of 6°C, average prosome length of males and females was reduced by approx. 8% in the warmest mesocosms at ΔT=6°C compared to the coldest ones at ΔT =0°C.

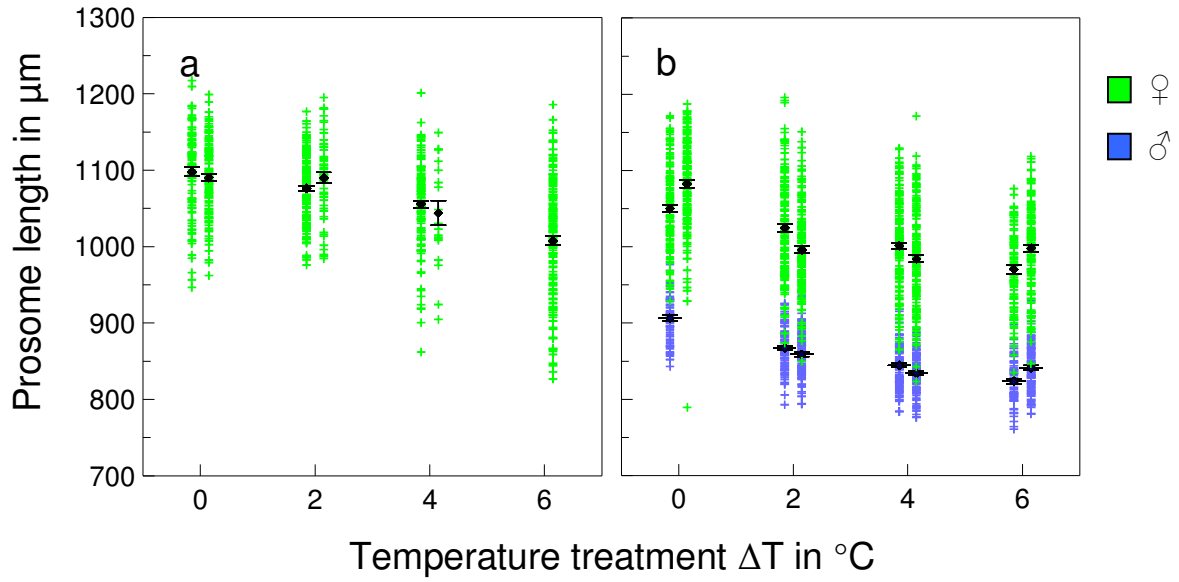

Fig. 17. Prosome length of adult *Pseudocalanus*. Prosome length (µm) for **a)** females in 2006 and **b)** for both sexes in 2007. Prosome length is plotted against the temperature treatment whereby the two mesocosms belonging to the same temperature are shown slightly shifted apart for better visualization. Green: females; blue: males 2007; black symbols: mean values; error bars: ± 1SE. In all temperature treatments: N > 55 in 2006 (except one mesocosm at ΔT=4 where N=18), and N = 150 in 2007.

Table 3. Prosome length (PL, in µm) of *Pseudocalanus* males (♂) and females (♀). Values given as means ± SE.

ΔT	0	0	2	2	4	4	6	6
♀ 2006	1098.0	1090.3	1078.0	1090.0	1055.4	1044.1	n.v.	1007.9
± SE	5.8	4.6	3.5	6.9	4.9	16.2	n.v.	5.6
♀ 2007	1050.0	1082.5	1024.8	995.9	1001.2	984.2	970.5	998.0
± SE	4.3	4.8	5.3	4.5	4.3	4.8	5.7	4.6
♂ 2007	906.2	n.v.	867.4	858.9	844.5	843.3	823.8	841.4
± SE	3.9	n.v.	3.0	2.7	2.7	2.4	3.5	3.1

Dependence of mean PL on temperature elevation ΔT according to the regression model: $f(x) = y_0 + a\,\Delta T$

	y_0	a	p
♀ 2006	1101.8	-13.83	***
♀ 2007	1152.9	-13.19	**
♂ 2007	892.0	-11.16	**

n.s. = not significant; n.v. = no value; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

C:N ratios

Male and female *Pseudocalanus* individuals were sorted out from the weekly zooplankton samples and processed for measurements of their elemental composition in terms of carbon (C) and nitrogen (N) content. In Figure 18, the time series of C:N ratios is given for both sexes. The first value within the sexes is identical in all treatments because the first measurements stem from the starting mixture of zooplankton that served for mesocosm stocking at the beginning of the experiment.

In general, there was wave-like basic pattern in the time series: first, C:N ratios increased above the Redfield ratio (C:N = 6.625, dotted line in the plots) and further, and then decreased below the Redfield ratio towards the end of the experiment. This pattern was similar for both sexes and most distinct in the coldest temperature treatment at ΔT=0°C, with peak values of C:N ranging from 12 to 15 on Julian Day 61 for both gender (Fig. 18a, e). Compared to the coldest treatment at ΔT=0°C, the C:N peak was more and more dampened at higher temperatures. In the warmest treatment at ΔT=6°C, C:N ratios dropped almost immediately from the start on and fluctuated most of the time close to or slightly below the Redfield ratio (Fig. 18d, h).

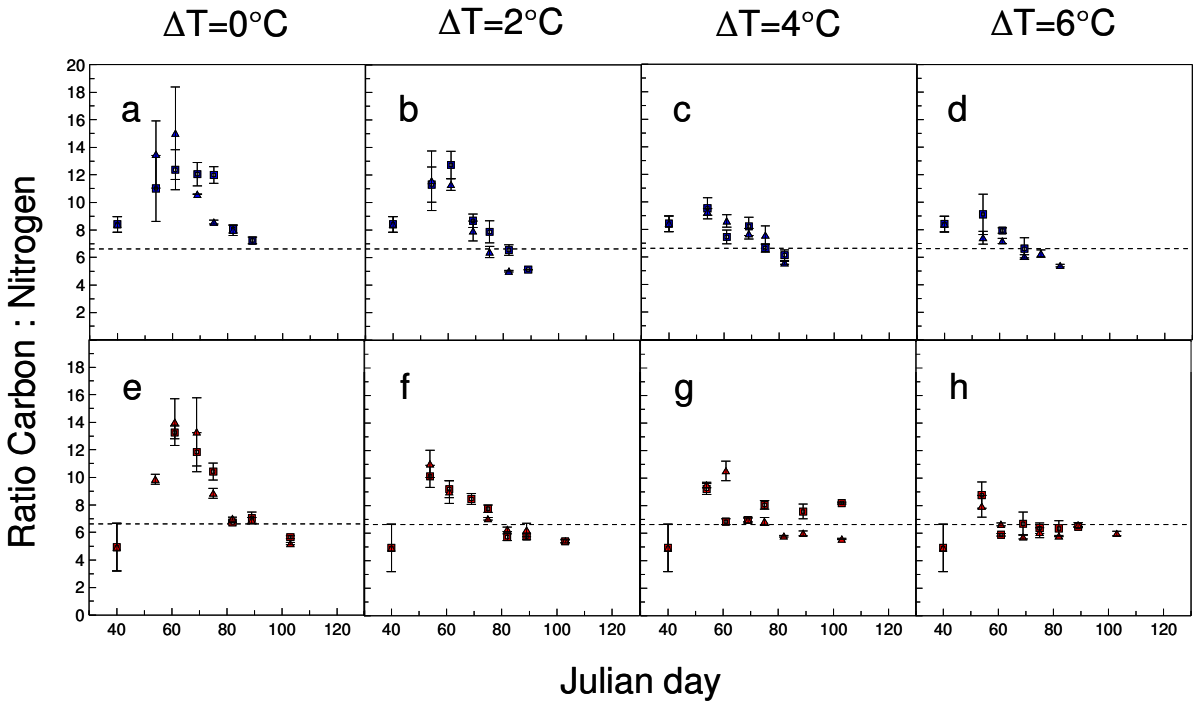

Fig. 18. Elemental composition in adult *Pseudocalanus* 2006. Time series of Carbon (C) to Nitrogen (N) ratios in the body tissue of *Pseudocalanus* shown for **a-d)** males and **e-h)** females across the thermal gradient of temperature treatments (from left to right). The dotted line depicts the Redfield ratio of C:N = 6.625. Triangles and squares represent the two parallel mesocosms within each temperature treatment.

Discussion

Population dynamics

The overall pattern of changing abundances were dominated by nauplii during both years because of their numerical dominance over copepodid stages. Nauplii patterns in turn followed closely the rates of egg production. There was a clear effect of temperature on the temporal aspect in population dynamics: in the colder treatments, processes occurred time delayed compared to the warmer treatments. This observation is a sum of temperature effects as well as the result of several other interconnected factors modifying the main determinants of population dynamics: reproduction, growth and mortality (immigration and emigration processes can be excluded for copepods in our system). This will be discussed in the following sections.

Fertilization and sex ratio

A prerequisite for population sustenance and growth is that mates find each other at a sufficiently high rate. Kiørboe and Bagøien (2005) investigated the swimming behaviour in *Pseudocalanus elongatus* and two other copepod species. Taking mating signaling into account, they established simple models to describe the resulting species-specific encounter rate. For *Pseudocalanus elongatus*, they estimated that male individuals are capable search 94 L day^{-1} in order to find mates. Based on this, female encounter rates in our experiments were always greater than E_F = 1 day^{-1} as long as males were above the detection limit (which was true most over the experimental period). In other words, a female individual was supposed to meet at least one male per day. *Pseudocalanus* belongs to the group of copepods with seminal receptacles and one single mating event is enough for a female to fertilize all eggs that will be laid. It is therefore likely, that population maintenance and growth was not impaired by insufficient mating, even at times when no males were detected.

In both studies, sex ratios in all treatments were skewed in favour of females over most of the experimental period. This fits to the typical pattern in the field: adult populations of pelagic copepods have usually a sex-ratio biased towards dominance of females (Kiørboe & Bagoien 2005). A possible explanation for skewed sex ratios in nature could be the shorter life span of males which do not feed in several species, such as

Pseudocalanus sp. (Corkett & McLaren 1978; Ohtsuka & Huys 2001; Kiørboe & Bagoien 2005). This suggestion is contradicted by Lee et al. (2003), who performed growth and reproduction experiments on *Pseudocalanus newmani* at different temperatures under saturated food conditions. They concluded, on basis of their data and further results from the literature, that skewed sex ratios in the field are probably due to sex change during juvenile development under the control of environmental factors, such as temperature, nutrition, or parasitism. What indeed triggered sex ratios in our experiments can not be clarified without further investigation.

Egg production rates as an output for growth

Copepods are characterized by determinate growth: after the last molt into the adult form, no further somatic growth occurs and body size remains stable. Instead, energy is allocated to reproductive tissues. Therefore the production of eggs and spermatophores can be regarded as adult growth. We calculated egg production rates (EPR) of *Pseudocalanus* to range from 0 to maximal 1.6 eggs female^{-1} day^{-1} in the experiment of 2006, and from 0 to maximal 4.7 eggs female^{-1} day^{-1} in the study of 2007. These results are comparable to the findings of Renz and Hirche (2007), who investigated the life cycle of *Pseudocalanus ascuspes* in the Central Baltic Sea. They found maximum EPR during late spring (April and May) with values up to 3.6 eggs female^{-1} day^{-1}. Field data for the congener species *Pseudocalanus elongatus* in the North Sea give maximal rates of 9.1 eggs female^{-1} day^{-1} (Renz *et al.* 2008) and 8.0 eggs female^{-1} day^{-1} in the German Bight (Halsband & Hirche 2001). Laboratory studies of Koski et al. (1998) on *Pseudocalanus elongatus* from the North Sea, reared at 15°C, give EPR of 2-5 eggs female^{-1} day^{-1}.

Factors influencing egg production

Food quantity is one of the main controlling factors for vital rates such as growth and fecundity (Renz *et al.* 2008). Investigations revealed that copepod egg production in the field is most of the time controlled by food supply (Frost 1985; Kiørboe & Johansen 1986; Kiørboe *et al.* 1988). Recently, Hirst and Bunker (2003) reviewed the literature on weight-specific fecundity and growth rates of copepods in relation to their body weight and *in situ* chlorophyll a contents and water temperature of their natural environments. They found that weight specific fecundity was positively correlated to chlorophyll a in several calanoid copepod genera, among those also in *Pseudocalanus*.

The dynamics of ER and derived EPR in our studies tracked closely the development of phytoplankton in the mesocosms: in 2006, phytoplankton biomass peaked at the beginning of the experiment and declined thereafter (Fig. 19a). The same pattern could be observed in ER and EPR. In 2007, phytoplankton blooms developed in midst of the experiment which is also true for ER and EPR peaks, which coincided with the phytoplankton biomass maxima (Sommer & Lengfellner 2008 and Sommer, unpublished data) (Fig. 19b). Hence, the production of eggs could be positively correlated to the amount of phytoplankton biomass in the water column of the mesocosms (Isla *et al.* 2008), thus corroborating findings of other authors.

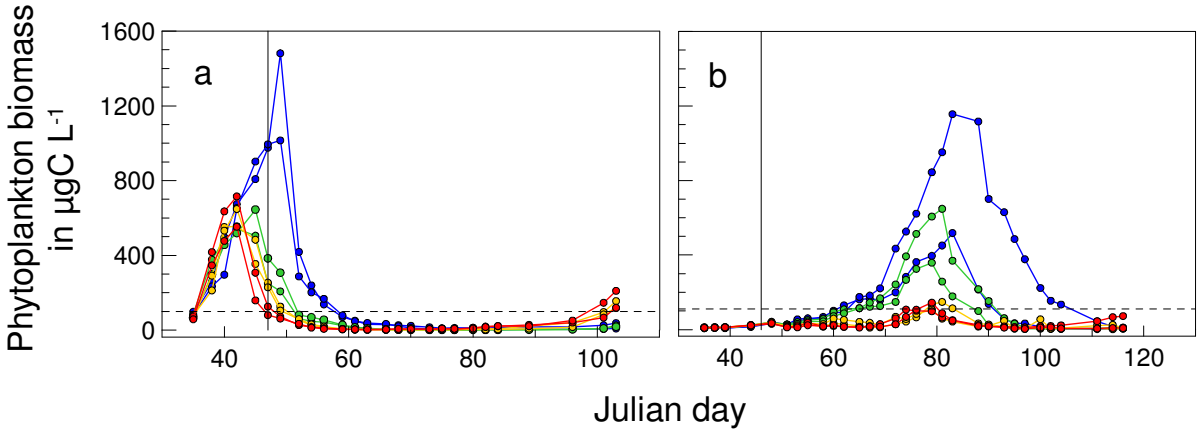

Fig. 19. Phytoplankton biomass dynamics in 2006 and 2007. Time series of phytoplankton biomass (µg C L^{-1}) shown for the different temperature treatments in **a)** 2006 and **b)** 2007. The vertical line marks the first day of egg ratio and egg production estimations, the horizontal line depicts the theoretical threshhold of 100µg C L^{-1} below which reproduction in *Pseudocalanus* is thought to be mainly food limited according to Corkett and McLaren (1978). Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Data from Sommer and Lengfellner (2008) and Sommer, unpublished data.

Stored energy reserves. Fecundity can also be fuelled by stored carbon rich compounds like lipids. An increased proportion of such components in copepod body tissue can be seen in rather high C:N ratios (Sterner & Hessen 1994; Hays *et al.* 2001). A study of Koski (1999) on *Eurytemora affinis* confirms that increasing food availability can elevate C:N in copepods. Our measurements in 2006 revealed that C:N ratios of both, male and female *Pseudocalanus,* stronger deviated from the Redfield ratio in the colder temperature treatments compared to specimens of the warmer treatments, whereby the C:N time series resembled the phytoplankton bloom dynamics, just with a certain time delay. Hence it seems likely that in this experiment, specimens from the cooler treatments were comparably better fed than those from the warmer treatments, and that they were able to invest additional energy reserves in survival and reproduction.

However, it has to be noticed that elevated C:N ratios in copepods can result from nutritionally unbalanced food resources: mesocosm experiments with natural plankton assemblies demonstrated that N-limitation in phytoplankton can translate into elevated C:N ratios in copepods (Van Nieuwerburgh *et al.* 2004), which in turn would have a negative effect on EPR (Kiorboe 1989; Koski *et al.* 2006). For the experiment in 2007 we have no data on the elemental composition of the studied copepods. Thus it is remains speculation whether the almost immediate production of eggs in all temperature treatments before the onset of the phytoplankton bloom was fuelled by stored energy reserves.

Temperature. Temperature is another key factor in controlling vital rates. In 2006 we observed that maximum ER and derived EPR were higher in the coldest temperature treatments at ΔT=0°C and ΔT=2°C at the beginning of the experiment, and continued to be at higher levels than those at ΔT=4°C and ΔT=6°C. In 2007, there was no clear trend across the temperature treatments in EPR. However, the underlying data on ER revealed a more pronounced difference between the warmest treatment at ΔT=6°C and the coldest treatment at ΔT=0°C. This indicates that clutch sizes were bigger at lower temperatures, but this was compensated at higher temperatures due to faster embryonic development, eventually resulting in rather similar EPR for both extreme temperature treatments. Nevertheless, the effect was not as clear across the thermal gradient as in 2006. A possible explanation is that temperature dependency of EPR becomes only evident above saturating food conditions: Corkett and McLaren (1978) found increasing EPR with increasing incubation temperature above a critical minimum phytoplankton carbon supply of ~100µg C L^{-1}. In the studies of Renz and Hirche (2006; 2007), EPR reached maximal values during times of phytoplankton spring bloom, but decreased thereafter though water temperature further increased till summer. These findings also outline the strong effect of food supply on egg production.

In our study in 2006, food conditions were probably satiating only at the beginning during the intense phytoplankton blooms in all mesocosms. However, within one week after the first zooplankton sampling, food levels dropped in all but the coldest temperature treatment below the theoretical threshold of 100µg C L^{-1}. In the coldest thermal regime at ΔT=0°C, food concentration fell below this critical threshold approximately one week later. From the findings of Corkett and McLaren (1978), temperature related differences in EPR would thus not be expected during the rest of the study period. A different picture emerged in 2007, where phytoplankton blooms were

more intense and lasted longer in the colder treatments at ΔT=0°C and ΔT=2°C than in the warmer treatments at ΔT=4°C and ΔT=6°C, where the critical food limit of 100µg C L^{-1} was only reached for a short time interval of one to several days. Hypothetically, this could mean that in the warmer treatments, egg production was down regulated by insufficient food supply whereas in the colder treatments low temperatures slowed egg development. Depending on how strong each factor regulated egg production, the observed pattern with highest rates at intermediate temperatures (ΔT=2 and ΔT=4°C) might have emerged.

Food quality. It should be mentioned that in general, food quality is also an important determinant of growth and reproduction. Two main characteristics determine the quality of food: the digestion resistance and the magnitude of stoichiometric imbalance between consumer and food resource (Hall *et al.* 2007 and references therein). Besides, species- and ontogenetically specific requirements for certain elements or essential biochemical compounds, such as vitamins, unsaturated fatty acids, sterols and amino acids play an important role (Urabe & Watanabe 1992; Kleppel *et al.* 1998; Breteler *et al.* 1999; 2005; Frost *et al.* 2005). For copepods, the nutritional balance of food has profound effects on egg production and juvenile growth (Bonnet & Carlotti 2001; Koski *et al.* 2006) as well developmental time (von Elert & Stampfl 2000). Further, toxic effects have been reported from specific diatom diets which can induce detrimental maternal food effects, such as reduced fecundity, disturbed oogenesis and lower hatching success (Ban *et al.* 1997; Lacoste *et al.* 2001), as well as generally retarded growth and malformation in nauplii offspring (Poulet *et al.* 1994; Ianora *et al.* 1996; Miralto *et al.* 1999).

Data on copepod grazing lacked in the studies of 2006 and 2007. Nonetheless, it could be speculated that egg production in 2006 might have been affected by the presence of *Thalassiosira* sp. (Sommer, unpublished data), a diatom that can negatively influence copepod fecundity (Halsband-Lenk *et al.* 2005). In the experiment of 2007, an intense bloom of the silicoflagellate *Dictyocha speculum* was observed in the colder treatments (Sommer, unpublished data) - a species that has also been reported to reduce copepod reproduction (Nejstgaard *et al.* 2001). Besides, EPR of *Pseudocalanus* has been positively linked to dietary nitrogen contents and negatively correlated to increased phytoplankton carbon:nitrogen ratios (Koski *et al.* 2006). Therefore nutrient limitation in phytoplankton as well as food quality upgrade by predation on ciliates should be considered, too.

Body size. Egg production is also indirectly affected by temperature through body size of females: larger female copepods are known to correlate with higher rates of reproduction. This has also been demonstrated for *Pseudocalanus* in controlled experiments with surplus food (Corkett & McLaren 1969) and in field studies (Halsband & Hirche 2001; Napp *et al.* 2005; Renz *et al.* 2007; 2008). With respect to body size (i.e. prosome length), we found that females at the end of both experiments tended to be bigger at colder temperatures (see section below). This is likely to have added to the other factors controlling egg production. However, it must be considered that the effect of body size on egg production was probably not constant but continuously gaining importance, because temperature in turn will have affected body size stronger in those individuals that had spent more life time in the mesocosm.

Altogether, the dynamics of reproduction can be explained very well by the interplay of temperature and food conditions: high levels of food supply translated into well fed females and high egg ratios. This was corroborated by the results of C:N measurements in 2006, which suggested that specimen were well nourished and probably had more energy reserves at colder temperatures. Further, females have been shown to be bigger at lower temperatures, which expectedly had an additional positive effect on fecundity. On the other hand, higher temperatures accelerated developmental times, which in turn resulted in higher egg production rates and may have compensated for smaller clutch sizes.

Temperature effects on body size

Body size is regarded as one of the most fundamental characteristics of an organism because it is related to lifespan, home range size, abundance, fecundity and other important life-history traits (Woodward *et al.* 2005; White *et al.* 2007). Potentially, variations in body size can have profound effects across multiple scales of biological organization, spanning from the individual level to whole ecosystems (Woodward *et al.* 2005 and references therein). We determined body size of adult *Pseudocalanus* (males and females) at the end of the experiments in 2006 and 2007. In both years, body size correlated negatively with temperature treatment. Simulation of a spring season, where temperatures lie 6°C above the decadal mean, resulted in smaller animals whose prosome length was on average 8% shorter. Converted into biomass, after the formulas

given by Corkett and McLaren (1978), this would translate into a loss of 25% in carbon content (dry weight).

Body size is known to be influenced by several aspects: size-selective predation pressure, quantity and stoichiometric quality of food resources as well as temperature effects on metabolic rates. As mentioned above, copepods did not face any predation in our set-up. Therefore, it can be assumed that changes in body size are a consequence of dietary and temperature related aspects. Logically, the same argumentation should hold true as for the rates of egg production because as a matter of fact, final body size is the cumulative result of growth. Similarly to EPR, maximal body size is thus dependent on food quantity, and above a critical minimum food supply, there is a switch where temperature becomes the key regulating factor (Corkett & McLaren 1978; Breteler & Gonzalez 1988). The study of Isla et al. (2008) demonstrated decreased net growth efficiencies in adult *Pseudocalanus* under climate warming conditions due to increased metabolic demands and increased proportions of carbon allocated to respiration. It can be expected that this finding can be extrapolated to growth in general (Bertalanffy 1957; Kozlowski *et al.* 2004).

In our studies, food concentrations varied temporally according to the phytoplankton bloom dynamics, and as mentioned in the section on EPR above (see Fig. 19), phytoplankton food supply was highest and longer lasting in the colder treatments at ΔT=0°C and ΔT=2°C compared to the warmer ones at ΔT=4°C and ΔT=6°C. Accordingly, quantitative food supply for copepod growth seems to have been better at lower temperatures, which could be a possible explanation of the final body size differences. As discussed for EPR, food quality aspects should also be taken into account for body size considerations, such as stoichiometry of phytoplankton and grazing on ciliates. Finally, it can not be excluded that differences in body size among the temperature treatments is partly due to a shifted overlap in generations: organisms generally tend to live longer at colder temperatures because less energy has to be expended on metabolism (Gillooly *et al.* 2001). For *Pseudocalanus newmani,* all stages have been shown to survive longer at colder temperatures (Tsuda 1994), and adult females *of Pseudocalanus elongatus* have been shown to survive more than 70 days at 5 to 7°C in the laboratory, without any food (Corkett & Urry 1968). In addition, better food conditions in the colder treatments could have sustained more individuals from the original stocking population. Hence, at colder temperatures more individuals from the starting stock could have been present at the end of the studies and thus have

influenced body size measurements. Taken together, this means that temperature effects probably became more pronounced and evident in the warmer treatments.

Mortality patterns on basis of the stage structure

From the weekly samples, *Pseudocalanus* specimens were separated and counted in a stage-specific manner. From this stage matrix, instantaneous mortality rates (m_i) were calculated according to the vertical life table method (Aksnes & Ohman 1996; Thor *et al.* 2008). In both experiments, m_i for nauplii were positive and ranged from 0.06 day^{-1} to 0.12 day^{-1} in 2006 and from 0.02 day^{-1} to 0.12 day^{-1} in 2007. Eiane and Ohman estimated mortality rates for *Pseudocalanus elongatus* from the Fladen Ground Experiment during spring 1976 (Eiane & Ohman 2004). Mortality rates were calculated for a time period with a pronounced phytoplankton bloom and water temperatures of approx. 6 to 7°C. On basis of the population surface method (Wood 1994) they found mortality rates for *Pseudocalanus* nauplii of stage N1 to be highest with 0.11 day^{-1} and constantly dropping m_i in older naupliar stages, down to <0.03 day^{-1} in stage N5. This is clearly the range found for our bulk estimates (all naupliar stages) in both years. Thor et al. (2008) investigated instantaneous mortality rates of epipelagic copepods during the post-bloom period in Disko Bay, Western Greenland, at water temperatures between 0.5°C and 2°C. They found m_i for nauplii of *Pseudocalanus* sp. with a mean of 0.05 day^{-1}. This also fits very well to our estimates.

For the copepodid stages of *Pseudocalanus elongatus*, Eiane and Ohman (2004) report extremely low values, except for stage C1 with a peak mortality of approx. 0.1 day^{-1}. However, no direct explanation is given for this peak. Thor et al. (2008) found a bi-modal increase of m_i in copepodid stages with highest mortality rates in stages C3 and C4 (m_i close to 0.1 day^{-1}). Our calculations in 2007 (m_i for nauplii and copepodid stages C4, C5), revealed that m_i seemingly increased with age. In the study of Thor et al. (2008), the mortality pattern was explained by increased susceptibility of larger sized stages to attacks from predators. But compared to field studies, our experiment was set up without any predators, or at least, their abundance was well below the detection limit. Therefore other factors are responsible for the shape of mortality patterns in the mesocosms. In our system, the main controlling factors are supposed to be temperature and food conditions. Studies by Vidal (1980b) and Finlay and Roff (2006) reveal that temperature and food affect copepod growth in a size-specific way: nauplii growth is

maximal at relatively low food concentrations whereas older and therefore bigger stages need increasingly more food to cover their energy demands. This is also true for smaller species (e.g. *Pseudocalanus* sp.) compared to bigger species (e.g *Calanus hyperboreus*). The critical level of food saturation in turn increases with increasing temperatures. Hence, at a given temperature nauplii can be expected to be less food limited than copepodid stages (though the trend probably reverses at starvation conditions). This could explain increasing mortality rates with age found in the experiment of 2007.

Generally, the calculations of m_i have to be considered with caution because Aksnes and Ohman (1996) suggested to make use of the vertical life table method in absence of strong cohort development. In our data, the stage distribution was however nonuniform with relatively higher abundances of distinct stages, and skewed data in successive stages did indicate cohort formation. On the one hand, this could be a consequence of the stocking procedure: we caught mesozooplankton with a plankton-net of 200µm mesh size and thus excluded nauplii stages from the starting population. On the other hand, egg production during the experiment of 2007 was discontinuous with a pronounced peak in midst of the study period. Hence, the presence of cohorts can not be excluded and hampering of the vertical life tables is possible. Furthermore, only data points were taken into account, where at least 14 individuals of successive stages were found (see Thor *et al.* 2008). Therefore many data had to be ignored. Finally, it should be noted that the model parameters for *Pseudocalanus* development are those of *Pseudocalanus elongatus*. We guess, however, that our specimens belong to *Pseudocalanus ascuspes*, and thus the coefficients of developmental time to be slightly different. It might be due to these drawbacks that no clear temperature trend appeared in instantaneous mortality patterns, which would have been expected from the findings of Vidal et al. (1980b), Finlay and Roff (2006), and the experiments with adult *Pseudocalanus* females performed by Isla et al. (2008) parallel to our study in 2006 and under the same conditions.

Conclusion

In this chapter, temperature induced effects were investigated on the population level. We focused on the copepod genus *Pseudocalanus*, which represents not only an

important link in the marine food web, but is known to be a key species in many temperate marine ecosystems, among those the Baltic Sea (Corkett & McLaren 1978; Hinrichsen *et al.* 2003; Möllmann *et al.* 2003a). *Pseudocalanus* is therefore a well studied organism and an avalanche of field and laboratory studies has investigated life-history traits of this genus, such as population dynamics, growth, reproduction, mortality and other important aspects. Our study for the first time focussed on *Pseudocalanus* reaction norms under the influence of simulated climate warming in almost natural food web surroundings. Together with information from the literature, our results indicate that higher temperatures increase individual metabolic demands, which in turn have to be covered by increased feeding activities (Aberle *et al.* 2007; Isla *et al.* 2008). If food is the limiting factor, temperature effects can be obscured and vital rates such as growth and reproduction may display no temperature related patterns (Vidal 1980a; Finlay & Roff 2006; Isla *et al.* 2008). At a given level of food supply, however, temperature effects become evident and have shown to be negative on egg production and final body size. Increasing temperatures can further accelerate population dynamics and probably increase rates of mortality (see Isla *et al.* 2008). Taken together, this might induce a negative feedback loop: at higher temperatures, more intense copepod grazing can be suspected, thus exerting a stronger top-down control on phytoplankton blooms during spring. Indeed, this was demonstrated in our mesocosm studies (Aberle *et al.* 2007; Sommer *et al.* 2007, see Chapter 4). Higher grazing pressure, could result in an earlier onset of low food availability, which in turn could hamper maturation of the new copepod generation. In addition, decreased egg production could negatively affect population size.

With respect to the key position of *Pseudocalanus* in many marine ecosystems, the detrimental effects of temperature on this genus are likely to propagate up the food web. *Pseudocalanus* is a major food resource for sprat and herring as well as larval cod in the Baltic Sea (Hinrichsen *et al.* 2002; Möllmann *et al.* 2003a). Hence, a temperature induced decrease in *Pseudocalanus* stocks could have negative effects on fish recruitment and might accentuate the current regime shift in the Baltic Sea, evident in the zooplankton by a change from formerly *Pseudocalanus* dominated copepod communities towards a dominance of *Acartia* (Alheit *et al.* 2005; Möllmann *et al.* 2008).

Chapter 4 - Temperature effects at the functional level

Introduction

Energy flux in ecological networks

From an energetic point of view, food webs can be regarded as networks of pathways where energy flows through ecosystems. Solar or chemical energy is captured by autotrophs in the first step, further converted to organic material and thus transformed and subsequently released by heterotrophic respiration along the food web pathway (Lindeman 1942). Which pathways are used and how efficiently energy is transferred from one consumer to the next depends on the characteristic traits of the involved species, their direct and indirect interactions and the number and complexity of linkages between them. Knowledge on food webs is of high heuristic value for ecological theory because food webs provide the basis for integrating population dynamics, community structure, species interactions, community stability, biodiversity and ecosystem stability, and offer possibilities for practical management of living resources (Link *et al.* 2005 and references therein).

The match-mismatch hypothesis

Amongst others, a prerequisite for efficient energy transfer between consumer and prey is a spatial and temporal overlap of their existence: only food resources, which are available at the right time and in the right place, can be exploited (theoretically) and thus sustain consumer populations. Cushing (1972) proposed this so called match-mismatch hypothesis for larval herring which is very food sensitive at certain stages and thus has to match zooplankton blooms that serve as prey and are in turn coupled to seasonal phytoplankton blooms. Climate change is supposed to create asynchronous shifts in consumer-resource relations, especially where consumer phenology is triggered by temperature (a cue altered by climate change) whereas resource seasonality is controlled via photoperiodicity (a cue not directly altered by climate change). A growing amount of field studies across various types of ecosystems affirms this expectation (see Introduction). From the marine sector, a prominent example is the study of Edwards and

Richardson (2004) who demonstrated that during the last decades, North Atlantic diatom blooms have remained rather fixed in time, whereas dinoflagellates and zooplankton have significantly moved forward in their seasonal cycle.

In our study we hypothesized a growing mismatch between autotrophic and heterotrophic dynamics with increasing spring temperatures. This assumption is based on the fact that photosynthetic activities of phytoplankton in temperate (and polar) regions are mainly light limited during the early season (winter-spring transition) and thus rather insensitive to ambient temperatures (Tilzer *et al.* 1986). Heterotrophic processes of poikilotherms, on contrary, directly depend on ambient temperatures and hence are supposed to be accelerated under warmer climate conditions.

Changes in top-down control

The temperature sensitivity of heterotrophic processes has a further implication: higher temperatures lead to higher metabolic rates in marine ectotherms (Ikeda 1985; Ivleva 1985; Clarke & Johnston 1999; Ikeda *et al.* 2001). This increases food demands and translates into enhanced feeding activities of heterotrophic organisms: at a given level of food supply, copepods are reported to increase ingestion rates at higher temperatures (Kiorboe *et al.* 1982; Dam & Peterson 1988; Durbin & Durbin 1992; Kleppel 1992), and similar observations exist on grazing of microzooplankton (Montagnes 1996; Montagnes & Lessard 1999; Verity *et al.* 2002). Thus, it could be expected that spring temperatures within the predicted range of global warming will diminish the amount of accumulating phytoplankton biomass in our system. This could also lead to shifts in phytoplankton species distribution because copepods have been demonstrated to be capable of inducing trophic cascades through selective feeding on large phytoplankton species and ciliates, thereby effectively releasing nanoplankton from ciliate grazing pressure (Kleppel 1993; Katechakis *et al.* 2002; Sommer & Stibor 2002). However, such changes in phytoplankton size structures will presumably depend on resource overlap between both types of grazers, ciliates and copepods.

Results

Biomass dynamics

Total phytoplankton biomass. Across all studies and temperature treatments, phytoplankton dynamics displayed a general pattern (Fig. 20): we observed distinct algae blooms (with maximal biomass values), followed by a decrease of biomass towards minimum values (the so called clear water phase) and a second growth period afterwards until the end of the experiments, usually only detectable in the warmer treatments (ΔT=2°C, ΔT=4°C and ΔT=6°C). The initial phase differed from experiment to experiment: in 2005 there was a decline of biomass within the first two to three weeks before the onset of the bloom (Fig. 20a-d), whereas in the other experiments, phytoplankton biomass showed positive growth rates right from the start on (Fig. 20e-l). In the study of 2007, this first period before the bloom was characterized by fluctuating phytoplankton biomass in the two warmer treatments at ΔT=4°C and ΔT=6°C whereas in the colder treatments at ΔT=0°C and ΔT=2°C biomass increased more steadily from the beginning on (Fig. 20i-l). Data from microscopic counting of phytoplankton supplied by Sommer (2007; 2008 and Sommer, unpublished data).

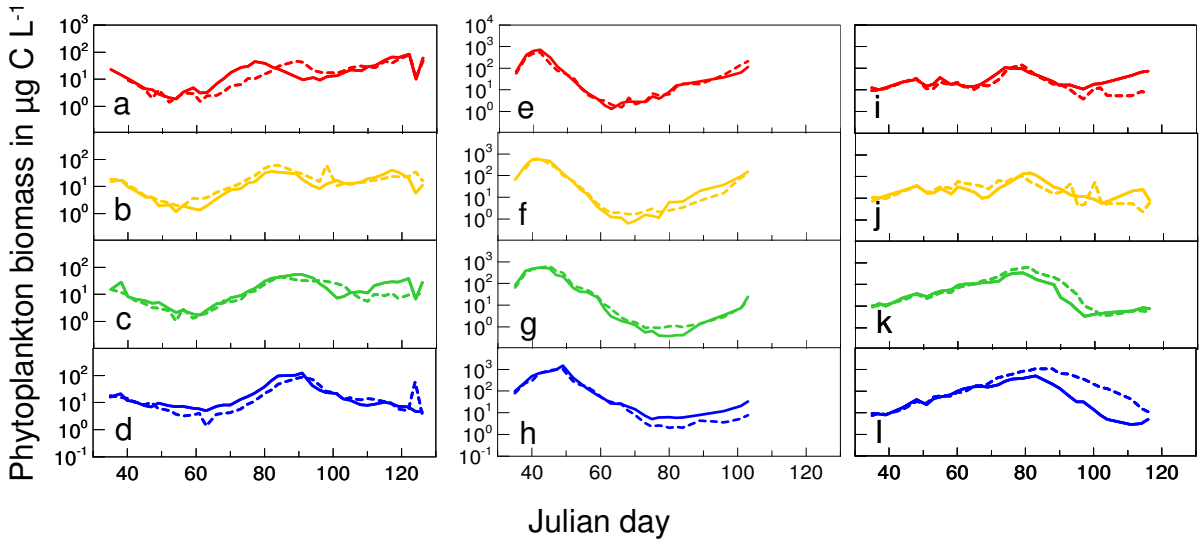

Fig. 20. **Total phytoplankton biomass dynamic**. Time series of total phytoplankton biomass (µg C L^{-1}) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Note that the logarithm scale on the y-axis varies between 2005 and 2006/ 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Data from Sommer et al. (2007), Sommer and Lengfellner (2008) and Sommer, unpublished data.

Total ciliate biomass. Common temporal patterns also emerged for the ciliate community (Fig. 21): a first biomass peak could be detected before, and at least one pronounced biomass peak followed after the phytoplankton bloom (timing of phytoplankton biomass maxima see Fig. 20). An exception to this was the experiment in 2006 where both ciliate peaks occurred after the phytoplankton bloom (Fig. 21e-h). Generally, ciliate biomass dynamics was characterized by rather strong fluctuations. In contrast to this, copepod dynamics (Fig. 22) were comparably smooth though it has to be noted that sampling intervals were only weekly for copepods and shorter for ciliates in most cases. Graphs based on ciliate data from Aberle (Aberle *et al.* 2007 and Aberle, unpublished data).

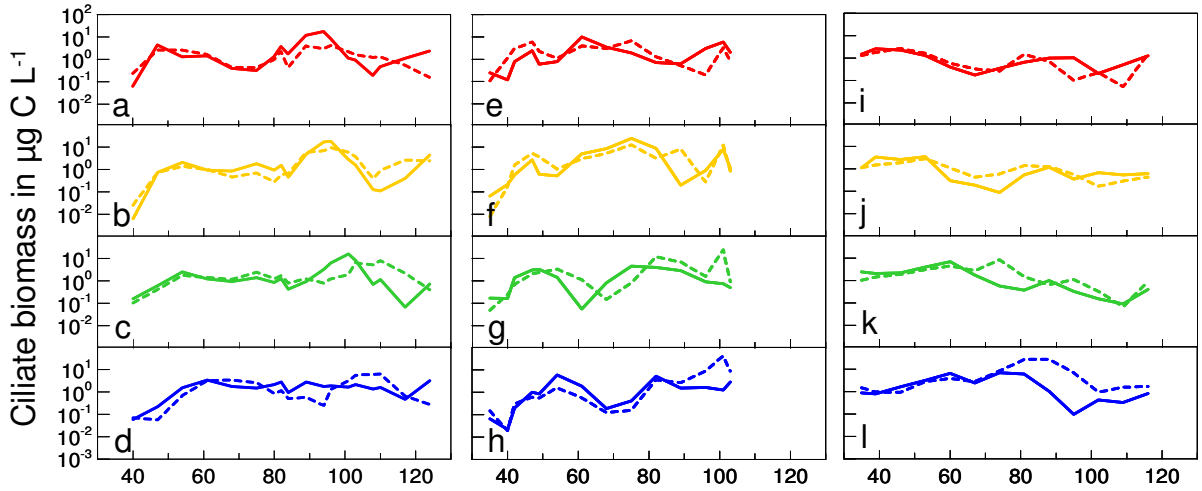

Fig. 21. Total ciliate Bomass dynamic. Time series of total ciliate biomass (µg C L^{-1}) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Note the logarithm scale on the y-axis. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Data from Aberle et al. (2007) and Aberle, unpublished data.

Total copepodid biomass. Copepodid biomass displayed no uniform pattern across the studies as growth rates were negative in all treatments in 2005 (Fig. 22a-d), positive in all treatments in 2007 (Fig. 22i-l) and initially positive in 2006, followed by biomass declines thereafter (Fig. 22e-h).

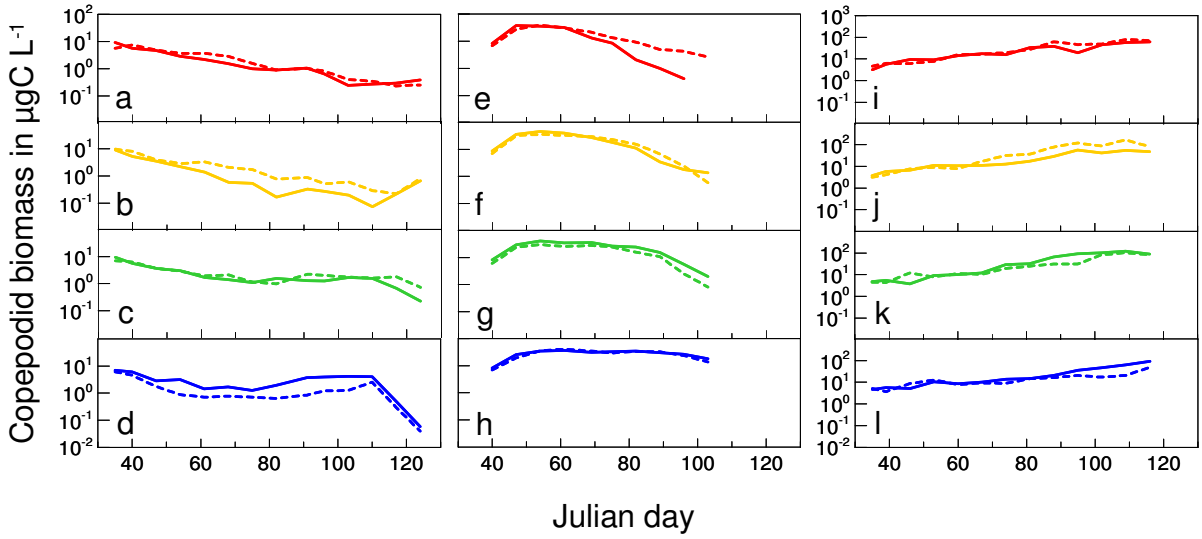

Fig. 22. Total copepodid biomass dynamic. Time series of total copepodid biomass (µg C L^{-1}) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Note that the logarithm scale on the y-axis varies between the years. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C.

Total naupliar biomass. Copepod nauplii, which formed only a small fraction of the total copepod biomass, displayed a temperature related, unimodal pattern that reoccurred more or less pronounced in the subsequent years (Fig. 23): peak biomass was reached earlier in the warmer treatments at ΔT=4°C and ΔT=6°C, and later in the colder treatments at ΔT=0°C and ΔT=2°C. In the study of 2007, nauplii peaks were not clearly separated but the growth phase before the peak showed a time delay at lower temperatures (Fig. 23i-l).

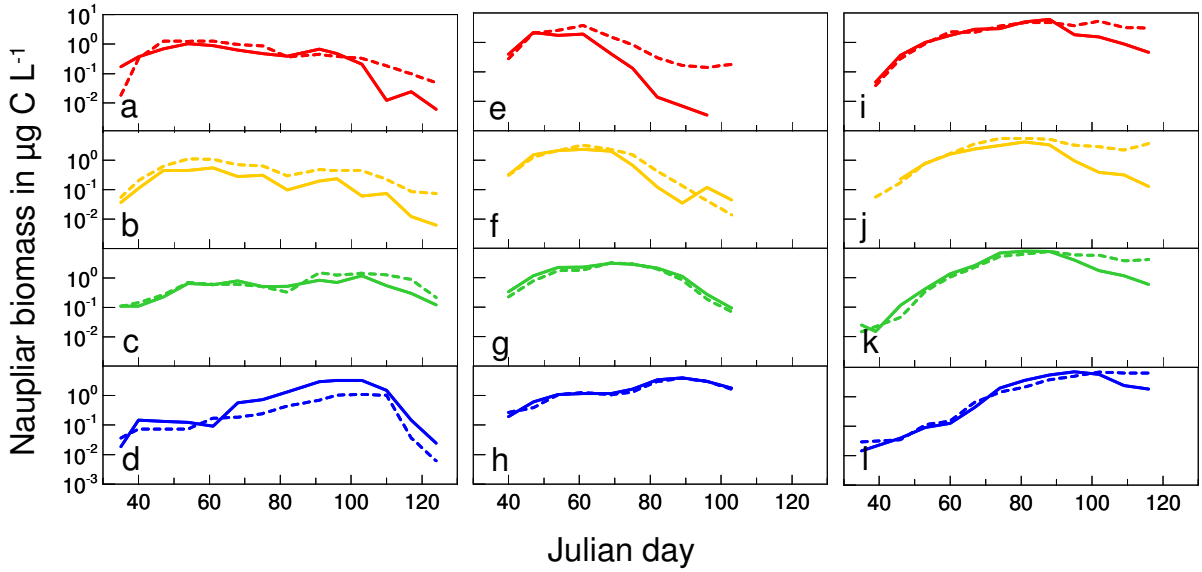

Fig. 23. **Total naupliar biomass dynamic**. Time series of total naupliar biomass (µg C L^{-1}) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Note the logarithm scale on the y-axis. Dotted and solid lines in represent the two parallel mesocosms of each temperature treatment. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C.

Peak timing

Temperature had an accelerating effect on the timing of biomass maxima of phytoplankton, ciliates and copepod nauplii: treatments with higher temperatures reached peak values earlier compared to cooler treatments (Fig. 24, Tab. 4).

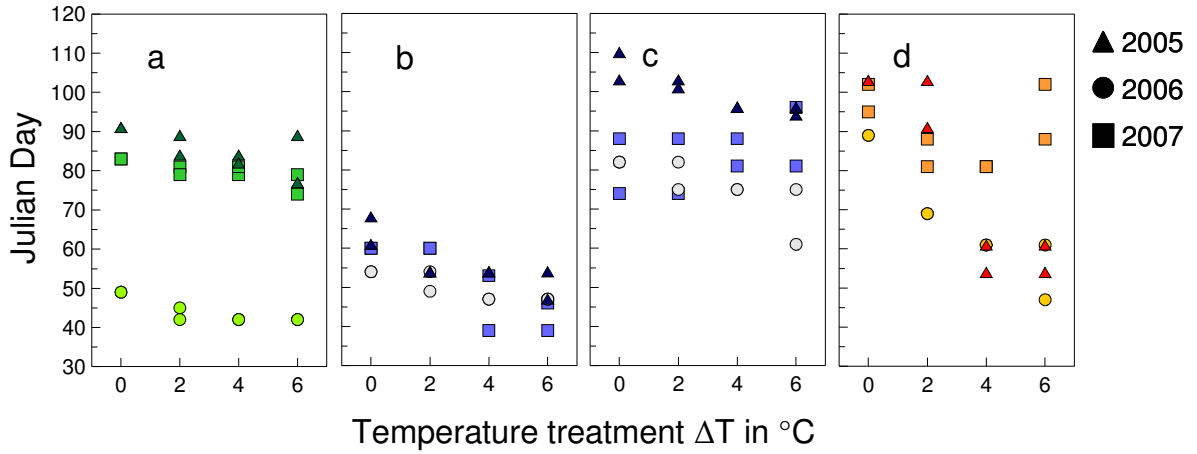

Fig. 24. Timing of biomass peaks. Timing of the biomass peaks (Julian day) in the different temperature treatments shown for **a)** phytoplankton and **b)** copepod nauplii in the subsequent years. For the ciliates, timing of the **c)** first and the **d)** second biomass maximum is shown. Triangles: 2005; circles: 2006; squares: 2007. Phytoplankton data from Sommer and Lengfellner (2008), ciliate data from Aberle et al. (2007) and Aberle, unpublished data.

Exceptions to this were the timing of the second ciliate peak (Fig.24c, squares) and the timing of nauplii peak (Fig. 24d, squares) in 2007, where no clear temperature related patterns appeared. Linear regression models show that in general the acceleration trend was lowest for phytoplankton peak timing with significant rates of 1.0 to 1.2 days $°C^{-1}$, intermediate at the ciliate level with 1.3 to 3.3 days $°C^{-1}$ (except second peak in 2007) and strongest in the nauplii fraction with 5.7 and 8.8 days $°C^{-1}$ (not considering 2007) (Tab. 4). For total copepod biomass, no maxima could be detected in the experiments of 2005 and 2007. In 2006, total copepod biomass did peak shortly after the start of the experiment and a weak temperature related trend could be detected in timing with 1.6 days $°C^{-1}$ (data not shown).

Table 4. Date of the biomass maximum (d, in Julian days) in phytoplankton (P), ciliates (Cil, first and second max.) and copepod nauplii (Nau) in dependance of temperature elevation (ΔT, in °C): Regression analysis according to the model: $d = y_0 + a\,\Delta T$

Group	y_0	a	p
P 2005	(90.0)	(-1.38)	(0.07)
P 2006	47.5	-1.13	**
P 2007	82.8	-0.98	0.02
Cil 2005 (first max.)	62.1	-2.1	0.02
Cil 2006 (first max.)	53.7	-1.3	**
Cil 2007 (first max.)	62.1	-3.3	**
Cil 2005 (sec.max.)	106.0	-2.0	**
Cil 2006 (sec.max.)	82.7	-2.3	0.02
Cil 2007 (sec.max.)	n.s.	n.s.	n.s.
Nau 2005	105.2	-8.8	**
Nau 2006	82.2	-5.7	***
Nau 2007	n.s.	n.s.	n.s.

n.s. = not significant; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

A direct statistical comparison of the different years i.e. the different light treatments is not possible because starting conditions and community compositions differed between the experiments. However, it can be noted that the timing of the phytoplankton bloom seemed to be positively linked to light treatment (i.e. light intensity I): comparing the three experiments, bloom peaks were reached earliest in the high light experiment of 2006 (64% I_0), whereas in the medium and low light experiments (32% I_0 in 2007 and 16% I_0 in 2005) the blooms occurred about five to six weeks later (Fig. 24a). Calculation of the mean light intensity (I_{mix}) in the mesocosms for the date of the bloom start revealed that I_{mix} ranged from 1.14 to 1.63 mol photons m^{-2} day^{-1} in the years 2005 and 2007, with a mean value of 1.34 mol photons m^{-2} day^{-1}. The high light experiment in 2006 started with 2.27 mol photons m^{-2} day^{-1} (Sommer & Lengfellner 2008). A similar but less clear pattern emerged for the second ciliate peak (Fig. 24c), which occurred earlier in the high light experiment of 2006 compared to the low light experiment of 2005. The peaks of the experiment in 2007 gave no clear trend and fell not clearly in between 2005 and 2006. In contrast to this, the first ciliate peaks as well as the nauplii peaks showed almost no year-to-year differences in timing (Fig. 24b, d).

Maximum carbon content

Total phytoplankton biomass at the bloom peak significantly declined with increasing temperatures (Fig. 25a). For phytoplankton peaks, fits were obtained with a polynomial inverse first order regression model $f(x) = y_0 + a(\Delta T+1)^{-1}$, indicating that changes in

maximum biomass content were most pronounced between the cooler treatments at ΔT=0°C and ΔT=2°C (Tab. 5). For the ciliates, total biomass peaks showed no significant temperature related trends in 2005 and 2006. In 2007, maximum biomass declined for both peaks with increasing temperature (models and results see Tab. 5). Nauplii biomass revealed no temperature related patterns when numbers were converted to carbon content with a mean conversion factor for all genera and all stages present in the mesocosms (Fig 25d). However, in the experiments of 2006 and 2007, *Pseudocalanus* nauplii were counted separately and respective carbon conversion revealed higher biomass maxima in the lower temperature treatments (Tab. 5).

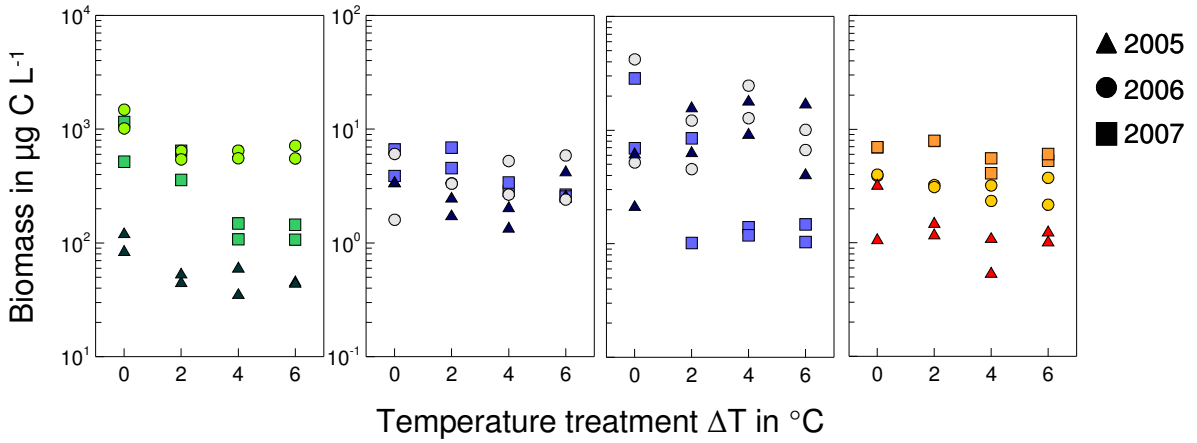

Fig. 25. Biomass maximum carbon contents. Maximum carbon content (µg C L^{-1}) in the different temperature treatments shown for **a)** phytoplankton and **b)** copepod nauplii (mean carbon conversion) in the subsequnt years. For the ciliates, timing of the **c)** first and the **d)** second biomass maximum is shown. Note the different scales on the y-axis. Triangles: 2005; circles: 2006; squares: 2007. Phytoplankton data from Sommer and Lengfellner (2008), ciliate data from Aberle et al. (2007) and Aberle, unpublished data.

Comparing the three years, the most intense phytoplankton blooms developed in the study of 2006 with 553 to 1482µg C L^{-1}, followed by the study in 2007 with 107 to 1156µg C L^{-1}. In 2005, phytoplankton biomass peaks were about one magnitude lower with values ranging from 36 to 123µg C L^{-1} (Fig. 25a). For the ciliates, no clear pattern emerged with respect to the different years whereby biomass maxima for the first peak ranged almost uniformly between 1 and 7µg C L^{-1} across the years (Fig. 25b) and biomass maxima of the second peak spanned from 1 to 55µg C L^{-1} (Fig. 25c). Nauplii biomass maxima were estimated twice: a conversion of individual numbers into biomass with a mean conversion factor for all copepod genera and all nauplii stages resulted in peaks that were highest in 2007 with 4 to 8µg C L^{-1}, intermediate in 2006 with 2 to 4µg C $L^{-1}$and lowest in 2005 with 1 to 3µg C L^{-1} (Fig. 25d). A more detailed carbon

conversion (*Pseudocalanus* nauplii and all other nauplii) yields biomass maxima of 4 to 9µg C L^{-1} in 2006 and 6 to 13µg C L^{-1} in 2007 (data not shown).

Table 5. Maximal biomass (B, in µg C L^{-1}) in phytoplankton (P), ciliates (Cil, first and second max.) and copepod nauplii (Nau, all and *Pseudocalanus* only) in dependance of temperature elevation (ΔT, in °C): Regression analysis acc. to various models: linear: $B = y_0 + a\,\Delta T$ or inverse first order: $B = y_0 + a(\Delta T + 1)^{-1}$

Group	Model	y_0	a	p
P 2005	inverse first order	32.58	70.71	**
P 2006	inverse first order	441.24	783.28	**
P 2007	inverse first order	58.65	811.13	**
Cil 2005 (first peak)	n.s.	n.s.	n.s.	n.s.
Cil 2006 (first peak)	n.s.	n.s.	n.s.	n.s.
Cil 2007 (first peak)	linear	6.29	-0.53	0.04
Cil 2005 (second peak)	n.s.	n.s.	n.s.	n.s.
Cil 2006 (second peak)	n.s.	n.s.	n.s.	n.s.
Cil 2007 (second peak)	inverse first order	-2.01	19.72	0.03
Nau 2005 (all)	n.s.	n.s.	n.s.	n.s.
Nau 2006 (all)	n.s.	n.s.	n.s.	n.s.
Nau 2007 (all)	n.s.	n.s.	n.s.	n.s.
Nau 2006 (*Pseudocal.*)	inverse first order	3.97	4.92	**
Nau 2007 (*Pseudocal.*)	linear	13.04	-0.81	0.03

n.s. = not significant; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

Functional groups

We assigned the various phytoplankton species to different functional groups according to their size (i.e. biovolume) and their taxonomic affiliation (i.e. diatom, flagellate or silicoflagellate) and thus established six groups: microdiatoms, nanodiatoms, microflagellates (mainly dinoflagellate species), nanoflagellates, silicoflagellates (i.e. *Dictyocha speculum*; "nano-" size category) and picophytoplankton. The ciliates were sub-divided according to their maximal lengths into three groups: small (<25µm), medium (25-50µm) and large (>50µm). Copepods (i.e. copepodid stages) were considered at a genus based resolution for the most abundant specimen: the small cyclopoid copepod *Oithona* and the calanoid genera *Pseudocalanus*, *Centropages*, *Temora* and *Acartia*. All functional groups are described in terms of biomass (carbon content). Data from microscopic counting of phytoplankton supplied by Sommer (2007; 2008 and Sommer, unpublished data) and ciliate data by Aberle (Aberle *et al.* 2007 and Aberle, unpublished data).

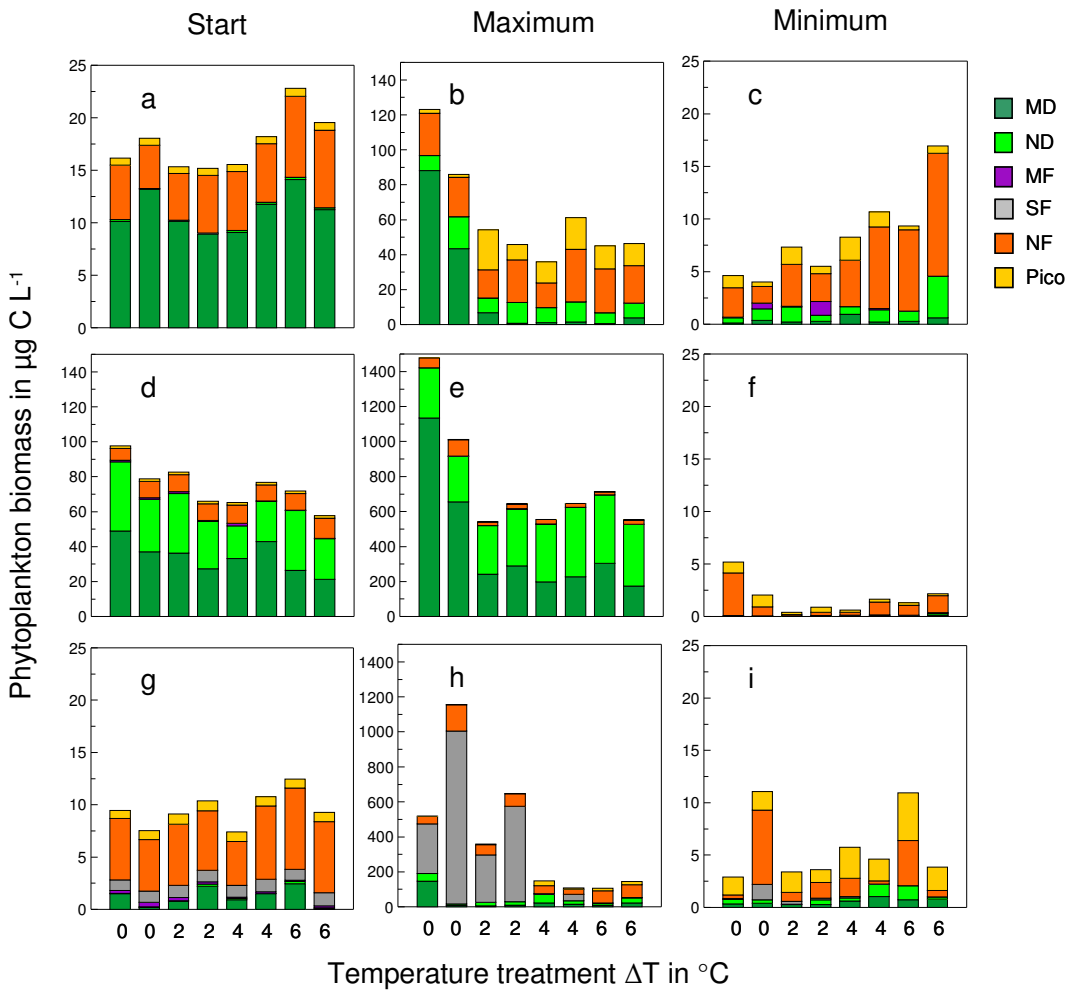

Fig. 26. Phytoplankton biomass composition. Phytoplankton biomass (µg C L^{-1}) shown for the different functional groups as stacked bar charts for the different temperature treatments in **a-c)** 2005, **d-f)** 2006 and **g-i)** 2007. The first column **(a, d, g)** shows the starting community, the second column **(b, e, h)** shows the composition of the biomass maximum (bloom peak) and the third column **(c, f, i)** depicts the composition of the biomass minimum during the clear water phase. Each mesocosm is shown seperately. Note the different scales on the y-axis. Dark green (MD): microdiatoms; light green (ND): nanodiatoms; purple (MF): microflagellates; grey (SF): silicoflagellates; orange (NF): nanoflagellates; yellow (Pico): picophytoplankton. Data from Sommer and Lengfellner (2008) and Sommer, unpublished data.

Phytoplankton composition. In 2005, the phytoplankton community was dominated by microdiatoms and, to a smaller amount, by nanoflagellates at the beginning of the experiment (Fig. 26a). At the bloom peak, this distribution was still found in the coldest treatment at ΔT=0°C, whereas in the warmer treatments at ΔT=2°C, ΔT=4°C and ΔT=6°C, phytoplankton blooms were clearly dominated by nanoflagellates and picophytoplankton (Fig. 26b). At the biomass minimum during the following clear water phase, phytoplankton communities in all mesocosms showed a prevalence of nanoflagellates (Fig. 26c). The phytoplankton community of 2006 was also dominated by diatoms at the beginning of the experiment, whereby microdiatoms and nanodiatoms were present in almost equal amounts. Nanoflagellates comprised only a small fraction

(Fig. 26d). These proportions persisted until the bloom peak in the all of warmer treatments (ΔT=2°C, ΔT=4°C and ΔT=6°C) and slightly changed in favour of microdiatoms in the coldest treatment at ΔT=0°C (Fig. 26e). Similar to the experiment in 2005, the biomass minimum of 2006 was characterized by a dominance of nanoflagellates and picophytoplankton in all treatments (Fig. 26f). In 2007, nanoflagellates dominated the starting stock of phytoplankton whereas the other functional groups appeared in smaller fractions (Fig. 26g). In both colder treatments at ΔT=0°C and ΔT=2°C, the biomass maximum during the bloom was made up by silicoflagellates (*Dictyocha speculum*) whereby in one of the coldest mesocosms at ΔT=0°C microdiatoms were found as a co-dominant group. At ΔT=4°C, the bloom was rather a mixture of several functional groups in varying proportions, but in the warmest treatment at ΔT=6°C nanoflagellates dominated more clearly (Fig. 26h). In contrast to this, the biomass minimum showed relatively high proportions of picophytoplankton and in some treatments dominance of nanoflagellates. In the warmer treatments at ΔT=6°C and ΔT=4°C, a slightly higher amount of microdiatoms could be found compared to the cooler treatments (Fig. 26i).

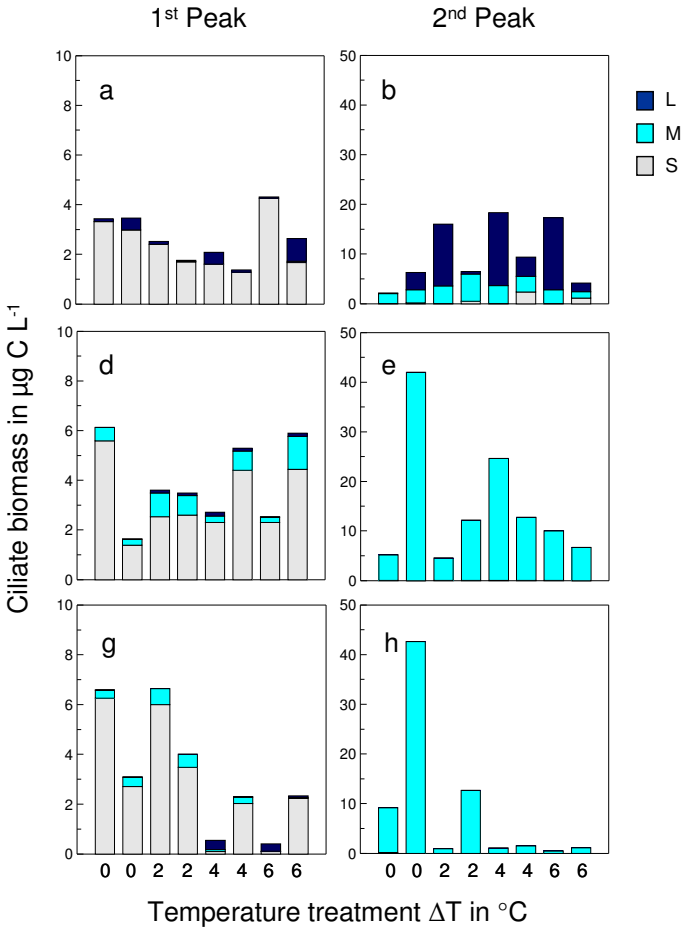

Fig. 27. Ciliate composition. Ciliate biomass (µg C L^{-1}) shown for the different size classes as stacked bar charts for the different temperature treatments in **a, b)** 2005, **c, d)** 2006 and **e, f)** 2007. The first column **(a, c, e)** shows the composition of the first biomass maximum (first peak), the second column **(b, d, f)** shows the composition of the second biomass maximum (second peak). Each mesocosm is shown seperately. Note the different scales on the y-axis. Light grey (S): small ciliates <25µm; medium blue (M): medium ciliates 25 - 50µm; dark blue (L): large ciliates >50µm. Data from Aberle et al. (2007) and Aberle, unpublished data.

Ciliate composition. In all experiments, the first biomass maximum was formed by small ciliates (dominated by the strobilidiid *Lohmanniella oviformis*, data not shown) (Fig 27a, c, e). An exception to this was the study of 2007 where in one mesocosm at ΔT=4°C and one mesocosm at ΔT=6°C large sized ciliates dominated the first biomass peak (Fig. 27e). The second biomass maximum in 2005 was comprised by medium sized and large sized species (Fig. 27b) whereas in the studies of 2006 and 2007 only medium sized ciliates were found (Fig. 27d, f).

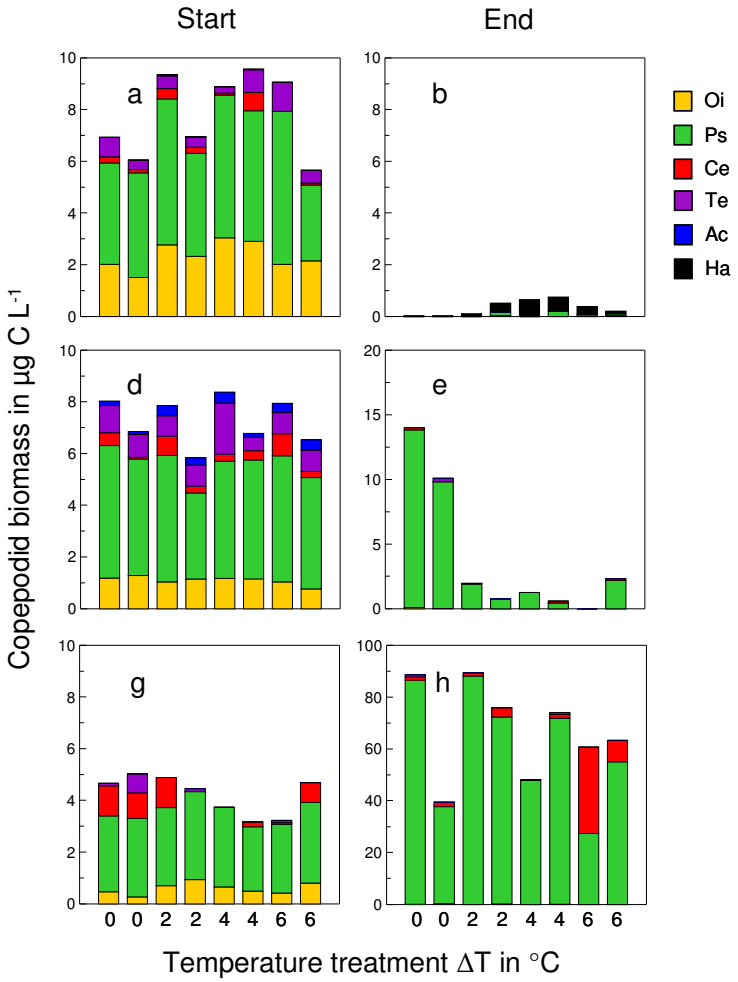

Fig. 28. Copepodid composition. Copepodid biomass (µg C L^{-1}) shown for the different copepod genera as stacked bar charts for the different temperature treatments in **a, b)** 2005, **c, d)** 2006 and **e, f)** 2007. The first column **(a, c, e)** shows the starting composition (start), the second column **(b, d, f)** shows the composition on the last sampling date (end). Each mesocosm is shown seperately. Note the different scales on the y-axis. Yellow (Oi): *Oithona* sp.; green (Ps): *Pseudocalanus* sp.; red (Ce): *Centropages* sp.; violet (Te): *Temora* sp.; blue (Ac): *Acartia* sp.; black (Ha): harpacticoid copepods.

Copepodid composition. In general, the starting stock of copepodids was characterized by a dominance of *Pseudocalanus* sp. in all experiments and a high proportion of *Oithona* sp. while *Temora* sp. *Centropages* and *Acartia* species appeared in smaller amounts (Fig. 28a, c, e). During all experiments, *Pseudocalanus* sp. and *Oithona* sp. continued to dominate during most of the studying period (data not shown) except that in 2007 *Centropages* gained importance until the end of the study (Fig. 28f), and in 2005 harpacticoid copepods finally began to dwell in the mesocosms (Fig. 28b).

Initial negative net growth of phytoplankton in 2005

Biomass (B) data of phytoplankton functional groups (microdiatoms, nanodiatoms, microflagellates, nanoflagellates and picophytoplankton) in 2005 were ln-transformed, and loss rates (r_L) for the initial phase of biomass decline (see Fig. 20a) derived by linear regression (linear regression model: $r = y_0+a(\ln B)$). Loss rates and regression of loss rates against temperature are displayed in Table 6.

Generally, at a given temperature and within a certain mesocosm, microdiatom biomass declined strongest and picophytoplankton biomass declined least, whereby r_L for the different groups was ordered as follows: microdiatoms > nanodiatoms > nanoflagellates > picophytoplankton for each mesocosm (Tab. 6). Loss rates ranged from 0.08 to 0.27 day^{-1} in microdiatoms, 0.09 to 0.23 day^{-1} in nanodiatoms, 0.05 to 0.11 day^{-1} in nanoflagellates and from 0.04 to 0.09 day^{-1} in picophytoplankton. Microflagellate biomass was below detection limit at the beginning of the study and thus no analysis could be performed. Regression of r_L against temperature within the groups revealed that the loss of microdiatom and nanoflagellate biomass was significantly accelerated at higher temperatures, whereby this effect was stronger in microdiatoms than in nanoflagellates (Tab. 6).

Table 6. Initial loss rates (r_L, day^{-1}) for phytoplankton biomass (B) of the different functional groups during exponential phase in 2005. r_L calculated according to the model: $r_L = y_0+a(\ln B)$.

ΔT	Microdiatoms			Nanodiatoms			Nanoflagellates			Picophytoplankton		
	y_0	a	p	y_0	a	p	y_0	a	p	y_0	a	p
0	6.33	-0.11	**	1.62	-0.10	***	3.69	-0.05	**	0.90	-0.04	****
0	5.39	-0.08	****	n.s.	n.s.	n.s.	3.87	-0.07	0.03	0.77	-0.04	****
2	8.31	-0.17	****	0.71	-0.09	***	4.49	-0.08	**	1.33	-0.05	****
2	12.00	-0.27	****	6.04	-0.23	**	4.96	-0.09	***	1.54	-0.06	***
4	11.27	-0.24	****	3.28	-0.14	**	5.25	-0.10	***	1.58	-0.06	0.03
4	11.14	-0.24	****	2.75	-0.13	**	4.73	-0.08	****	1.34	-0.05	**
6	11.67	-0.26	****	5.77	-0.22	**	5.72	-0.10	****	n.s.	n.s.	n.s.
6	11.93	-0.27	****	4.95	-0.19	****	6.06	-0.11	**	2.63	-0.09	***

Dependence of r_L on temperature elevation ΔT according to the regression model: $f(x) = y_0+a\ \Delta T$

	y_0	a	p
Microdiatoms	-0.125	-0.026	**
Nanodiatoms	n.s.	n.s.	n.s.
Nanoflagellates	-0.625	-0.008	**
Picophytoplankton	n.s.	n.s.	n.s.

n.s. = not significant; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

Discussion

The timing of biomass maxima

We hypothesized that autotrophs of temperate regions will only weakly respond to rising temperatures during the early season in contrast to heterotrophic organisms, which should react more temperature dependent. Basis of this hypothesis is the assumption that light is the limiting factor in terms of primary production during spring time, whereas heterotrophic processes are temperature limited in ectothermic organisms. Our studies confirmed this expectation by demonstrating that elevated temperatures do accelerate the timing of spring bloom events and that the intensity of changes varies among the different trophic levels: phytoplankton showed the lowest acceleration rates of the three main groups (phytoplankton, ciliates and copepods) with rates about r = 1 day $°C^{-1}$. Ciliate biomass peaks advanced more strongly than phytoplankton with rates of approx. r = 1 to 3 days $°C^{-1}$, and copepod nauplii peaks displayed the highest sensitivity to temperature increase in two out of three experiments, with acceleration rates of approx. r = 6 and 9 days $°C^{-1}$. Field studies show similar trends of spring peak advancement under recent climate warming: Edwards and Richardson (2004), for example, analyzed North Sea data from the Continuous Plankton Recorder and extracted the timing of the seasonal peaks of 66 plankton taxa for the period from 1958 till 2002, during which North Sea surface temperatures increased by 0.90°C. Despite from intertaxon variation, diatom spring (and autumn) peaks were shown to remain rather static, and mean movement of the total phytoplankton spring bloom was zero days over the whole time series. For the copepod genera *Oithona*, *Pseudo-Paracalanus* and most Dinoflagellates, significant advances in peak timing (though in summer) were reported and advancing but insignificant trends were found for *Centropages*, *Acartia* and *Temora*, too (data in the supplementary information of the paper). This trend of rather static phytoplankton bloom timing and advancing copepod phenology also emerged from the data series of Helgoland Roads, a station of well-mixed coastal waters in the German Bight (Wiltshire *et al.* 2008). Earlier ciliate peaks at warmer thermal conditions in our mesocosms also meet expectations, such as increasing food supply and rising temperatures are known to induce rapid numerical responses whereby growth rates increase linearly with temperature (Weisse & Montagnes 1998; Montagnes & Lessard 1999; Montagnes *et al.* 2003; Johansson *et al.* 2004).

With respect to the rather fixed phytoplankton spring bloom timing, Edwards and Richardson (2004) suggested that the phenomenon of could be due to the predominance of phytoplankton taxa which germinate from resting spores and thus are controlled by photoperiodicity, not by ambient temperature. This idea arose from the observation that environmental conditions were very variable over the analyzed time series. For our experiments, this germination theory does not hold because our mesocosm set-up did not contain benthic features (except for the first experiment in 2005). It seems more likely that the slow advancement of phytoplankton in our experiments is attributable to light-limited primary production. This is supported by the study of Siegel at al. (2002) who found that throughout the North Atlantic, and thus over a broad latitudinal scale, a relatively uniform critical light dose I_C of 1.3 mol photons m^{-2} day^{-1} (in the mixed surface layer) initiates phytoplankton spring bloom. Consistently, exponential growth of phytoplankton set in at a mean light intensity of 1.34 mol photons m^{-2} day^{-1} in our low light and medium light experiment (2005 and 2007). In the high light study of 2006, phytoplankton grew exponentially right away from the start, presumably because starting light dose of 2.27 mol photons m^{-2} day^{-1} already surpassed I_C (Sommer & Lengfellner 2008).

Changing characteristics of phytoplankton spring bloom and top-down control

We found temperature dependent patterns in the magnitude and composition of biomass maxima at the primary producer level: phytoplankton peaks were highest in the coldest temperature treatments and tended to decrease in the warmer mesocosms throughout the subsequent years. Across the thermal gradient, a reduction in microdiatom portions with increasing temperatures could be observed. Changes in magnitude of phytoplankton biomass can be expected for two reasons: first, higher temperatures speed up metabolic processes and thus increase phytoplankton respiration rates. At given light (and nutrient) conditions, this could translate into lower net primary production at higher temperatures and therefore less phytoplankton biomass accumulation in warmer treatments. Enhanced respiration at higher temperatures is also reported for microbes (e.g. Vazquez-Dominguez *et al.* 2007) and zooplankton (e.g. Ikeda *et al.* 2001), and is likely to promote higher grazing activities, thus exerting a stronger top-down control on phytoplankton. This is supported by a mesocosm study of

Keller et al. (1999) on spring plankton communities from Narragansett Bay, USA, who demonstrated increased losses phytoplankton biomass at higher temperatures due to zooplankton grazing and filter feeding blue mussels. Further support, though to a limited amount, is given by grazing experiments of Aberle et al. (2007): in the mesocosm study of 2005 grazing rates of ciliates and copepods tended to be higher in the warmer treatments compared to the control ($\Delta T=0°C$) during phytoplankton bloom conditions. The study of Aberle et al. (2007) further revealed a strong overlap in feeding preferences between both grazer guilds for micro- and nanodiatoms. This seems a likely explanation for the resulting shift in phytoplankton functional groups and the different bloom compositions across the gradient of thermal treatments. Observations from the first part of the study in 2005 provide additional evidence for grazing imprints shaping the phytoplankton community: during the first weeks, losses due to grazing seemingly exceeded phytoplankton growth, resulting in overall negative net growth rates and declining phytoplankton biomass. A detailed analysis of the different phytoplankton functional groups revealed that most of all, microdiatoms were removed from the water column, and that this occurred in a temperature dependent way, with stronger reductions at higher temperatures. Nanoflagellate loss was less affected by temperature and picophytoplankton biomass decreased with similar rates in all temperature treatments. In consistency with the grazing experiments of Aberle (2007), this suggests temperature dependent grazing with grazer preferences for microdiatom food. Losses due to sedimentation can be ruled out because of sufficient mixing in the mesocosms.

Alterations of functional group composition in phytoplankton have major implications in terms of food web energy fluxes. Firstly, blooms comprised by smaller species are likely to reduce vertical energy transfer by lower sinking velocities, thus providing a lower amount of energetically rich material for benthic organisms and retarding the biological pump (Bopp *et al.* 2001). It can be hypothesized that more bloom derived material will be degraded and regenerated in the water column then. Furthermore, blooms of nanoplankton may have negative effects on up-coming generations of copepods such as copepods have been shown to preferentially graze on microplankton (Sommer *et al.* 2002; Sommer & Sommer 2006).

Impact on peak magnitude and composition at the grazer level

Except for the study of 2007, temperature and total biomass were not correlated in ciliates, neither for the first nor for the second ciliate peak. Ciliates are fast growing organisms and capable of matching the growth rates of their algal food so it could be expected that their yields in biomass reflect those patterns found in phytoplankton. The observed lack of such a temperature dependency in ciliate maximal biomass might be explained by a mixed effect of variations in food resources, coupling strength and interaction with copepods over the experimental temperature gradient: at colder temperatures, phytoplankton blooms tended to be more intense but ciliates could only respond to this increase of food with a certain time lag. At higher temperatures, this time-lag shortened, presumably due to shorter generation times and thus tightened the temporal coupling to the food resource. However, at higher temperatures net primary production was probably lower, and food competition as well as predation by copepods could have been assumed to be stronger (Aberle *et al.* 2007). It is further likely, that top-down control of copepods shaped the ciliate composition to a certain extent: in 2005, large sized ciliates prospered after the phytoplankton bloom peak, especially at higher temperatures. In this study, copepod biomass constantly declined, even faster at higher temperatures (data are given in Sommer *et al.* 2007), and thus predation on ciliates became probably negligible and promoted a bloom of large ciliates. In 2006 and 2007, the ciliate community was dominated by medium sized ciliates which could be probably attributed to a stronger top-down control by comparably high numbers of copepods in both years. However, it has to be noted that bacterivore ciliates species were highly abundant in 2006 (data not shown), so that the dominance of medium sized ciliates could also be related to resource use.

Due to methodological biases, results on nauplii biomass have to be treated with caution. A negative correlation of peak biomass and temperature could be found in 2006 and 2007, depending on the conversion of abundance data into carbon content. Certainly, it can be stated that when regarding offspring of the genus *Pseudocalanus* alone, higher nauplii abundances were found at colder temperatures. However this does only translate into higher biomass when the same stage distribution is assumed at all temperatures, which is likely oversimplified. Concerning the composition of the copepod community, temperature did not show any clear effect: in all temperature treatments, copepodids of *Pseudocalanus* relatively increased and clearly dominated in all three

experiments. An exception to this uniform pattern was found in both mesocosms of warmest treatment (ΔT=6°C) in 2007, where abundances of the genus *Centropages* constantly increased and formed a big proportion of up to 50% of copepodid biomass at the end of the study. This latter observation meets expectations at least to some extent: climate warming induces poleward range retractions of species adapted to colder temperatures whereas species stemming from warmer environments expand their ranges towards the poles. This phenomenon has been demonstrated in many species, among those copepods inhabiting the North Atlantic (Beaugrand *et al.* 2002). For our study we thus hypothesized a concordant shift from copepod species (or genera) typically found during winter to a composition of summer species at higher temperatures, i.e. a shift from *Oithona*, *Pseudocalanus*, *Paracalanus* to *Acartia*, *Temora* and *Centropages* (Behrends 1996). Hypothetically, the starting stock of copepods contained all these genera in all three studies, though *Acartia* was almost absent in 2005 and 2007. So far, no explanation can be given on the striking dominance of *Pseudocalanus*.

Match and mismatch at the food web basis

A core question we sought to answer with our mesocosm studies was whether climate change can disrupt the successional pattern of plankton spring bloom by asynchronous shifts in autotrophic and heterotrophic processes, thus decoupling primary and secondary production. As discussed in the sections above, we found temperature induced acceleration of peak biomass formation with low sensitivity at the phytoplankton level, intermediate temperature dependence at the ciliate level and highest acceleration rates in copepod nauplii. In case of ciliates, this resulted in tightened coupling between the second ciliate peak (forming after the phytoplankton bloom) and the phytoplankton maximum.

It is only over the last years, that scientists have acknowledged the key role of ciliates in marine trophodynamics (Calbet 2008 and references therein). On global scales, ciliates act as main consumers of phytoplankton primary production, ingesting on average up to 60% of primary production and 20% of algal standing stock per day. In turn, they have been found to form on average 30% of the copepod carbon ration, whereby amounts vary according to the trophic state of the respective ecosystem (higher in oligotroph regions, lower in more productive regions). Ciliates have been shown to be important consumers, especially during spring blooms, as they can

potentially ingest more food than mesozooplankton and are able to respond more quickly to increasing food availability due to higher production rates. In terms of energy flow, ciliate production is regarded to diminish transfer efficiency to higher trophic levels as they form an additional link, thus retaining primary produced material in the water column (Johansson *et al.* 2004). Taken together, a stronger coupling between ciliate and phytoplankton dynamics at higher temperatures could lead a higher input of energy into the microbial loop, thus reducing the amount of energy which hypothetically could be utilized to fuel top-predator levels.

Concerning the strong acceleration of nauplii peaks, the question, whether this high temperature sensitivity eventually induces temporal mismatch on the copepod level or not, seemed to depend on the interplay of temperature and light: above a critical threshold, exponential phytoplankton growth can be initiated (Sommer & Lengfellner 2008). At high light conditions, warmer temperatures could thus offer favourable condition for copepods, because growth rates increase and developmental times shorten (Fig. 29b). At low light conditions, however, colder temperatures have shown to be advantageous, because metabolism was presumably slower, resulting in longer survival of copepodid stages at low food conditions and time delayed nauplii peaks that could temporally match a phytoplankton bloom developing late in the year (Sommer *et al.* 2007) (Fig. 29d). We can not derive from our studies whether temporally matching nauplii cohorts would have successfully developed into a second generation of adults. Experiments were to still too short to rear the next generation and extension was not possible due to increasing wall growth in the set-ups. However, from biomass dynamics in the copepodid fraction we can conclude that optimal conditions for copepods existed in the medium light study of 2007, however with no difference between temperature treatments at the copepodid level (Fig. 29c, f).

Durant et al. (2005; 2007) proposed to add a further dimension to the match-mismatch hypothesis: originally, the hypothesis stated that predator (i.e. any type of consumer) and prey have to overlap temporally and spatially in order to match and thus promote predator recruitment (Cushing 1972). However, similarly important to fulfil match conditions is a suitable amount of prey. Thus, abundance (or biomass) can be seen as a third axis, along which the quality or intensity of the match event is determined (Durant *et al.* 2005; 2007). We demonstrated that phytoplankton blooms were generally less intense at higher temperatures. Combined with the suggested extension of the match-mismatch hypothesis, it can be concluded that even at perfect temporal and/or

spatial match, the amount of energy that could be transferred from phytoplankton to zooplankton is likely to be diminished under climate warming. Hence, a general mismatch in terms of biomass could be expected at elevated temperatures. It could be even hypothesized, that the match-mismatch hypothesis is expandable in other prey related aspects, for example prey quality, which may also undergo changes as environmental conditions alter under global warming.

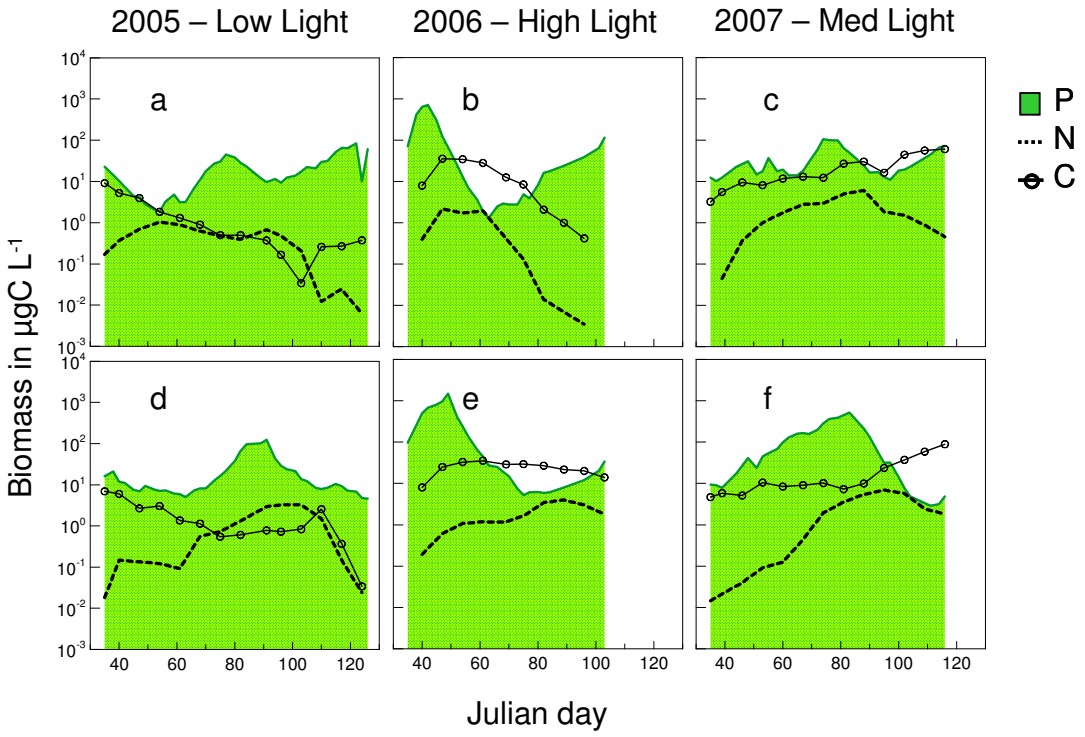

Fig. 29. Match and mismatch. Time series of total phytoplankton, nauplii and copepodid biomass (µg C L^{-1}) shown for **a, b, c)** one of the +6°C temperature treatments and **d, e, f)** one of the +0°C temperature treatments from the different experiments. The first column **(a, d)** shows data from 2005, the second column **(b, e)** from 2006, and the third column **(c, f)** from 2007.
a, d) At low light conditions, timing of the nauplii peak matched the timing of the phytoplankton bloom peak best at colder temperatures, but food levels where too low and copepod populations declined. **b, e)** At high light conditions, food levels were higher, but blooms of phytoplankton occurred early and decayed fast so that even at high temperatures, where nauplii peaks developed closest to the food peaks, copepod populations showed no increase. **c, f)** At medium light conditions, food conditions seemed optimal and nauplii peaks temporally matched phytoplankton blooms at all temperatures and copepod populations increased in all treatments. Green area plot (P): phytoplankton; dotted line (N): copepod nauplii; solid line with open circles (C): copepodids. Phytoplankton data from Sommer and Lengfellner (2008) and Sommer, unpublished data.

Further implications arise from temperature induced shifts in phenology of other plankton organisms: Kirby et al. (2007), for example, report an advancement in spring time recruitment of meroplankton larvae in the North Sea. Depending on the annual spring situation this could pose additional competitive stress on holoplankton herbivores, including copepods, or even reduce food resources ahead of the copepods'

reproductive window. Intensified food shortage for the individual could be also imposed by propagated density-dependence in mismatch-situations (Philippart *et al.* 2003; Visser *et al.* 2004). Maybe most importantly, temperature related shifts to higher trophic levels should be considered. First feeding fish larvae are especially sensitive to food shortage and synchrony with their food resources is vital for yields of strong year classes. Consequently, efficient transfer in the marine pelagic depends strongly on the synchrony of successive trophic levels and timing of their production peaks. In North Sea waters, Edwards and Richardson (2004) have already demonstrated shifts in seasonality plankton seasonality to a varying extent at species and functional level. The study of Beaugrand et al. (2003) links these asynchronies in combination with strong fishing pressure to the decline of North Sea cod stocks. Similar scenarios are quite conceivable for the Baltic Sea or other temperate marine environments

Conclusion

This chapter points out possible impacts of climate warming on the level of primary producers (i.e. phytoplankton) and adjacent heterotrophic levels of primary and secondary consumers (ciliates and copepods). We demonstrated that the different trophic levels display differential temperature sensitivity in biomass dynamics and eventually spring bloom formation: whereas phytoplankton peak timing was rather insensitive to temperature elevation, ciliate peaks, and most of all peaks of copepod nauplii revealed comparably strong advancement: nauplii peaks occurred several weeks earlier across the temperature gradient of 6°C (except in 2007). Moderate advancement of ciliate peaks, emerging after the phytoplankton blooms, resulted in stronger coupling of this consumer-resource pair at elevated temperatures. This has major implications for trophic energy transfer such as it can be expected that global warming shifts more primary produced material towards the microbial loop via the fast growing microzooplankton fraction. This could eventually reduce the available amount of energy for higher trophic levels such as fish, seabirds or marine mammals. The acceleration in copepod recruitment can promote both, match and mismatch situations: the outcome strongly depends on the interaction of light and temperature which trigger

phytoplankton phenology and magnitude of biomass peak, as well as grazing activities of ciliates, which in turn act as food competitors and prey items at the same time.

We have further demonstrated that higher temperatures alter maximal phytoplankton biomass accumulation and functional group composition, most importantly a reduction of microphytoplankton and the promotion of smaller sized phytoplankton groups at higher temperatures. This could be expected to enhance the energy flux in the microbial loop at least in two ways: by reduction of sinking velocity of phytoplankton bloom material and by reduced direct energy transfer from the primary producer to the copepod level.

Chapter 5 - Changes in diversity and size structure of plankton communities under global warming conditions

Introduction

Diversity matters

Changes in species abundance and temporal dynamics are not only interesting with respect to energy flow in the food web, but also provide information on community structure in terms of biodiversity and underlying species evenness. Why does biodiversity matter? Generally, it has been demonstrated that species diversity of a given trophic level is positively related to productivity in terms of biomass (reviewed by Hooper *et al.* 2005), whereby most of the studies investigated diversity effects in terrestrial primary producers such as grassland communities. Experimental studies on aquatic microbes revealed, that similar effects occur in aquatic systems: increasing species richness enhances resource use und thus productivity (McGradySteed *et al.* 1997; Naeem & Li 1997; Steiner *et al.* 2005). Besides this positive effect on productivity, it is hypothesized that more diverse mixtures of species have a higher probability to include forms that are pre-adapted or more tolerant to environmental stress and thus could buffer food webs against environmental disturbance (insurance hypothesis; Yachi & Loreau 1999). Only recently, this stabilizing diversity effect was demonstrated in planktonic autotrophs from limnic as well as marine systems (Ptacnik *et al.* 2008).

In our experiment, we investigated plankton spring succession under climate warming conditions. This seasonal event is typically characterized by a succession of species with different requirements concerning light intensity and nutrient supply on the primary producer level as well as specific thermal and food demands in secondary producers. In the first part of this chapter, we will investigate whether temperature elevation alters the temporal patterns of species richness, species evenness and resulting biodiversity, thus possibly destabilizing community structure and functioning.

Community and population size structure

Body size distribution is a further fundamental characteristic of networks, because it relates to many life-history traits such as numerical abundance, home range, competitive and facilitative relations to other food web members, trophic status, ingestion and secondary production, fecundity, nutrient turnover, life-span as well as fasting endurance (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; White *et al.* 2007). Changes in body size are therefore likely to have severe consequences for individuals, populations, communities and even entire ecosystems (Woodward *et al.* 2005 and references therein). There is a vast amount of literature dealing with the temperature effect on body size. Several ecological rules and hypothesis have been put up to describe global trends in body size of populations and communities found in studies on contemporary, historic and fossil records across various temporal and spatial scales (reviewed partly by Millien *et al.* 2006). The second part of this chapter therefore surveys our experimental results related to size structure on the population and community level, and discusses the findings in the context of established body size theories in ecology.

Results

Time series of species richness and evenness

Richness and evenness are given over the whole experimental period for phytoplankton and ciliate species (R_S and E_S) as well as for copepodid stages on the genus level (R_G and E_G). Nauplii stages were not included because of low taxonomic resolution. Symbols depict the timing of the biomass maxima for the respective groups in each mesocosm (phytoplankton bloom peak in phytoplankton, and first and second ciliate biomass maximum in ciliates). In the copepodid plots, symbols mark the timing of the phytoplankton bloom. No data are given on copepodids of 2005 because abundances were very low. Data from microscopic counting of phytoplankton supplied by Sommer (2007; 2008 and Sommer, unpublished data) and ciliate data by Aberle (Aberle *et al.* 2007 and Aberle, unpublished data).

Phytoplankton species richness. In 2005, the phytoplankton community comprised 14 species at the beginning of the experiment, though only 13 were found on the first day

in one of the coldest mesocosms at ΔT=0°C. The general trend was an initial decline in R_S in all treatments with elevated temperatures (ΔT=2°C, 4°C and 6°C), followed by an increase of R_S until maximum values between Julian Day 77 and 101. Maximal species number varied between 19 and 21 without any temperature dependent trend. After the R_S maximum, the number of species declined in all treatments in a fluctuating, but overall constant manner. The timing of both, phytoplankton peak and maximal R_S coincided in most of the treatments (not among treatments) but differed in the warmest treatment at ΔT=6°C (Fig. 30a-d). In 2006, the experiment started with an average R_S of 23, varying between 21 and 24 among the mesocosms. R_S increased within the first two weeks and peaked between Julian Day 40 and 49, temporally coinciding with the phytoplankton biomass maximum. Maximal R_S was highest in the coldest treatment at ΔT=0°C, with R_S = 28 and 29. In the warmer treatments (ΔT=2°C, 4°C and 6°C), between 24 and 26 phytoplankton species were found. At the timing of the phytoplankton bloom peak, R_S was significantly negatively correlated with temperature (inverse first order regression model: $f(x) = 23 + 5.16(\Delta T+1)^{-1}$; p = 0.002). R_S dropped in all treatments after the peak and reached minimum values earliest at higher temperatures (linear regression model: $f(x) = 83.6 - 3.83\Delta T$; p = 0.0003), whereby the minimal species number was lower at ΔT=0°C and ΔT=2°C (R_S=10 to 12) compared to the warmer treatments at ΔT=4°C and ΔT=6°C (R_S=13 to 17). Thereafter, R_S fluctuated but overall increased in all mesocosms (Fig. 30e-h). The study of 2007 started with an average number of 20 phytoplankton species, varying between 16 and 22 among the mesocosms. Dynamics of R_S were characterized by fluctuating but rather stable values and declining trends after Julian Day 80 at ΔT=4°C and ΔT=6°C. An exception to this was one mesocosm at ΔT=4°C, where R_S continuously declined. In the colder treatments at ΔT=2°C and ΔT=0°C, R_S showed a pronounced, broad peak, temporally coinciding with the phytoplankton biomass maximum. There was a significant negative correlation between R_S at the timing of the phytoplankton bloom peak and temperature (linear regression model: $f(x) = 28 - 1.38\Delta T$; p = 0.005). Maximally found R_S was lower at ΔT=4°C and ΔT=6°C (R_S=22 to 23) compared to the cooler mesocosms at ΔT=0°C and ΔT=2°C (R_S=27 to 29) (Fig. 30i-l).

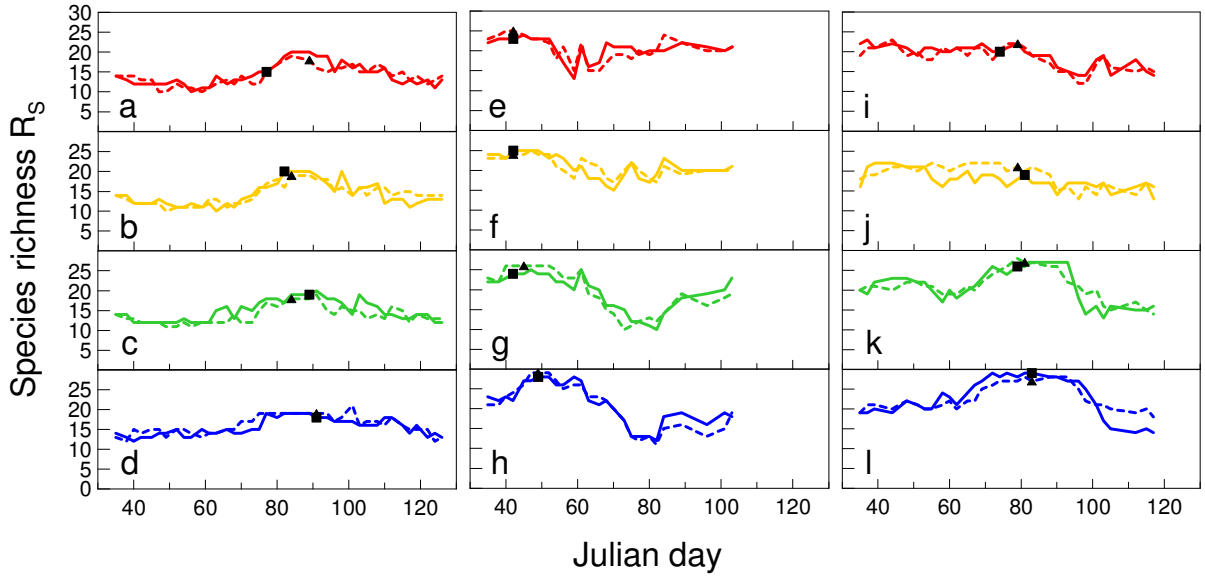

Fig. 30. Phytoplankton species richness. Timeseries of phytoplankton species richness (R_S) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm. Data from Sommer, unpublished data.

Phytoplankton species evenness. All three experiments started at an intermediate level of species evenness between E_S = 0.4 and 0.5. In 2005, E_S fluctuated at the beginning and started to decrease from around Julian Day 50 onwards in all mesocosms. The treatments differed in that minimum values of E_S were soonest reached in the coldest treatment at ΔT=0°C and thereafter oscillated, whereas in all warmer treatments, lowest values for E_S were reached about 10 to 20 days later. Phytoplankton bloom peaks coincided with E_S minima or nearly minimum values at ΔT=2°C, 4°C and 6°C, whereas in the coldest treatment, E_S had already passed the minimum point. At the timing of the phytoplankton bloom, E_S was negativle correlated to temperature (inverse first order regression model: $f(x) = 0.091 + 0.45(\Delta T+1)^{-1}$; p = 0.0008) (Fig. 31a-d). In 2006, patterns of species evenness are characterized by an initial drop to minimum values of E_S, which coincided in most cases exactly with the timing of the phytoplankton bloom peak. Minima of E_S were negatively correlated with temperature (linear regression model: $f(x) = 0.26 - 0.022\Delta T$; p = 0.007). Thereafter, E_S steeply increased in all mesocosms and fluctuated at rather constant levels, except for one mesocosm at ΔT=0°C where E_S continuously decreased towards the end of the experiment (Fig. 31e-h). The dynamics in 2007 were also marked by an initial drop of E_S whereby minima were reached first in the warmer treatments at ΔT=2°C, 4°C and 6°C and last in the coldest ones at ΔT=0°C. E_S steeply increased afterwards and reached highest or nearly highest levels at the timing of

the phytoplankton bloom peak. An exception to this was one mesocosm at ΔT=0°C and one mesocosm at ΔT=2°C (Fig. 31i-l).

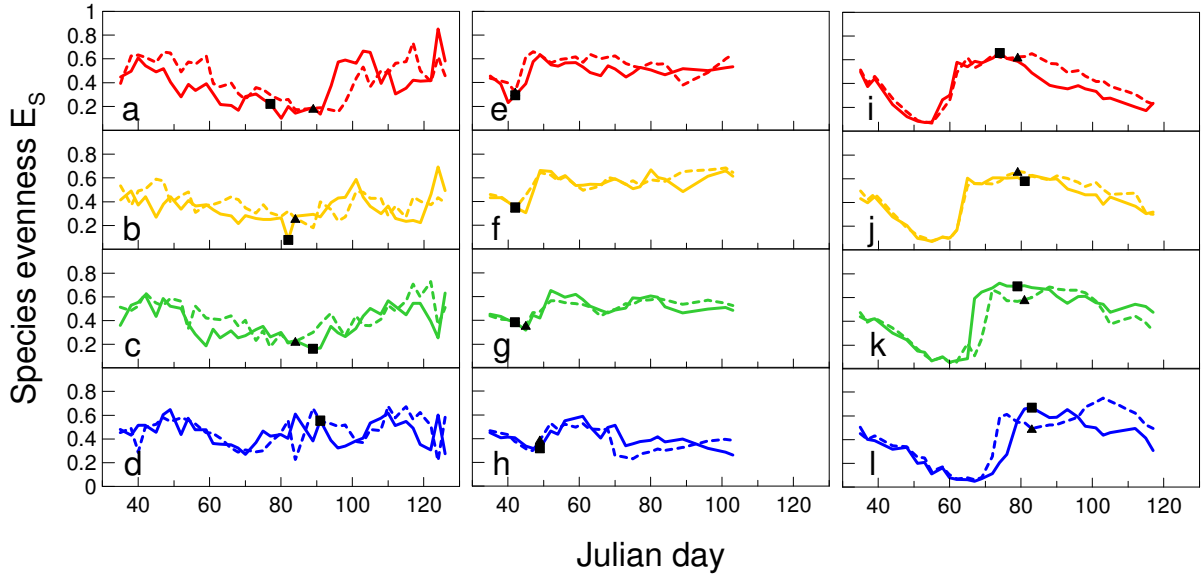

Fig. 31. **Phytoplankton species evenness**. Timeseries of phytoplankton species evenness (E_S) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm. Data from Sommer, unpublished data.

Ciliate species richness. At the beginning of the experiment in 2005, between one and three ciliate species were found in the starting communities. In the first half oft the experiment, where the first ciliate biomass maximum occurred, R_S kept rather constant at values near R_S = 3 in all treatments. It increased around Julian Day 75 and maximum R_S was reached between Julian Day 90 and 100. The second ciliate biomass maximum coincided with R_S maxima or near maximal values at ΔT=2°C, 4°C and 6°C. In the coldest treatment at ΔT=0°C, R_S already declined at the time when ciliate biomass peaked. Maximal ciliate species richness did not show any temperature related pattern (Fig. 32a-d). In the study of 2006, one to four ciliate species were counted on the first sampling date. Generally, R_S displayed strong fluctuations in all mesocosms during this study and the timing of the two ciliate biomass maxima coincided with maxima, minima or intermediate levels of R_S, hence lacking any clear pattern (Fig. 32e-h). The experiment of 2007 was characterized by very stable ciliate species richness: starting with two to five species, R_S oscillated between these values over the whole experimental period uniformly in all mesocosms. Only in one mesocosm at ΔT=0°C there was a single drop to R_S = 1 (Fig. 32i-l).

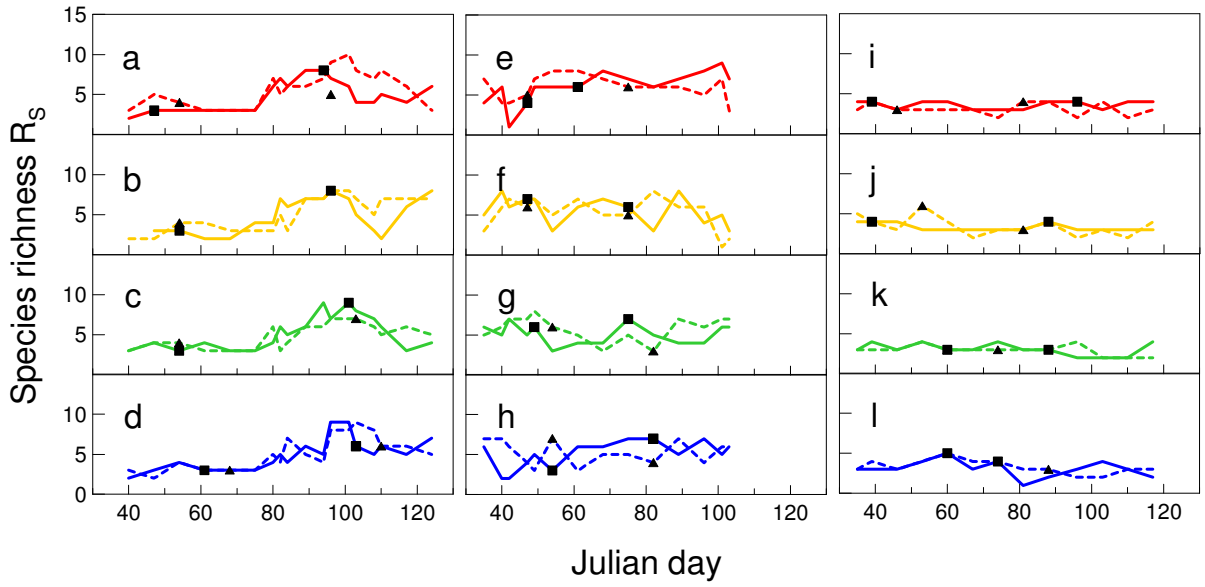

Fig. 32. Ciliate species richness. Timeseries of ciliate species richness (R_S) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the ciliate maxima (first and second peak) of the respective mesocosm. Data from Aberle, unpublished data.

Ciliate species evenness. Ciliate species were very evenly distributed at the beginning of the experiment in 2005, with E_S ranging from 0.8 to 1.0. The only exception was one of the warmest mesocosms at ΔT=6°C, where species evenness was much lower with E_S= 0.5. Within the first weeks, E_S continuously declined and reached minimum values first in the warmest treatments and thereafter in the colder treatments (linear regression model: f(x) = 60.3 - 2.1ΔT; p = 0.0003) whereby values for minimum E_S did not show any temperature dependency. In most mesocosms, minimum E_S and first ciliate biomass maximum coincided. Exceptions were one mesocosm at ΔT=0°C and one mesocosm at ΔT=6°C. Evenness generally increased from then on until around Julian Day 110, and in some mesocosms declined after that date until the end of the study. Dynamics were subject to strong fluctuations. The second ciliate biomass maximum occurred during this period but without any temperature related pattern concerning evenness (Fig. 33a-d). In 2006, the starting community was also characterized by a high species evenness (E_S = 0.7 to 1.0) and a steep decline in E_S within the first weeks. Minimum values of E_S were reached first in the warmer treatments and with a time lag in the colder treatments (linear regression model: f(x) = 53 - 1.75ΔT; p = 0.002). In most cases, the first ciliate biomass peak coincided with minimum values of E_S. Thereafter, E_S sharply increased and fluctuated until the end of the study. The second ciliate biomass peak happened in most mesocosms when E_S passed an intermediate minimum. No further temperature related

patterns in E_S were found (Fig. 33e-h). The initial ciliate community in the study of 2007 displayed a more variable evenness with E_S ranging between 0.5 and 1.0. Similar to the other experiments, E_S declined at first in all temperature treatments. In the warmest treatment at ΔT=6°C, E_S increased steeply after passing the minimum, and values fluctuated at a relatively high level until the end of the experiment. In the other treatments, E_S also increased after the minimum but apparently lower temperatures slowed down this dynamic. Timing of the first ciliate biomass maximum coincided with minimal E_S only in four out of eight mesocosms. No relation was found between temperature and minimum values of E_S. Timing of the second ciliate biomass maximum coincided with minimal E_S in two out of eight mesocosms. At the timing of the second ciliate biomass maximum, E_S was positively correlated with temperature treatment (linear regression model: $f(x) = 0.75 + 0.12\Delta T$; $p = 0.005$) (Fig. 33i-l).

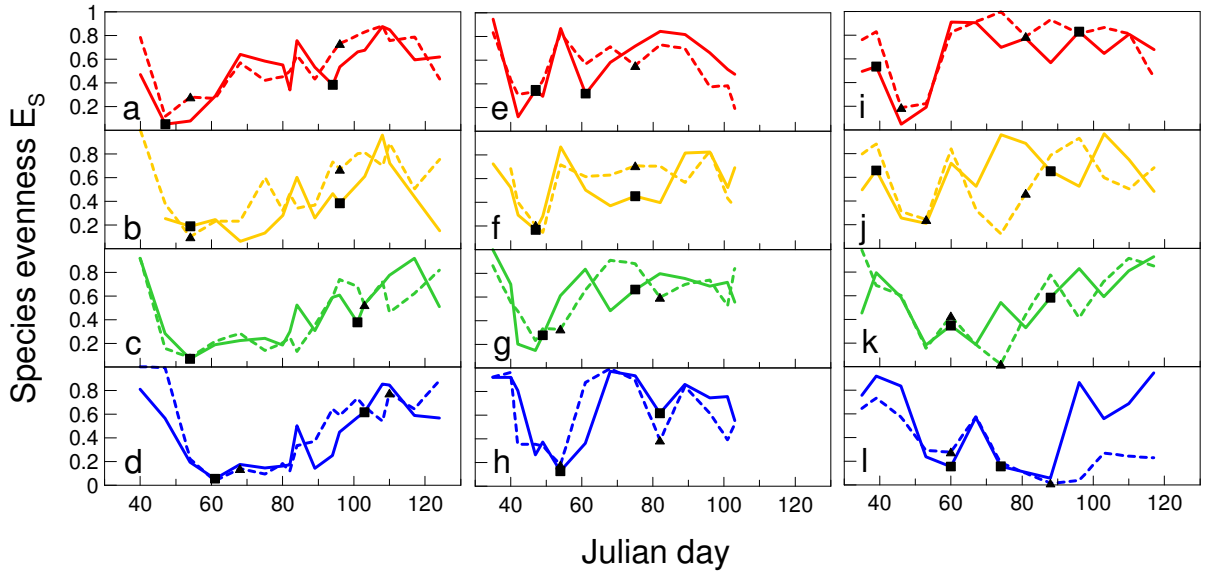

Fig. 33. Ciliate species evenness Timeseries of ciliate species evenness (E_S) shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and f solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the ciliate biomass maxima (first and second peak) of the respective mesocosm. Data from Aberle, unpublished data.

Copepod genus richness. The study of 2006 started with a copepod community comprised of five genera. This level was kept in all mesocosms at least until Julian Day 60. Consequently, R_G was identical for all treatments at the timing of the phytoplankton bloom. After Julian Day 60, R_G declined first in one of the warmest mesocosms at ΔT=6°C and successively in the other temperature treatments. In the coldest mesocosms, the five genera were still found until Julian Day 80 (Fig. 34a-d). In the experiment of

2007, between two and four different copepod genera were detected on the first sampling date. In the course of the experiment, R_G fluctuated most of the time around values of $R_G = 4$, thereby displaying no differences between the temperature treatments. Hence, no temperature dependent pattern appeared in R_G for the timing of the phytoplankton bloom (Fig. 34e-h).

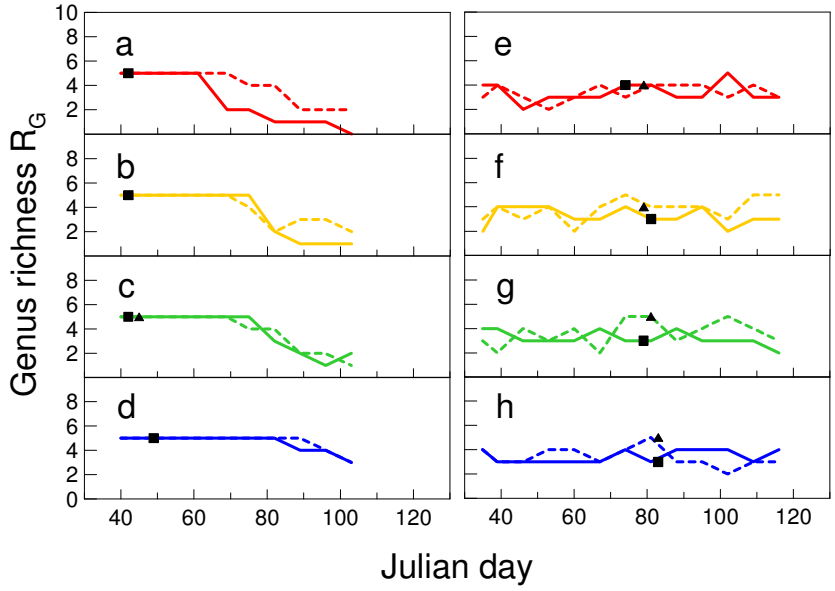

Fig. 34. Copepodid genus richness. Timeseries of copepodid genus richness (R_G) shown for the different temperature treatments in **a-d)** 2006 and **e-h)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm.

Copepod genus evenness. Genus evenness was uniformly $E_G = 0.6$ at the beginning of the study in 2006 and only changed little over the short period until the phytoplankton biomass maximum was reached. At the timing of the phytoplankton bloom, E_G was weakly positively correlated with temperature treatment (linear regression model: $f(x) = 0.55 + 0.0059\Delta T$; $p = 0.05$). In the coldest temperature treatment at ΔT=0°C, E_G declined until the end of the experiment. In all warmer treatments (ΔT=2°C, 4°C and 6°C), E_G also declined but there was a trend of increasing E_G from around Julian Day 89 onwards (Fig. 35a-d). In the experiment of 2007, initial E_G ranged from 0.6 to 1.0. In the warmest mesocosms at ΔT=6°C, E_G first increased to values close to 1.0 and then declined to an intermediate minimum, followed by a second peak. At ΔT=4°C, there was also a peak in E_G dynamics during the first part of the experiment, however, values constantly declined thereafter. At ΔT=2°C, E_G first fluctuated around its initial value and then declined. In the coldest mesocosms, E_G was also rather stable until Julian Day 70 and peaked at Julian Day 81 in one mesocosm while it peaked on Julian Day 102 in the other mesocosm. At the timing of the phytoplankton bloom, E_G was weakly negatively

correlated with temperature treatment (inverse first order regression model: f(x) = 0.42 + 0.36(ΔT+1)$^{-1}$; p = 0.05) (Fig. 35e-h).

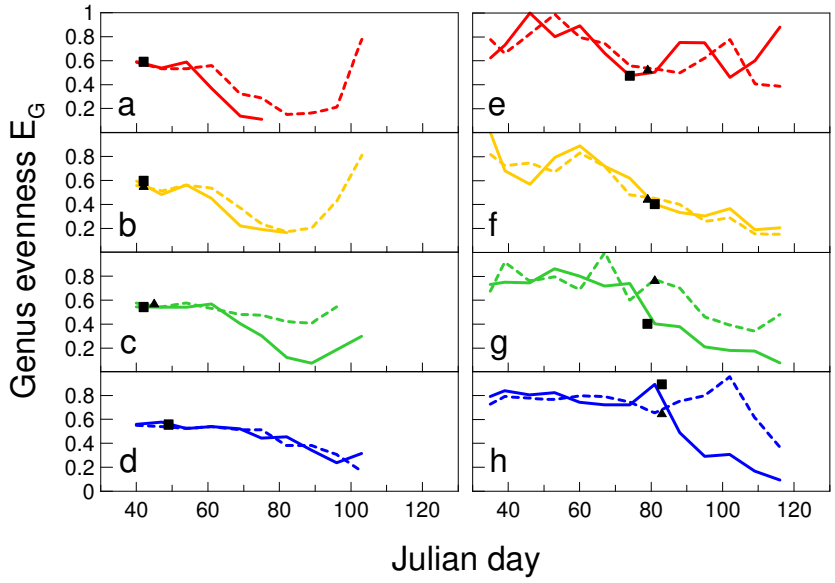

Fig. 35. Copepodid genus evenness. Timeseries of copepodid genus evenness (E_G) shown for the different temperature treatments in **a-d)** 2006 and **e-h)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm.

Mean richness

Mean richness was calculated as an average of all richness estimates within a mesocosm for the respective group (phytoplankton, ciliates, copepods). Data for mean richness of the different years are displayed in Figure 36.

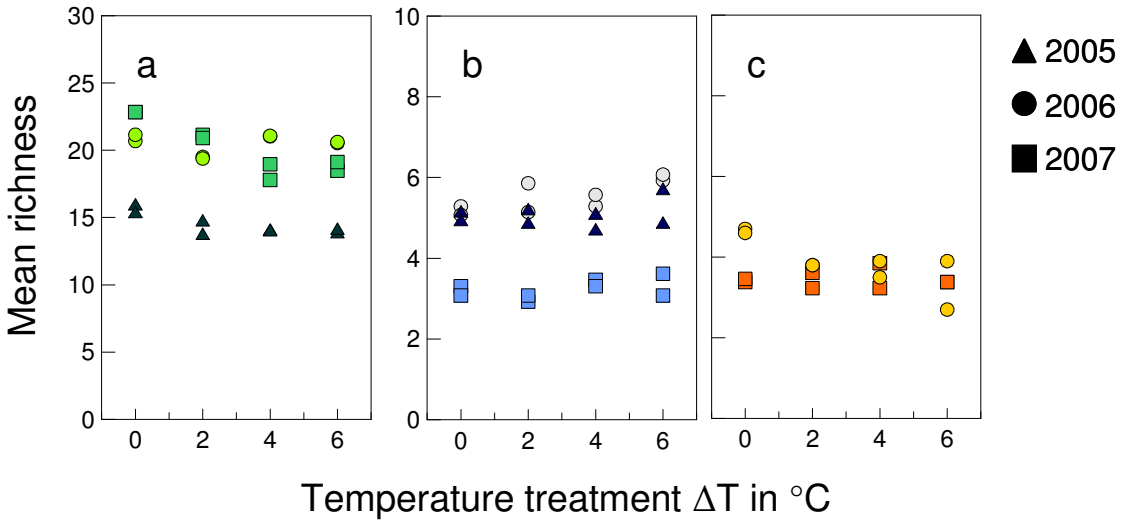

Fig. 36. Mean richness. Mean richness over the whole experimental period of **a)** phytoplankton, **b)** ciliates and **c)** copepodids plotted against temperature treatment for the different years. Triangles: 2005; circles: 2006; squares: 2007. Note the different scales on the y-axis. Phytoplankton data from Sommer, unpublished data and ciliate data from Aberle, unpublished data.

Phytoplankton mean richness was negatively correlated with temperature treatment in the experiments 2005 and 2007 (in both cases inverse first order regression model: $f(x) = 13.7 + 1.99(\Delta T+1)^{-1}$; $p = 0.002$ and $f(x) = 18.26 + 4.78(\Delta T+1)^{-1}$; $p = 0.003$). No temperature trend was found in 2006 (Fig. 36a). Ciliate mean richness was positively correlated with temperature treatment in 2006 (linear regression model: $f(x) = 5.17 + 0.12\Delta T$; $p = 0.04$). No temperature related trends were found in 2005 or 2007 (Fig. 36b). Mean richness of copepodids displayed a negative relation with temperature treatment in the experiment of 2006 (inverse first order regression model: $f(x) = 3.28 + 1.39 (\Delta T +1)^{-1}$; $p = 0.01$), but no relation in 2007 (Fig. 36c).

Mean evenness

Mean evenness was calculated as an average of all evennness estimates within a mesocosm for the respective group (phytoplankton, ciliates, copepods). Data for mean evenness of the different years are displayed in Figure 37.

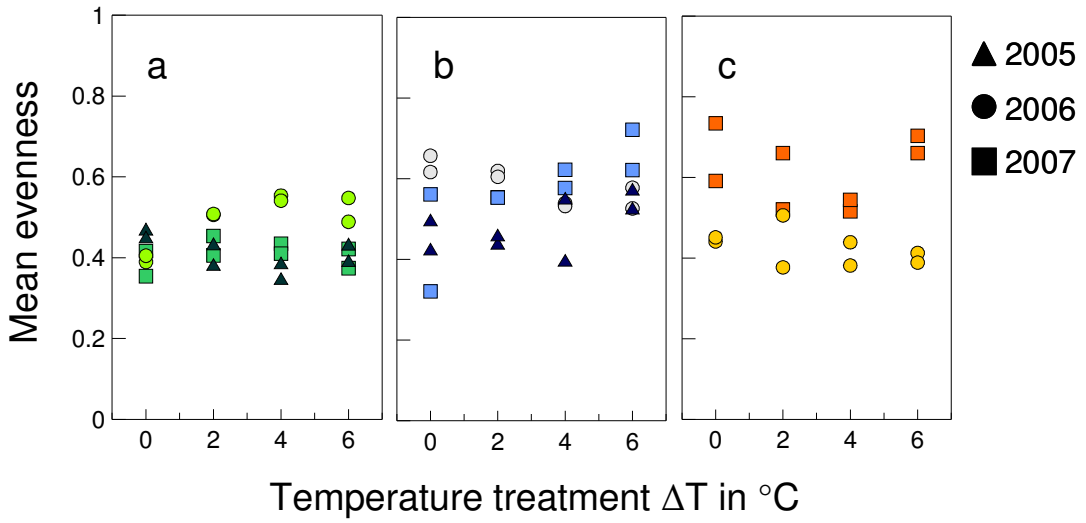

Fig. 37. Mean evenness. Mean evenness over the whole experimental period of **a)** phytoplankton, **b)** ciliates and **c)** copepodids plotted against temperature treatment for the different years. Triangles: 2005; circles: 2006; squares: 2007. Phytoplankton data from Sommer, unpublished data and ciliate data from Aberle, unpublished data.

Phytoplankton mean evenness was negatively correlated with temperature treatment in the study of 2005 (inverse first order regression model: $f(x) = 0.38 + 0.081(\Delta T+1)^{-1}$; $p = 0.04$) and gave an unimodal response to temperature treatment in 2006, whereby an internal maximum was found near $\Delta T=4°C$ (cubic regression model: $f(x) = 0.4+0.072\Delta T + 0.0087(\Delta T)^2 + 6*10^{-6}(\Delta T)^3$; $p = 0.009$). No trend emerged in 2007 (Fig. 37a). Ciliate mean

evenness showed no temperature relation in the study of 2005, but was negatively correlated with temperature treatment in 2006 (linear regression model: f(x) = 0.63 + 0.017ΔT; p = 0.01) and positively correlated with temperature treatment in 2007 (linear regression model: f(x) = 0.46 + 0.037ΔT; p = 0.02) (Fig. 37b). No significant correlations were found for copepodid evenness and temperature treatment in any year (Fig. 37c).

Diversity time series

Biodiversity (H') was calculated after Shannon and Weaver (1963) on basis of species data (H_S) for phytoplankton and ciliates and on basis of genus data (H_G) for copepodid stages. Nauplii stages are not included due to low taxonomic resolution. No copepodid diversity is given for 2005 because copepod abundance declined rapidly and was very low for most of the experimental period. Figures 38, 39 and 40 show the time series of H_S and H_G. Symbols depict the timing of the biomass maxima for the respective groups in each mesocosm (phytoplankton bloom peak in phytoplankton and first and second ciliate biomass maximum in ciliates). In the copepodid plots, symbols mark the sampling date closest to the timing of the phytoplankton bloom. Data from microscopic counting of phytoplankton supplied by Sommer (2007; 2008 and Sommer, unpublished data) and ciliate data by Aberle (Aberle *et al.* 2007 and Aberle, unpublished data).

Diversity time series of phytoplankton. Generally, phytoplankton diversity patterns resembled those in phytoplankton evenness. In 2005, starting values for H_S ranged between 0.95 and 1.35. At ΔT=2°C, 4°C and 6°C, diversity declined in a fluctuating manner, passed minimum values between Julian Day 73 and 89 around the timing of the phytoplankton biomass maximum. Thereafter H_S increased again towards the end of the experiment. In the coldest treatment at ΔT=0°C, H_S oscillated over the experimental period and passed an intermediate peak at the timing of the phytoplankton biomass maximum. There was no significant correlation between H_S and temperature at the phytoplankton biomass maximum, neither with linear or non-linear regression models (Fig. 38a-d). In the study of 2006, initial values for H_S ranged from 1.37 to 1.44. H_S declined in all temperature treatments and reached minimum values at the timing of the phytoplankton bloom between Julian Day 40 and 50. Minimal H_S was reached faster at higher temperatures (linear regression model: f(x) = 47.05 - 0.98ΔT; p = 0.001). H_S at the phytoplankton biomass peak tended to be slightly lower in the warmer mesocosms (linear regression model: f(x) = 1.22 - 0.04ΔT; p = 0.05). Thereafter, H_S increased in all

treatments and fluctuated at relatively stable levels in the warmer mesocosms at ΔT=2°C, 4°C and 6°C, whereas H_S declined again at ΔT=0°C. H_S peak values between Julian Day 50 and 60 were reached first at higher temperatures and with a time lag at colder temperatures (linear regression model: f(x) = 55.65 - 1.43ΔT; p = 0.02) (Fig. 38e-h). The study of 2007 started with H_S values between 1.20 and 1.51. H_S declined from the beginning on and passed a minimum between Julian Day 53 and 65. Minimum values of H_S were reached earlier in the warmer mesocosms (linear regression model: f(x) = 64.2 - 1.9ΔT; p = 0.0001). Afterwards H_S increased in all treatments to maximal or nearly maximal values at the timing of the phytoplankton biomass peak, and then declined until the end of the study. No temperature dependency was found for H_S at the timing of the phytoplankton biomass peak (Fig. 38i-l).

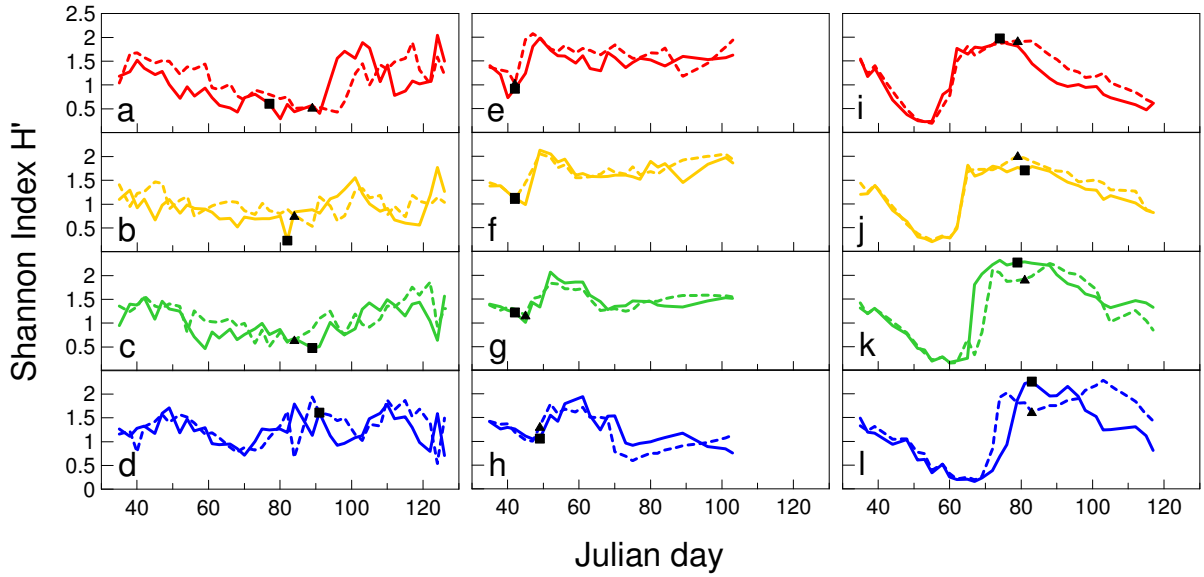

Fig. 38. Phytoplankton diversity. Timeseries of phytoplankton diversity (Shannon index, H') shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm. Data from Sommer, unpublished data.

Diversity time series of ciliates. The dynamics of ciliate diversity generally resembled those of ciliate evenness. In 2005, initial values for H_S ranged from 0.33 to 1.10. H_S first declined in all treatments and reached minimal values at the timing of the first ciliate biomass maximum between Julian Day 47 and 68. Thereafter, H_S gradually increased towards the timing of the second ciliate biomass maximum between Julian Day 94 and 110. No significant correlation between diversity and temperature emerged at any biomass maximum (Fig. 39a-d). The experiment of 2006 started with H_S values between

0.64 and 1.31. Dynamics of H_S were characterized by an initial decline and strong fluctuations over the whole experimental period in all temperature treatments (Fig. 39e-h). In 2007, H_S ranged between 0.50 and 1.29 at the beginning of the study and dynamics were subject to strong fluctuations over the whole experimental period. The general trend was a decline in H_S values from the start on and an increase thereafter. Due to fluctuations, the timing of minimum H_S was difficult to determine but overall it seemed that dynamics were slowed down in the colder treatments compared to the warmer ones. H_S was positively correlated to temperature at the second ciliate maximum (linear model: $f(x) = 0.06 + 0.17\Delta T$; $p = 0.003$) (Fig. 39i-l)

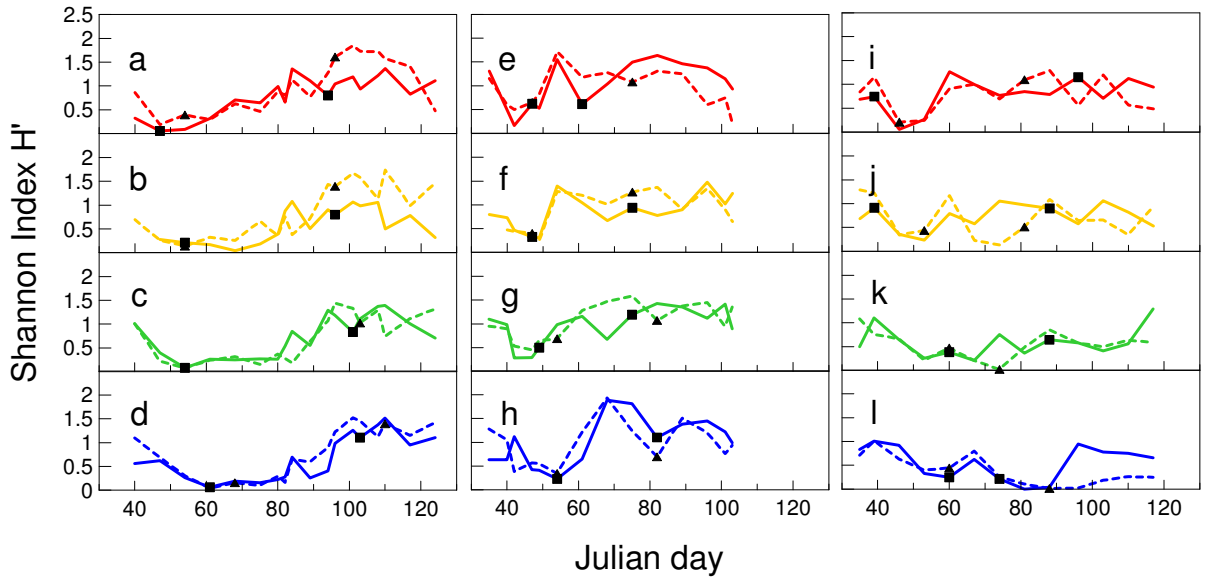

Fig. 39. Ciliate diversity. Timeseries of ciliate diversity (Shannon index, H') shown for the different temperature treatments in **a-d)** 2005, **e-h)** 2006 and **i-l)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of ciliate biomass maxima (first and second peak) of the respective mesocosm. Data from Aberle, unpublished data.

Diversity time series of copepodids. In the experiment of 2006, H_G ranged between 0.87 and 0.96 at the beginning, and continuously declined until the end of the study. This seemed to happen faster at higher temperatures. No significant trend was found for copepod diversity at the timing of the phytoplankton bloom (Fig. 40a-d). The study of 2007 started with H_G ranging from 0.69 and 1.10. H_G fluctuated at rather stable levels until Julian Day 70 in all treatments and thereafter declined at ΔT=0°C, 2°C and 4°C until the end of the experiment. In the warmest treatment, at ΔT=6°C, H_G kept further stable. No trend emerged for H_G at the timing of the phytoplankton biomass peak. However,

H_G at this point was higher in the coldest treatment at ΔT=0°C compared to most of the warmer treatments (Fig. 40e-h).

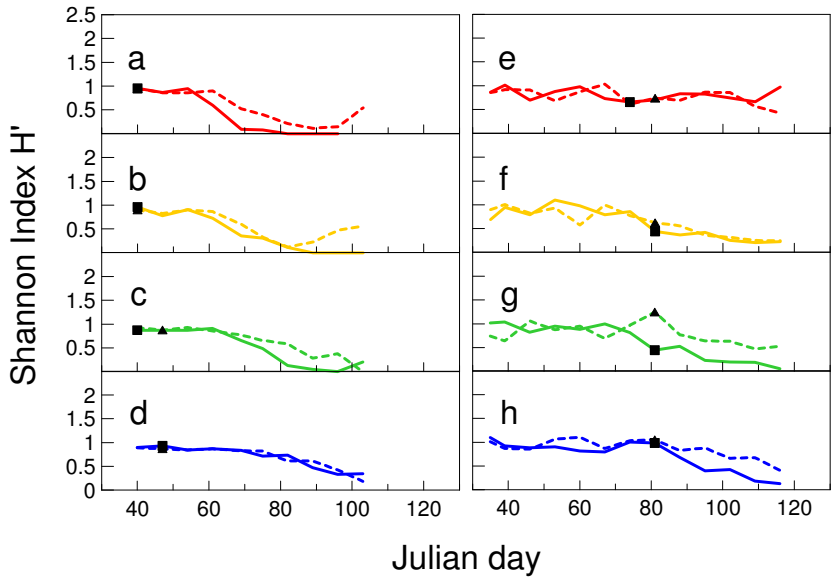

Fig. 40. Copepodid diversity. Timeseries of copepodid genus diversity (Shannon index, H') shown for the different temperature treatments in **a-d)** 2006 and **e-h)** 2007. Blue: ΔT=0°C; green: ΔT=2°C; yellow: ΔT=4°C; red: ΔT=6°C. Dotted and solid lines represent the two parallel mesocosms of each temperature treatment. Black symbols (triangle or square) mark the timing of the phytoplankton biomass maximum of the respective mesocosm.

Mean diversity

Mean diversity was calculated as an average of all diversity estimates within a mesocosm for the respective group (phytoplankton, ciliates, copepods). Data for mean diversity of the different years are displayed in Figure 41.

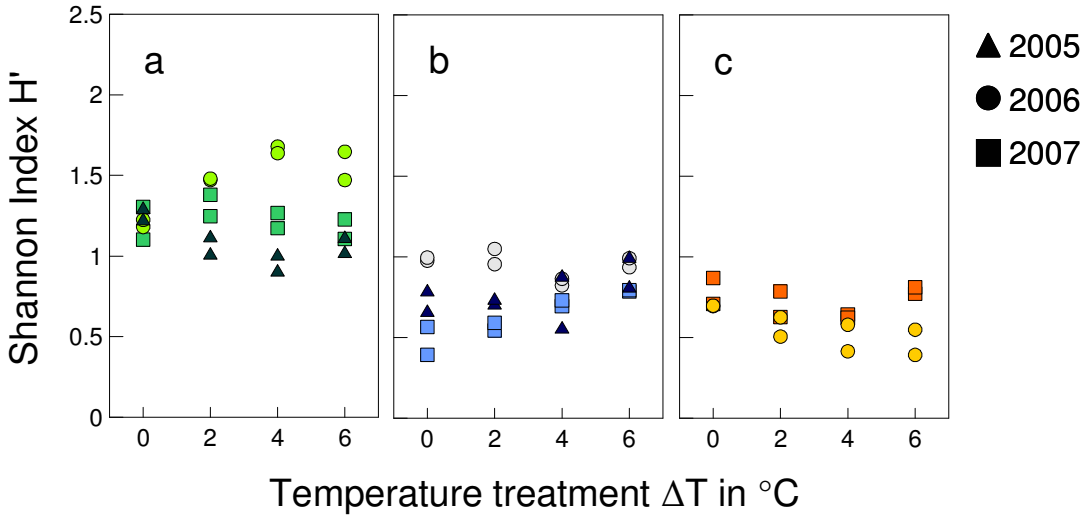

Fig. 41. Mean diversity. Mean diversity over the whole experimental period of **a)** phytoplankton, **b)** ciliates and **c)** copepodids plotted against temperature treatment for the different years. Triangles: 2005; circles: 2006; squares: 2007. Phytoplankton data from Sommer, unpublished data, ciliate data from Aberle et. al. (2007) and Aberle, unpublished data.

Phytoplankton mean diversity displayed a negative unimodal response to temperature treatment in the experiment of 2005, and a positive unimodal response to temperature treatment in the study of 2006. The internal minimum of the model for 2005 was found near ΔT=4°C, the internal maximum in 2006 was also found near ΔT=4°C (cubic regression models: $f(x) = 1.2 - 0.096\Delta T - 0.0061(\Delta T)^2 + 0.0028(\Delta T)^3$; $p = 0.04$ and $f(x) = 1.2 + 0.013\Delta T + 0.013(\Delta T)^2 - 0.01(\Delta T)^3$; $p = 0.009$). No temperature trend was found in 2007 (Fig. 41a). Ciliate mean diversity was not related to temperature in 2005 and 2006, but positively correlated with temperature treatment in 2007 (linear regression model: $f(x) = 0.47 + 0.54\Delta T$; $p = 0.0008$) (Fig. 41b). Mean diversity of copepodids displayed a negative relation with temperature treatment in the experiment of 2006 (linear regression model: $f(x) = 0.67 - 0.037\Delta T$; $p= 0.03$), but no relation in 2007 (Fig. 41c).

Mean size at the biomass maximum

Mean size was calculated in terms of carbon content per cell for phytoplankton and ciliates at the respective biomass maxima (phytoplankton bloom peak, first and second ciliate biomass maximum) of each experiment. Similarly, the carbon content per individual was calculated for adult female *Pseudocalanus* specimens at the end of the experiment in 2006 and for adult females and males at the end of the study in 2007. Results are presented in Figure 42, regression parameters and models are given in Table 7.

Taken together, in all studies, there was a clear tendency of decreasing mean size with increasing temperature treatment for phytoplankton at the bloom peak, whereby the steepest decline was found in the study of 2007 ($p \ll 0.01$ in each case; inverse polynomial regression models) (Fig. 42a). For ciliates, no significant trends could be found except for the second ciliate peak in 2007, where mean size was positively correlated to temperature (Fig. 42c, d). Adult *Pseudocalanus* copepod mean size of both gender decreased with increasing temperature treatment (Fig. 42b).

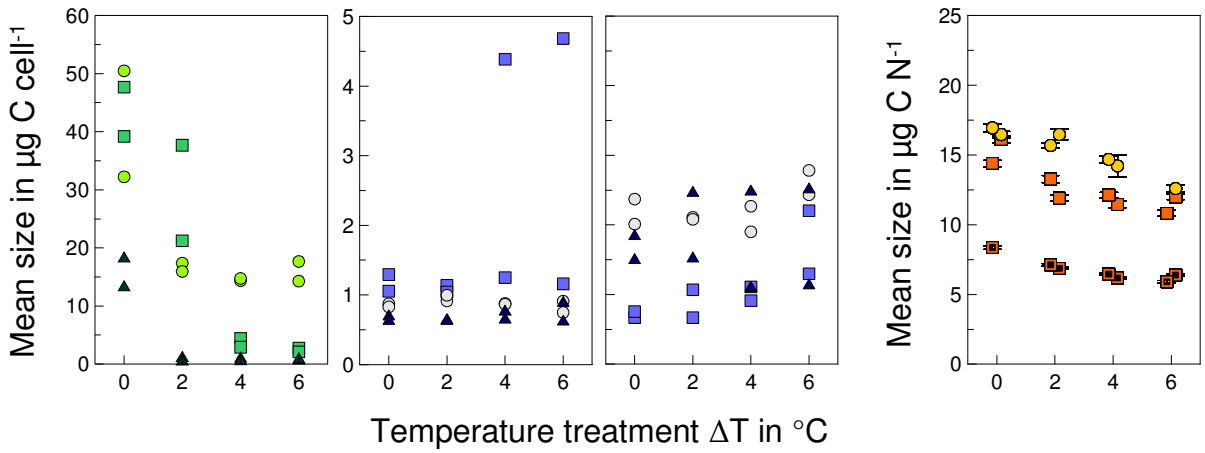

Fig. 42. Mean size. Mean size at the biomass peak plotted against temperature treatment for the different years. Mean size (µg C cell^{-1}) shown for **a)** biomass maximum of phytoplankton, **b)** the first and the **c)** second ciliate biomass maximum. Mean size (µg C N^{-1}) for **d)** adult *Pseudocalanus* copepodids shown at the end of the experimental period. Triangles: 2005; circles: 2006; squares: 2007. For copepodids in 2007: full squares: females; open squares: males. Phytoplankton data from Sommer and Lengfellner (2008), ciliate data from Aberle et. al. (2007) and Aberle, unpublished data.

Table 7. Mean size (m, in µg C cell^{-1}) in phytoplankton (P), ciliates (Cil, first and second max.), and mean size (m , in µg C N^{-1}) in adult male or female *Pseudocalanus* (Ps♂ or Ps♀) in dependance of temperature elevation (ΔT, in °C). Regression analysis according to various models:
linear: $m = y_0 + a\,\Delta T$ or inverse first order: $m = y_0 + a(\Delta T + 1)^{-1}$

Group	Model	y_0	a	p
P 2005	inverse first order	-3.04	18.56	****
P 2006	inverse first order	8.75	31.96	**
P 2007	inverse first order	0.79	45.22	**
Cil 2005 (first max.)	n.s.	n.s.	n.s.	n.s.
Cil 2006 (first max.)	n.s.	n.s.	n.s.	n.s.
Cil 2007 (first max.)	n.s.	n.s.	n.s.	n.s.
Cil 2005 (sec.max.)	n.s.	n.s.	n.s.	n.s.
Cil 2006 (sec.max.)	n.s.	n.s.	n.s.	n.s.
Cil 2007 (sec.max.)	linear	434.42	165.72	0.02
Ps♀ 2006	inverse first order	17.67	-0.67	***
Ps♀ 2007	inverse first order	10.93	4.37	***
Ps♂ 2007	inverse first order	5.9	2.57	***

n.s. = not significant; **** = $p \leq 0.0001$; *** = $p \leq 0.001$; ** = $p \leq 0.01$

Discussion

Diversity, richness and evenness on the primary producer level

Mean phytoplankton diversity displayed different patterns in the subsequent studies: it tended to be negatively related with temperature treatment in the experiment of 2005 (nonlinear trend), positively related to temperature in 2006 (nonlinear trend) and not influenced by temperature increase in 2007. Diversity time series of the different years display some similarities: apart from fluctuations, diversity tended to decline in the first period of each study, and in 2005 and 2006 diversity had reached minimum values most treatments at the timing of the phytoplankton bloom peak (exceptions was ΔT0=°C in 2005). In 2007, the picture diverged such as diversity was almost maximal in all treatments when the phytoplankton bloom peak was reached. Realized diversity is derived from species numbers (i.e. richness) and the relative number of individuals (i.e. evenness). As diversity trends and dynamics in phytoplankton resembled those of phytoplankton evenness, it can be noted that in our case diversity was mainly driven by emerging dominance of some species and less by changes in the detected number of species.

Two patterns could be expected to overlap in our experiments, determining the basic dynamics of diversity: first, in absence of further disturbance, the typical pattern of a natural succession sequence. This pattern is marked by a slow increase in diversity over time and an increase in evenness during much of the successional sequence, which may saturate or decline during late successional stages, when competitively dominant species monopolize the community biomass (Sala & Knowlton 2006). Second, data from the literature suggest that climate warming can reduce species evenness and diversity: Walker et al. (2006) performed a meta-analysis on data from standardized warming experiments in 11 locations across the tundra biome. Results indicated a rapid decline in primary producer species evenness and biodiversity within two growing seasons.

In our studies, phytoplankton species richness (R_S) increased during the build-up phase of the phytoplankton bloom and declined thereafter. Exceptions to this were both warmer treatments in the study of 2007, because R_S did not change considerably until the bloom peak. The general trend therefore conforms to the picture of a natural succession sequence. Either rare species gained importance and increased to numbers above the detection limit, or new species, which were introduced with the small weekly

portion of refill water from Kiel Bight, successfully established in the mesocosms. A mixture of both processes seems possible.

Phytoplankton species evenness displayed a pattern somewhat opposing the predictions of succession dynamics: whereas species richness increased towards the phytoplankton bloom, species evenness reached minimal values at this time point (except the coldest treatment in 2005). Similarly, evenness in the study of 2007 continuously declined within the first weeks (in all treatments) though it could have been expected to increase steadily until the bloom peak. Nonetheless, this could be seen as a typical feature of phytoplankton spring blooms in temperate, shallow water bodies such as Kiel Bight: winter mixing enriches the water column with nutrients, and increasing day length and light intensity promotes algae growth. However, depending on the ratio of dissolved silicate (Si) to nitrogen (N), either diatoms (high Si:N ratio) or flagellate species (low Si:N ratio) are favoured due to their competitive abilities. Within these groups, dominance arises according to the prevailing light conditions (Sommer 1994).

Apart from interspecific competition effects within the phytoplankton community, dominance patterns can further arise from trophic interactions. It has been suggested that while abiotic factors (e.g., physical conditions) tend to predict species richness patterns, biotic factors (e.g. grazing) at population or community levels are more likely to be responsible for controlling species densities and thus realized evenness (Therriault & Kolasa 1999). Grazing by herbivores such as ciliates and copepods can have a strong imprint on phytoplankton community because preferred food items are likely to be stronger depleted and thus dominance may shift towards disdained or grazing resistant phytoplankton species. Supposedly, consumer induced effects on phytoplankton evenness are strong during phases of low primary production (i.e. biomass build up). The low light experiment in 2005 was characterized by an initial phase of declining phytoplankton biomass (see Chapter 4). Losses due to sedimentation could be ruled out in our case due to sufficient mixing. Therefore it can be concluded that strong grazing pressure outbalanced primary production. Selective grazing for certain diatom species was reported for both types of grazers, ciliates and copepods (Aberle *et al.* 2007). In combination with higher activity in the warmer treatments, this might serve as an explanation for the observed temperature dependent shifts in evenness at the beginning of the experiment in 2005: at high temperatures, evenness dropped to lower values than in the colder temperature treatments. A similar explanation might hold true for the both warmer temperature treatments ($\Delta T=4°$ and $\Delta T=6°C$) in the study in 2007: biomass

fluctuated strongly for almost three weeks before the onset of the bloom, indicating strong top-down control. Presumably, this induced or contributed to declining phytoplankton evenness, however does not suffice as explanation for the pattern in both cooler treatments (ΔT=0° and ΔT=2°C), where evenness dropped in the same way.

Temperature appeared to have an accelerating effect on both dynamics, those of phytoplankton species richness and evenness. Further, there was an impact on the magnitude of fluctuations, at least in the studies of 2006 and 2007, where higher numbers of species appeared at colder temperatures during bloom conditions. When richness was averaged across the whole time series, a negative relation emerged between mean richness and temperature treatment in 2005 and 2006. These findings partly confirmed that warming may reduce richness on the primary producer level. In contrast to this, no conclusive picture emerged for temperature effects on absolute values of species evenness: minimum or maximum values as well as mean evenness responded either positively, negatively or not at all to temperature treatment. The results therefore suggest that in the course of phytoplankton spring succession, temperature elevation within the applied range does not promote increased dominance in terms of abundance. These findings, however, only represent numerical relations and thus have to be carefully distinguished from the actual shifts in functional groups (Chapter 4), which are also documented in other studies (e.g. Andersson *et al.* 1994). Further, the outcome could be completely altered by the invasion of non-native species. If climate change highly disturbs the local community, this could open up niche space for species better adapted to warmer conditions and thus potentially restructure the food web.

Diversity, richness and evenness on the grazer level

For copepods, a negative relation between mean diversity and temperature was observed in 2006 and declining trends in diversity time series were retarded in the coldest mesocosms compared to the warmer ones. No clear pattern emerged in 2007; however, diversity kept at a high level in the warmest treatment whereas it declined in all other treatments. The underlying pattern of genus richness was either stable (in 2007) or declined in the course of the experiment (in 2006). As copepods were only distinguished at the genus level, changes in species numbers could be masked and thus actual changes in species richness might have been missed. Considering only the genus level, the findings meets expectations: long-term field studies on the local genera (*Oithona*,

Pseudocalanus & *Paracalanus*, *Centropages*, *Acartia* and *Temora*) reported a continuous presence in Kiel Bight at least between February and May (Behrends 1996). Under climate warming conditions, however it was suggested that richness declines. This was partly confirmed as in the experiment of 2006, genus richness declined earlier at higher temperature treatments, by trend. In contrast to this, no such pattern was observed in the study of 2007. Considering that both experiments were run with the same temperature regimes and similar initial copepod densities, this discrepancy might be attributable to the feeding conditions: in 2006, the phytoplankton bloom occurred within the first two weeks and rapidly decayed in all treatments. The following phase was characterized by low amounts of food (see Chapter 4, Fig. 19b) and competition among grazers was probably high, thus pushing rare genera below the detection limit. In the study of 2007, the phytoplankton bloom occurred in the middle of the experiment whereby phytoplankton biomass before the bloom kept stable in both warmer treatments (ΔT=4° and ΔT=6°C) and increased in the colder treatments (ΔT=0° and ΔT=2°C). Seemingly, this was enough to sustain genus richness in copepods.

Genus evenness generally declined in 2006 as well as in 2007 (increasing levels of evenness at the end of 2006 are due to reappearance of one genus biasing the calculations) and dynamics were accelerated by higher temperature treatment. On the one hand, this conforms to the naturally increasing dominance of the genus *Pseudocalanus* from early spring towards summer season in Kiel Bight (Smetacek 1985; Behrends 1996). On the other hand this fits to observations from freshwater crustaceans: increasing temperatures have been reported to reduce species evenness in pond *Daphnia*, whereby this trend was especially pronounced in phases of high growth rates (McKee *et al.* 2002).

Dynamics in ciliate species richness followed the proposed successional pattern by Sala and Knowlton (2006) only in the experiment of 2005, where richness and evenness increased over time, and maximal species numbers coincided with the timing of the second ciliate biomass maximum (following the phytoplankton bloom peak). In the study of 2006, richness maxima were less prominent and obviously lacked in the experiment of 2007. It could be suspected that lower levels of richness in the latter studies might have simply resulted from different ciliate communities in Kiel Bight and the absence of new ciliate species which could have colonized the mesocosms via the weekly inoculum. A detailed look to the data, however, revealed that true succession patterns of different ciliate species occurred throughout all experiments, but experiments differed

with respect to the number of species present at the same time (Aberle, unpublished data). The establishment of rich ciliate communities in 2005 was likely a synergistic effect of increasingly diverse food supply and release from copepod predation and food competition, because copepod numbers were very low during the second phase of this experiment. In the subsequent studies, ciliates probably interacted stronger with copepods, especially in the study of 2007, where copepod numbers continuously increased. Hence rare species were either not able to surpass detection limits or could not gain foot hold in our set up. With respect to temperature treatment, a positive relation on mean richness was found in 2006, where on average more species were present at the same time. In contrast, a negative relation of temperature treatment and evenness was found. Generally, patterns in ciliate evenness were difficult to interpret. Presumably, they were also a result of species specific food requirements, actual food diversity and concentration and temperature requirements, and as ciliates are capable of fast growth, dynamics can be expected to show strong fluctuations. Overall, temperature increase seemed to accelerate evenness dynamics. This led to highly even ciliate communities during the phytoplankton bloom and at the timing of the second ciliate biomass peak in the warmer treatments in 2007, opposed to the colder treatments. Mean evenness was positively correlated with temperature treatment in 2007 and the overall resulting ciliate mean diversity was hence positively correlated with temperature.

It is difficult to disentangle possible causes for the observed patterns in richness, evenness and diversity. Especially as experiments that analyse the effects of biodiversity, usually manipulate species richness or evenness - which was not the case in our approach. Hence, it is also not possible to establish causal relationships between diversity and other parameters such as productivity or diversity of adjacent trophic levels. Further investigations may shed light on the complex interactions. Up to date, only few studies exist on multitrophic interactions with respect to diversity effects, and results are strongly context dependent and often diverge from investigations on single trophic levels (Duffy *et al.* 2007).

Changes in community size structure

In all three experiments, significant temperature effects on community size structure emerged for phytoplankton at the biomass maximum and for adult *Pseudocalanus* specimen at the end of the experiments: temperature increase led to a decrease in mean

size (biomass : number of individuals). In case of the phytoplankton, this could be attributed to a shift in dominance patterns whereby the proportion of smaller species increased. Within the copepod community, the effect was caused by actual reductions in prosome length at higher temperatures, hence a decline in size-at-stage within the population. Possible explanations arising from the direct experimental context are discussed in Chapter 4 for phytoplankton size shifts and in Chapter 3 for copepods. Briefly, phytoplankton size trends were supposed to be, at least, partially induced by herbivore grazing (positively selection for bigger phytoplankton cells), whereas copepod size reduction was suggested to be linked to temperature dependent food supply and overall reduced net growth efficiency at higher temperatures. Within the ciliate community, no consistent trend emerged across the years and only for the second ciliate peak in 2007, a significant correlation between temperature and mean cell size was found. However, this trend contrasted to those of phytoplankton and copepods, such as mean ciliate size at the biomass peak increased at elevated temperatures. This seems against expectations because if it is assumed that no changes in actual ciliate body size occurred, this finding contradicts the general trend in ectotherms (Atkinson 1994; see section below). Two explanations seem possible: first, it has to be noted that estimates yielded a mean cell size at the biomass maximum, which is only expected to change if pronounced shifts in species distribution take place. It can not be ruled out, that temperature may have had an actual effect on ciliate cell size though not operating on the population level. In this case, temperature effects would have been masked. Indeed it is likely that actual cell size did change because interannual comparisons revealed variations in size (Aberle, unpublished data). It should be noted, that actual changes in cell size may have occurred in phytoplankton, too. Generally, this could be expected from a comprehensive meta-analysis by Atkinson et al. (2003) who found an average cell size reduction of 2.5% volume per °C increase in protists across various taxa, including amoebae, diatoms, ciliates, dinoflagellates and flagellates. A second explanation for the observed counterintuitive mean size tendency in ciliates is the strength of interaction effects: processes like predation and competition might have had a stronger impact than climatic factors or may have interacted with these (Stenseth *et al.* 2002), obscuring direct effects of temperature on community size structure.

Where do our observations fit into the long lasting debate on body size clines of organisms? The observed decline in phytoplankton community size largely conforms to the Bergmann rule (1847), which was originally formulated for mammal species and

states, that warmer areas tend to be inhabited by smaller species of a given genus. As temperature can be roughly correlated with latitude, this rule is regarded as a biogeographic hypothesis. Bergmann argued that larger species have a smaller surface area-mass-relation and thus heat loss in cold habitats is minimized in larger organisms. Of course, it could be questioned whether optimized heat control is the actual target of selection because many other life-history traits are also linked to body size. Further, this rule did also hold for ectothermic animal groups. Nonetheless, the majority of examined and re-examined species so far follows the typical Bergmann cline. Atkinson (1994) extended the hypothesis to individual body size in ectotherms and established the so called temperature-size rule: based on extensive empirical data sets, including animals, plants and protists, Atkinson concluded that in 83,5% of the investigated cases, colder rearing temperatures led to an increase in actual body size. As for most rules, exceptions were documented which displayed opposite variations, and therefore several different hypothesis have been established, such as the converse Bergmann rule (Park 1949; Mousseau 1997) and the countergradient variation (Conover & Present 1990). Authors suggested that the contradictory patterns found in nature are not mutually exclusive because these patterns seem to have different underlying mechanisms - temperature and seasonal length - and hence should be regarded as two ends of a continuum where all intermediate clines are theoretically possible (Blanckenhorn & Demont 2004). Recently, West et al. and others (West *et al.* 1997, 1999; Gillooly *et al.* 2001; Gillooly *et al.* 2002; Brown *et al.* 2004) formulated the metabolic theory of ecology (MTE), which should somewhat simplify theory and settle the questions on body size patterns and related temperature effects. Initially, this theory was put forward to explain the frequent observation of allometric scaling in biological parameters. For example whole organism metabolic rate is often proportional to body mass M, raised by the power of ¾ (Kleiber 1932). The authors claimed that virtually all characteristics of organisms vary predictably with their body size, temperature and chemical composition: mass specific metabolic rates should be determined by uptake rates of resources across cell surfaces and enzymatic reactions which exponentially increase with temperature. Corroborated by the findings of Allen et al. (2002), MTE suggests for example that at given rates of supply, increasing temperatures should reduce the carrying capacity and result in lower numbers of individuals fluxing material and energy at higher rates. Alternatively, the same amount of individuals could be supported if their body size (i.e. body mass) declines. MTE therefore claims to explain observed temperature related clines in body size, global

species richness and various other ecological relevant parameters that are linked to body size. However, this theory can be criticized for many reasons (for detailed discussion see O'Connor *et al.* 2007), and in the case of protists, the underlying assumptions are not even met: MTE assumes that energy and material is transported within organisms through quasi-fractal distributional networks, such as blood vessels, and that optimization of transport costs through these networks necessitates allometric scaling with an exponent of ¾. Besides the lack of evidence that fitness is actually hampered by transport costs, no such distributional networks exist in protists or copepods. Therefore our experimental data are not likely to support MTE. In summary, conclusive mechanistic explanations are lacking so far, and results remain as empirical support for the temperature-size rule and the Bergmann rule.

Conclusion

This chapter focussed on two community characteristics that might be altered under future climate warming: biodiversity and body size. Both features are known to be central features, structuring ecological communities and determining ecosystem functioning and food web dynamics. To our knowledge, this is the first time that both parameters are investigated in the context of spring successional patterns under climate warming conditions. Hence, observations can be regarded as valuable information and basis for further investigations. Concerning biodiversity, our results suggest that temperature does not necessarily alter species richness or evenness in a directional manner but more likely acts on process rates such as higher temperatures have been observed to accelerate the temporal dynamics of richness and evenness within trophic levels. Interactions in multitrophic systems are complex and therefore more detailed studies are needed to link temperature, diversity and ecosystem functions such as production or community stability. With respect to body size and community size structure we were able to partly corroborate empirical findings of other authors, stating that temperature increase should lead to reductions in individual body size or towards a dominance shift within the community towards smaller species. Together with data from the literature, this general tendency towards smaller organisms could be put forward as a third rule dictated by climate change: besides the globally observed biogeographic shifts

in habitat range (tracking the retreating isotherms) and temporal shifts in species phenology, global warming may overall favour smaller species (Daufresne *et al.* submitted).

Chapter 6 - Final conclusions and outlook

A characteristic of ecosystems is the nonlinear and mutually dependent reaction of their components. This arises from specific differences in species physiological tolerance, life-history strategy, probabilities of extinction and colonization and dispersal abilities. For many species, the primary impact of climate change may be mediated through effects on synchrony with food and habitat resources, which can lead to disruption of predator-prey cycles, resulting in trophic uncoupling, regime shifts and overall decline.

Results and implications from the Kiel mesocosm studies

Our experiments demonstrated that temperature changes up to 6°C above the decadal mean of ambient temperatures in Kiel Bight can induce temporal trophic mismatch between phytoplankton and copepod offspring: phytoplankton bloom timing was rather insensitive to temperature elevation (Sommer *et al.* 2007; Sommer & Lengfellner 2008) whereas nauplii peaks strongly advanced (Sommer *et al.* 2007 and Lengfellner, unpublished data). This was probably a result of accelerated development at higher temperatures. However, the underlying dynamic of egg production have been shown to depend on temperature as well as on food conditions (Isla *et al.* 2008). Because timing of the phytoplankton bloom was linked to the mixed water column mean of daily light dose (Sommer & Lengfellner 2008), the ultimate outcome in terms of match or mismatch between food demand in copepod nauplii and food supply by phytoplankton as well as the trend in copepod population development was determined by the interplay of both, light and temperature.

Mismatch between nauplii and phytoplankton may adversely affect the trophic transfer of energy and have far reaching consequences for the food web: early naupliar stages have been shown to be the stages most sensitive to starvation (Tsuda 1994; Lopez 1996; Irigoien *et al.* 2003). Without food they do not moult and quickly die, even faster when temperatures are higher. Nauplii form the most important food item for many first-feeding fish larvae: in the Baltic Sea, naupliar stages of *Pseudocalanus* are a major food

resource for sprat and herring (Hinrichsen *et al.* 2002; Möllmann *et al.* 2003a). The observed mismatch in nauplii and phytoplankton could thus propagate up the food web, lower fish recruitment and might add additional stress to commercially already overexploited fish stocks. In turn, the loss of top predators is critical for ecosystem functioning because they can stabilize ecosystems and may serve as insurance against regime shifts (Sala 2006; Chapron *et al.* 2008; Heithaus *et al.* 2008).

The effect of increased spring temperatures on fast growing grazers like ciliates was completely different from those observed in copepods. Their advantage is the capability to rapidly respond to changing food conditions, and thus to be closely coupled to the dynamics of the focal prey. Traditionally, protozoans have been underrated in their role as grazers but actually they are major herbivores in marine systems, usually exceeding mesozooplankton in terms of grazing rates (Calbet 2008). Our experiments revealed that ciliates were clearly temperature sensitive and higher temperatures strengthened the coupling between ciliates and phytoplankton (Aberle *et al.* 2007; Sommer *et al.* 2007 and Aberle, Sommer, unpublished data): at elevated temperatures, the timing of ciliate biomass peaks advanced faster than the timing of phytoplankton peaks. This has several implications: on the one hand, this leads to a stronger energy flux through the microbial loop and thus reduces the efficiency of energy transfer to higher trophic levels. On the other hand, stronger grazing pressure by ciliates is likely to enforce food competition between ciliates and copepods and to reduce the magnitude of phytoplankton biomass accumulation (i.e. bloom magnitude).

Grazing was apparently enhanced in copepods, too: experiments demonstrated that higher temperatures increased metabolism in the key species *Pseudocalanus*, which led to higher rates of food ingestion (Aberle *et al.* 2007; Isla *et al.* 2008). However, net growth efficiency was reduced at the same time (Isla *et al.* 2008). Similar to the impact of ciliates on phytoplankton bloom magnitude, higher consumption rates in copepods have apparently contributed to the reduction of phytoplankton bloom magnitude observed at higher temperatures (Sommer & Lengfellner 2008).

Additionally, intense grazing of both grazer guilds could be linked to shifts in phytoplankton bloom composition, which were characterized foremost by reductions of microphytoplankton and increased proportions of nanoflagellates at higher temperatures

(Sommer & Lengfellner 2008). In blooms of small sized phytoplankton, sinking velocities are reduced, which means that more material is retained in the water column and less energetically rich food reaches benthic communities. This could have further implications for the global carbon cycle because less fixed carbon dioxide might be deposited on the sea floors (i.e. a weakening of the biological pump). In deep water bodies, rising temperatures will promote stratification which leads to both, reduced nutrient supply and increased light efficiency. Regionally this can translate into either positive or negative primary and export production as productive areas will shift poleward (Richardson & Schoeman 2004). Overall export production however is expected to be reduced because smaller species should be favoured under nutrient deplete, stratified conditions (Bopp *et al.* 2005). This general trend also applies to freshwater systems: Winder et al. (2008) investigated historical datasets of Lake Tahoe, USA, and found that higher temperatures induced shifts in the diatom community, biased towards smaller species with reduced sinking velocities. In concert with predicted reductions in net carbon uptake by terrestrial ecosystems until the end of this century (IPCC 2007), changes in the efficiency of the biological pump are likely to amplify climate change.

Changes in size were also detected in copepods, where adult prosome length in *Pseudocalanus* individuals was reduced at higher temperatures (Daufresne *et. al.* submitted, and Lengfellner, unpublished data). Body size is a central feature in ecology and linked to virtually all aspects of life-history (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; White *et al.* 2007). In case of *Pseudocalanus* (and other copepods), for example, body size positively correlates with encounter rates (Kiørboe & Bagoien 2005) and fecundity (Corkett & McLaren 1969; Halsband & Hirche 2001; Napp *et al.* 2005; Renz *et al.* 2007; 2008). On the other hand, larger individuals are more conspicuous to visually orientated predators. In any case, changes in size are therefore likely to translate into modified populations dynamics. Further, it can be expected that changes in individual body size or community size structure may alter energy fluxes through the food web: if prey items become smaller, the effort per catch presumably increases and a higher amount of energy has to be allocated to foraging. If prey doesn't have the appropriate size, this could even result in mismatch situations (Beaugrand *et al.* 2003; Platt *et al.* 2003).

Temperature has been demonstrated to generally accelerate dynamics and processes. In our study, this also applied in most cases to the dynamics of species richness and evenness and the resulting realized diversity. The underlying mechanisms can not be clarified from the conducted experiments because our multitrophic systems were characterized by complex interactions, and predictions based on single trophic level studies are not easily transferable to such systems (Duffy *et al.* 2007). Nevertheless, the resulting picture shows an interesting aspect of climate change: fluctuations in the community structure may occur faster. Theoretically, this might, for example, increase the pace at which alien species gain foothold or predation resistant species come to dominate, but it could also act in the reverse direction. The consequences probably depend on how fast other food web components react. Taking into account that we noticed clear differences in temperature sensitivity across the trophic levels, it could be suspected that food webs may become less stable under global warming conditions.

Due to its experimental nature, the present study can not cover the full range of possible climate change impacts on plankton spring succession. We were able to establish complex plankton communities and reproduce natural succession patterns that can be observed *in situ* in Kiel Bight (Smetacek 1985; Behrends 1996; Sommer 1996). Nonetheless, there were logistic constraints on temporal and spatial scales and hence, many aspects of the natural environment could not be included and important relations between interaction parameters might have been missed. This opens room for new questions and further investigations.

Open questions

Our study gave insight into possible consequences of climate warming for plankton spring communities in temperate regions, and several aspects have certainly a more general and global character. On basis of our experiments and with respect to the current literature, many interesting questions arise concerning climate change, and some of them are listed here:

Can species adapt fast enough to keep pace with current and future temperature increase?

Visser (2008) suggests that microevolution will play the most important role in determining whether species can adapt to changing conditions. Microevolution has already been observed in some terrestrial species (Bradshaw & Holzapfel 2006). More detailed knowledge on the temporal trends in life-history and the underlying mechanisms of phenotypic plasticity will be needed to develop models that could help to predict species capabilities to adapt.

Will there be a replacement of species? And if yes, will they fulfil similar ecosystem functions?

A well known phenomenon of climate change is geographical shift in habitat range (e.g. Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2006). Beaugrand et al. (2003) reported on the dramatic effect of species replacement in the North Sea, where the copepod *Calanus finnmarchicus* (cold water preferring species) has been replaced by *Calanus helgolandicus* (warm water preferring species). Though taxonomically closely related, these two species have completely different phenologies: *C. finnmarchicus* numbers peak in spring whereas *C. helgolandicus* peaks in autumn. Planktivorous fish that spawn in spring and rely in this copepod food resource are now faced with food shortage under the new copepod community.

Will warmer winters promote or decrease overwintering stocks of zooplankton? What will be the consequences for the subsequent spring bloom?

In the light of our experiments, it could be suspected that increasing temperatures increase the energetic costs of overwintering, and likewise increase mortality rates, especially as during winter, food levels are usually low. Further investigations will help to clarify this issue.

What will be the impact on resting eggs of copepods?

Several copepod species (such as *Acartia*, *Centropages* and *Temora* in the Baltic Sea) can produce resting eggs from which a new generation hatches in the following year. It should be investigated how the timing and success of emergence responds to temperature increase. Models for the cladoceran herbivore *Daphnia* have shown that

spring populations hatching from resting eggs are at risk to temporally mismatch their algal prey at climate change conditions (Domis *et al.* 2007).

Are future temperatures beyond tolerance?

Trends in surface temperatures in the North Sea and the Baltic Seas now exceed those at any time since instrumented measurements began in 1861 and 1880, respectively. Baltic Sea summer temperatures since 1985 have increased at nearly triple the global warming rate, which is expected to occur during the 21st century, and they have risen two to five times faster than those in other seasons (Mackenzie & Schiedek 2007). Taking this into account, warming effects of other seasons than spring should be investigated to gain a more holistic picture of the interactions between seasonal events under global warming conditions. Presumably, some species are already at the limit of their thermal tolerance and hence may be especially vulnerable to increases in annual maximum temperatures.

Will future food loose quality?

On the one hand, temperature has been shown to alter metabolic rates. This could translate into changes of individual elemental composition due to enhanced respiration rates. On the other hand, temperature alters species distribution and geographical habitat range. In combination, this could result in less valuable prey of low energy content and finally have detrimental effects on populations. Traditionally, this "junk food" hypothesis is linked to marine top-predators such as sea lions or piscivorous seabirds (reviewed by Österblom *et al.* 2008). Nonetheless it could also apply to lower trophic levels.

What will be the effect of combined stressors?

Current global change is not constituted of temperature change alone. Our planet is facing a concert of anthropogenic impacts, among which habitat destruction, ocean acidification (caused by increased carbon dioxide emissions), pollution and introduction of alien species can be seen as major stressors for marine environments. The combined effect of these influences may have more severe or completely different consequences than one variable alone.

Climate change has advanced to one of the top-priority issues in ecological research and recent years have brought about important knowledge on historic and contemporary responses to increasing temperatures. However, we are still at the beginning to understand the far reaching consequences of changes to come. Research in the marine sector is vital because oceans are major drivers of global climate and carbon cycling processes. With respect to this, plankton organisms can be seen as beacons for climate change (Richardson 2008): they are globally distributed and most of them are not commercially exploited, so that trends in their dynamics and compositions reflect true environmental changes (e.g. temperature, nutrient loads) and are not confounded by anthropogenic exploitation. They are sensitive indicators of temperature change as they respond quickly in their physiological processes to altered temperatures, due to their poikilothermic nature. As many plankton species are short lived (less than one year), their population dynamics can be expected to be closely coupled to climate (Hays *et al.* 2005). Further, impacts on the community are likely to be non-linear, so subtle changes in environmental conditions will be amplified. Given these natural, sensitive indicators we should not miss the chance but make use of this valuable "tool", carefully track their reactions and watch out for alerting signals.

Appendix - Carbon conversion factors for copepods

Adult Copepods	C in µg N^{-1}	Reference
Oithona similis	0,58	Kiorbøe and Sabatini (1994)
Pseudocalanus elongatus	8,50	Paffenhöfer and Harris(1976)
Centropages hamatus	7,60	Breteler at al. (1982)
Centropages typicus	12,40	Kiorboe and Johansen (1986)
Centropages mean value	10,00	
Temora longicornis	16,00	Breteler at al. (1982)
Acartia sp.	4,00	Landry (1983)
Microsetella sp.	like Oithona	Pedersen et al. (2005)
Pseudocalanus nauplii	0,26	mean, taken from Davis (1984)
Centropages typicus nauplii	0,06	length acc. Liang et al. 1996 for C. *abdominalis*
Oithona sp. nauplii	0,02	length from Murphy (1923) for O. *nana*
Rest nauplii (as mixture of C. and O.)	0,04	length-carbon relation from Sabatini and Kiorboe (1994)
mean all nauplii	**0,11**	
Pseudocalanus sp. eggs	0,06	Davis (1984)
Oithona sp. eggs	0,01	conversion acc. to Huntley and Lopez (1992) P. egg diameter 125µm (Royal Netherlands Institute of Sea Research http://www.nioz.nl/) O. egg diameter 57µm; North Sea (Nielsen *et al.* 2002)

Carbon estimated as mean for copepodid stages C1-3 and C4-6; respective percentage of adult carbon content calculated according to ratio found in Davis and Alatalo (1992)

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Publications arising from this work

Daufresne M, **Lengfellner K**, Sommer U (submitted) Global warming benefits the small: patterns from a meta-analysis in aquatic biota.

Gaedke U, Ruhenstroth-Bauer M, Tirok K, Aberle N, Breithaupt P, **Lengfellner K**, Wohlers J, Sommer U (submitted) Spring phytoplankton dynamics depend on temperature, cloudiness, grazing and overwintering biomasses – a process oriented modelling study based on mesocosm experiments.

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Lengfellner K, Aberle N, Sommer U: Temperature effects on plankton spring succession under different light conditions. 3rd AQUASHIFT-Workshop, Kiel, November 2006

Lengfellner K, Aberle N, Hansen T, Sandow M, Sommer U: The impact of climate change on plankton spring succession: a mesocosm study. ASLO 2006 Summer Meeting, Victoria, British Columbia, Canada, 4-9 June 2006

Lengfellner K, Aberle N, Hansen T, Sandow M, Sommer U: Plankton spring succession in response to winter warming. 2nd AQUASHIFT-Workshop, Kiel, September 2005

Posters

Sommer U, Aberle N, **Lengfellner K**, Hansen T, Sandow M, Hoppe H-G, Koppe R, Bleck S, Wohlers J, Zöllner E, Riebesell U: AQUASHIFT-Kiel: plankton spring succession under a changing climate. IfM-GEOMAR Evaluation, Kiel, September 2005

Lengfellner K, Aberle N, Hansen T, Sommer U: AQUASHIFT - Auswirkungen des Klimawandels auf aquatische Ökosystems. Kieler Woche, Kiel, Juni 2005

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Erklärung

Hiermit erkläre ich, dass diese Arbeit - abgesehen von der Beratung durch meine akademischen Lehrer - nach Inhalt und Form meine eigene ist und keine weiteren als die angegebenen Hilfsmittel und Quellen verwendet wurden. Ich habe bisher keinen anderen Promotionsversuch unternommen, und diese Arbeit hat weder im Ganzen noch zum Teil an anderer Stelle im Rahmen eines Prüfungsverfahrens vorgelegen. Bei der Erstellung dieser Abhandlung habe ich mich an die Regeln guter wissenschaftlicher Praxis gehalten.

Kiel, den 15. Oktober 2008

Kathrin Lengfellner