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ORIGINAL PAPER

# Warming induces shifts in microzooplankton phenology and reduces time-lags between phytoplankton and protozoan production

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**Abstract** Indoor mesocosm experiments were conducted to test for potential climate change effects on the spring succession of Baltic Sea plankton. Two different temperature (Δ0 °C and Δ6 °C) and three light scenarios (62, 57 and 49 % of the natural surface light intensity on sunny days), mimicking increasing cloudiness as predicted for warmer winters in the Baltic Sea region, were simulated. By combining experimental and modeling approaches, we were able to test for a potential dietary mismatch between phytoplankton and zooplankton. Two general predator–prey models, one representing the community as a tri-trophic food chain and one as a 5-guild food web were applied to test for the consequences of different temperature sensitivities of heterotrophic components of the plankton. During the experiments, we observed reduced time-lags between the peaks of phytoplankton and protozoan biomass in response to warming. Microzooplankton peak biomass was reached by 2.5 day $°C^{-1}$ earlier and occurred almost synchronously with biomass peaks of phytoplankton in the warm mesocosms (Δ6 °C). The peak magnitudes of microzooplankton biomass remained unaffected by temperature, and growth rates of microzooplankton were higher at Δ6 °C ($\mu_{\Delta 0\ °C} = 0.12$ $day^{-1}$ and $\mu_{\Delta 6\ °C} = 0.25$ $day^{-1}$). Furthermore, warming induced a shift in microzooplankton phenology leading to a faster species turnover and a shorter window of microzooplankton occurrence. Moderate differences in the light levels had no significant effect on the time-lags between autotrophic and heterotrophic biomass and on the timing, biomass maxima and growth rate of microzooplankton biomass. Both models predicted reduced time-lags between the biomass peaks of phytoplankton and its predators (both microzooplankton and copepods) with warming. The reduction of time-lags increased with increasing $Q_{10}$ values of copepods and protozoans in the tritrophic food chain. Indirect trophic effects modified this pattern in the 5-guild food web. Our study shows that instead of a mismatch, warming might lead to a stronger match between protist grazers and their prey altering in turn the transfer of matter and energy toward higher trophic levels.

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## Introduction

The potential restructuring of communities in response to climate warming is one of the current topics in ecology (McGowan et al. 2003; Smol et al. 2005; Walther 2010). It is predicted that warming will affect the different trophic levels unequally, which results in a temporal mismatch between predators and their prey (Durant et al. 2007; Thackeray et al. 2010). However, temporal match of zooplankton peaks with the spring phytoplankton bloom is required to provide an efficient energy transfer up the food web at the start of the growing season. Thus, the mismatch of phytoplankton with its zooplankton grazers under

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warming, that has been found in the freshwater as well as in the marine pelagic realm (Edwards and Richardson 2004; Winder and Schindler 2004), is a reason for concern. Previous studies were largely restricted to mesozooplankton as consumers of phytoplankton. However, microzooplankton has an important role as trophic intermediary between primary producers and mesozooplankton (Johansson et al. 2004; Sommer et al. 2005) and as major primary consumer of autotrophic production in the plankton (Landry and Calbet 2004; Calbet 2008). It is assumed that warming will strengthen top-down control of phytoplankton by microzooplankton communities (Rose and Caron 2007) as the growth of heterotrophic protists is much more temperature dependent than that of autotrophs. This assumption directly links to the 'metabolic theory of ecology' (MTE; Brown et al. 2004) as described by Lopez-Urrutia (2008). The present study focuses on the effects of temperature on the phenology of microzooplankton communities (ciliates and heterotrophic dinoflagellates <200 µm).

Besides temperature directly affecting microzooplankton, altered light levels (due to, e.g., increased cloudiness and atmospheric water vapor content) also influence microzooplankton growth indirectly by altering the availability of phytoplankton prey. Therefore, we hypothesized that the time-lag between autotrophic and heterotrophic processes in the plankton will be altered by light availability as well.

We used a cardinal point approach to analyse time-lags between phytoplankton and microzooplankton during the spring succession of Baltic Sea plankton in relation to changing temperature and light conditions. Cardinal points are considered as sensitive indicators of climate change-induced shifts in phenology such as shifts in the timing of phytoplankton spring blooms (Straile and Adrian 2000; Wiltshire and Manly 2004; Thackeray et al. 2008). However, as stated by Gaedke et al. (2010), the analysis of cardinal points does not provide a mechanistic understanding of climate change-related impacts on plankton succession. Thus, in addition to the analysis of time series of the community structure during the experiments, we conducted model simulations using a modified Rosenzweig and MacArthur (1963) predator–prey model incorporating temperature-dependent growth, grazing and mortality rates of autotrophic and heterotrophic components. We compared the phenology of two different simulated food webs under warming to gain insight into the role of trophic interactions and food web structure influencing the effects of temperature. Additionally, we tested how different temperature sensitivities of predators affect the simulated phenology by varying $Q_{10}$ values of copepods and protozoans independently.

Based on the observations of Rose and Caron (2007), we hypothesized that warming will lead to:

1. Acceleration of microzooplankton growth and species turnover.
2. Reduced time-lags between autotrophs and heterotrophs in plankton communities (taking additionally into account potential effects from changing light availability).
3. Stronger top-down bloom control by microzooplankton and enhanced dietary competition with mesozooplankton.

## Methods

### Experimental set-up

The experimental set-up consisted of twelve mesocosms made of food safe polyethylene in four temperature-controlled culture rooms. Each mesocosm had a volume of 1,400 L (1 m depth) and was filled with water from the Kiel Bight: sea water was pumped from the institute's pier (from 6 m depth) into an intercepting tank and was distributed further to the mesocosms by hosepipes. Hence, we were able to fill all mesocosms simultaneously and guarantee almost identical starting conditions. Damage by the pumping procedure was tolerable for phytoplankton and microzooplankton, but mesozooplankton organisms did not survive this transfer. Thus, we added mesozooplankton from net catches at natural densities (ca. 10–20 ind $l^{-1}$, dominated by the copepod *Oithona* sp. at the beginning), gathering the organisms by vertical hauls with a 200 µm WP2 net (Hydrobios, Kiel, Germany) at several stations in Kiel Bight. After filling, water columns were stirred moderately with agitators. Stirring speed was slow enough to ensure that mesozooplankton was not harmed.

The temperature programme was based on the decadal mean (1993–2002) of water temperatures in Kiel Bight, Baltic Sea. Two temperature treatments, called Δ0 °C and Δ6 °C for brevity (0 and 6 °C elevation above the decadal mean, respectively), were established. Δ6 °C mimicked the most drastic temperature scenario predicted by the IPCC (2007) for the end of the century. The natural seasonal temperature increase during spring was simulated starting with mean temperatures of 2.4 (Δ0 °C) and 7.8 °C (Δ6 °C). The light set-up simulating daily triangular light curves and seasonal changes in light climate was calculated using the astronomic model published by Brock (1981). Natural surface irradiance was reduced to 49, 57 and 62 % of sea surface irradiance on sunny days ($I_0$) to simulate three different light scenarios. The highest $I_0$ (62 %) was based on a mixed water column mean light intensity during cloudless days at 10 m mixing depth (depth of the halocline in situ) and a vertical attenuation coefficient ($k$) of 0.18 $m^{-1}$. 49 and 57 % simulated light reduction by cloud

cover or any combination of less clouds and higher attenuation coefficient. Light was supplied by computer-controlled light units (Profilux II, GHL Groß Hard- and Software Logistics, Kaiserslautern, Germany) above each mesocosm, which contained fluorescent tubes with different light spectra (T5 'Solar Tropic' and T5 'Solar Nature', JBL, Neuhofen, Germany) in order to mimic solar irradiance. The starting date for the light and temperature programs was set to 15th February (Day of the year 46; referred to as DOY thereafter) and each temperature and light level was replicated twice. The actual experimental period lasted from February 6 until March 26, 2008.

### Microzooplankton sampling and identification

Microzooplankton samples were taken once a week by sampling seawater from the mixed water column (30 cm water depth) with a silicone tube. 250 ml of the sampled seawater was transferred to brown glass bottles and fixed with acidic Lugol's iodine (2 % final concentration). 100 ml of each sample was transferred to sedimentation chambers and microzooplankton was counted by the inverted microscope method (Utermöhl 1958) at a 200× magnification with a Zeiss Axiovert 135. The whole area of the bottom plate was counted for each sample in order to guarantee comparability of the counting method both at periods of high and low microzooplankton abundance. Microzooplankton was identified to the lowest possible taxonomic level (species or genus level) according to Kahl (1932), Foissner et al. (1991, 1992, 1994, 1995), Strüder-Kypke et al. (2002), Tomas (1996), and Scott (2005). For biovolume calculations, geometric proxies were used according to Hillebrand et al. (1999) and carbon biomass was calculated using the conversion factors given in Putt and Stoecker (1989).

### Microzooplankton growth rates

The growth rate $\mu$ (day$^{-1}$) of microzooplankton was calculated as the slope of a regression of ln biomass on time. DOY 46 was set as start of the growth rate calculation and DOY 60 as end for the linear portions in the warm mesocosms, while DOY 67, 74 or 81 were the end points in the cold mesocosms.

### Phytoplankton and copepod sampling and classification

Samples for phytoplankton counts were taken three times per week, fixed with Lugol's iodine and counted using the inverted microscope method (Utermöhl 1958). To account for phytoplankton cells <5 µm, samples for flow cytometry were taken at the same intervals and analyzed on a Becton Dickson, FACScalibur system. For analysis, mesocosm water was pre-filtered by a 64-µm net in order to exclude big particles that might clog the cytometer. Phytoplankton was measured live from the unfixed water samples.

Biovolume calculations were conducted using approximations according to Hillebrand et al. (1999) and converted into carbon content as described by Menden-Deuer and Lessard (2000). Phytoplankton was subdivided into small-sized (particle size < 1,500 µm$^3$) and medium-sized algae (1,500–45,000 µm$^3$). The small-sized algae comprised autotrophic pico- and single-celled nanophytoplankton, that is, diatoms, autotroph athecate and thecate dinoflagellates, Haptophyceae, Chrysophyceae and Cryptophyceae. The medium-sized algae were dominated by diatoms contained micro- and chain-forming nanophytoplankton, but also silicoflagellates, Chryptophyceae, Chlorophyceae and autotrophic athecate and thecate dinoflagellates. Large-sized algae (>45,000 µm$^3$) were not included as these species, for example, *Coscinodiscus* sp., *Ceratium* spp. are not preferred prey items of the dominant microzooplankton species present in our mesocosms.

Copepod samples were taken once a week by vertical net tows with a plankton net (Apstei-type, Ø12 cm, 35 cm length, 64 µm mesh size, Hydro-Bios, Kiel, Germany). Copepod samples were counted under a dissecting microscope and converted into biomass using conversion factors by Paffenhöfer and Harris (1976), Landry (1983) and Castellani et al. (2005). Naupliar carbon content was calculated with a mean conversion factor from literature values (Davis 1984; Castellani et al. 2005), assuming an equal mixture of the dominating genera. For the total copepod carbon biomass, values of nauplii and copepodites were pooled.

### Cardinal point definitions

In order to characterize the timing of the microzooplankton bloom cardinal points, a sigmoidal fit with the equation

$$f(t) = a/(1 + \exp(-(t - t0)/b)$$

where $t$ = time was used (Fig. 1). The sum of microzooplankton biomass during the experimental period was set as 100 % and the dates (or days) when 25, 50 and 75 % of the total cumulative biomass were reached were defined as: (1) $D_{25}$: time when the cumulative biomass surpassed the 25 % threshold, (2) $D_{50}$: time when the cumulative biomass surpassed the 50 % threshold and (3) $D_{75}$: time when the cumulative biomass surpassed the 75 % threshold. The timing of the microzooplankton biomass maximum ($D_{max}$) was defined as the day when microzooplankton biomass reached its peak.

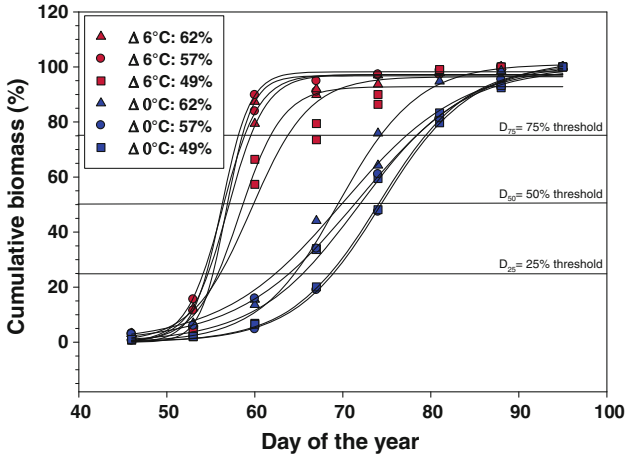


**Fig. 1** Sigmoidal fit showing the cumulative microzooplankton biomass (%) over the whole duration of the experiment. *Solid lines* indicate the thresholds of cumulative biomass defined as $D_{25}$, $D_{50}$, and $D_{75}$

## Statistical analysis

In order to test for significant effects of the factors light and temperature on the timing of microzooplankton bloom maxima, a two-way ANOVA using 'Timing of microzooplankton maximum ($D_{max}$)' as dependent variable and 'Temperature' and 'Light' as independent variables was performed. To test for significant effects of the different temperatures (mean actual temperatures in the Δ0 °C and Δ6 °C treatments over the whole duration of the experiment) on the response variables (1) timing of microzooplankton maximum ($D_{max}$) and (2) timing of cumulative biomass ($D_{25}$, $D_{50}$ and $D_{75}$), statistical tests using regression analysis were conducted. 'ΔT °C' was used as independent factor and 'Day' as dependent factor. We used STATISTICA 6.0 for analyses.

## Predator–prey model

We constructed two modified Rosenzweig and MacArthur (1963) predator–prey models with 3 and 5 species, incorporating temperature-dependent growth, grazing and mortality rates. In the tritrophic model, the biomass of phytoplankton ($A$), protozoans ($P$), and copepods ($C$) were simulated, where copepods grazed both protozoans and phytoplankton, while the protozoans consumed phytoplankton. In the model with 5 species, we distinguished between small- ($A_1$) and medium-sized ($A_2$) algae, between ciliates ($P_1$) and heterotrophic dinoflagellates ($P_2$) and copepods (C). Here, only ciliates grazed small-sized algae, while dinoflagellates and copepods consumed medium-sized algae. Copepods grazed both protozoan groups in this model. The biomass dynamics of the phytoplankton ($A_i$), protozoans ($P_j$), and copepods ($C$) is described by the following equations:

$$\frac{dA_i}{dt} = \text{prod} \cdot A_i - \sum_j g_{ij} \cdot P_j - g_{iC} \cdot C,$$

$$\frac{dP_j}{dt} = \left( e \cdot \sum_i g_{ij} - d \cdot eT_{\text{HP}} \right) \cdot P_j - g_{jC} \cdot C,$$

$$\frac{dC}{dt} = \left( e \cdot \left( \sum_i g_{iC} + \sum_j g_{jC} \right) - d \cdot eT_{\text{HC}} \right) \cdot C.$$

where the parameter $e$ is the growth efficiency and $d$ is the mortality rate of the predators at the reference temperature (2 °C) (for parameter values used see Table 1).

We assumed temperature-sensitive logistic growth for phytoplankton. Thus, the production rate ($day^{-1}$) of phytoplankton was calculated as:

$$\text{prod} = r' \cdot eT_A \cdot \left( 1 - \frac{\sum_i A_i}{K} \right),$$

where $r$' is the potential growth rate of phytoplankton at 2 °C (reference temperature). Temperature regulation factors for autotrophic ($eT_A$) and heterotrophic ($eT_{\text{HP}}$, $eT_{\text{HC}}$) processes were calculated as $eT = Q_{10}^{\frac{T(t)-2}{10}}$. For calculating $eT_A$, we used $Q_{10} = 1.5$. To test the effect of different temperature dependencies of grazers, we conducted simulations with $Q_{10} = 2$, 4, and 6 for copepods and protozoans ($eT_{HC}$, $eT_{HP}$, resp.). The $Q_{10}$ chosen were in the range of those found in studies on copepods (Leandro et al. 2006; Isla et al. 2008) and protozoans (Nielsen and Kiorboe 1994; Rose and Caron 2007), although it is controversially discussed in the literature whether protozoan growth increases rather linearily than exponentially with increasing temperature (Montagnes et al. 2003). We assumed the same $Q_{10}$ values for dinoflagellates and ciliates in the 5-guild model.

**Table 1** Abbreviations, values, and description of parameters used in the simulation models

| Parameter | Value (unit) | Description |
|---|---|---|
| $r$' | 1.6 ($day^{-1}$) | Maximum growth rate of phytoplankton at $T = 2$ °C |
| $e$ | 0.35 ($day^{-1}$) | Growth efficiency of predators |
| $d$ | 0.02 ($day^{-1}$) | Mortality rate of predators at $T = 2$ °C |
| $K$ | 1,000 (μgC/l) | Carrying capacity |
| $g'_C$ | 0.15 ($day^{-1}$) | Potential grazing rate of copepods |
| $g'_P$ | 0.3 ($day^{-1}$) | Potential grazing rate of protozoans |
| $M$ | 50 (μgC/l) | Half-saturation constant of grazers |

$T(t)$ indicates temperature values taken from the time series of the experiment. Grazing exponentially increased with temperature according to the classical $Q_{10}$ relationship.

Grazing rates of protozoa on phytoplankton ($g_{ij}$) were given by:

$$g_{ij} = eT_{\mathrm{HP}} \cdot g'_P \frac{A_i}{\sum_i A_i + M}.$$

$g'_P$ was the potential maximum grazing rate at 2 °C, estimated from measurements at 6 °C (Loeder et al. 2011), using a $Q_{10} = 4$.

Grazing of copepods on phytoplankton ($g_{iC}$) and protozoans ($g_{jC}$) was given by:

$$g_{iC} = eT_{\mathrm{HC}} \cdot g'_C \cdot \frac{A_i}{\sum_i A_i + \sum_j P_j + M},$$

$$g_{jC} = eT_{\mathrm{HC}} \cdot g'_C \cdot \frac{P_j}{\sum_i A_i + \sum_j P_j + M}.$$

$g'_C$ is the potential maximum grazing rate of copepods at the reference temperature (2 °C). We studied the simulated time series of the groups during the first 50 time steps (days) of model simulations. This is a transient period, where the biomass maxima were relatively sensitive to the initial biomasses. Thus, to focus on the effects of temperature and food web structure on the phenology of the simulated communities, we set the initial values for the biomasses 20 µgC/l for all groups instead of using the initial values from the experiments.

## Results

### Microzooplankton biomass, cardinal points, and growth rates

At the beginning of the experiment, microzooplankton biomass increased in all mesocosms until it reached the biomass maximum ($D_{max}$) and declined to initial biomass levels thereafter (Table 2; Fig. 2a–f). $D_{max}$ was reached more rapidly in the warm mesocosms compared with the cold ones (Table 2) showing a strong acceleration of 2.5 day °C$^{-1}$ by temperature ($y = -2.5x + 80$, $r^2 = 0.66$, $p < 0.05$). At Δ6 °C, the timing of the phytoplankton and the microzooplankton biomass maximum ($D_{max}$) occurred almost simultaneously (Fig. 2a–c), while $D_{max}$ was significantly delayed at lower temperatures (Δ0 °C; Fig. 2d–f; $p = 0.027$, $F = 24.0$, Table 3). The factor light did not significantly affect $D_{max}$ and did not enter the model ($p = 0.6297$, $F = 0.50$; Table 3). The timing of cumulative biomass ($D_{25}$, $D_{50}$ and $D_{75}$) showed a significant temperature dependency (Table 2). $D_{25}$ was significantly correlated with temperature showing an acceleration of 1.8 day °C$^{-1}$ ($y = -1.8x + 70$, $r^2 = 0.82$, $p < 0.05$). Even stronger accelerations were observed for $D_{50}$ (2.7 day °C$^{-1}$; $y = -2.7x + 80$, $r^2 = 0.92$, $p < 0.05$) and $D_{75}$ (3.3 day °C$^{-1}$; $y = -3.3x + 87$, $r^2 = 0.89$, $p < 0.05$).

**Table 2** Cardinal points of microzooplankton growth (in days of the year = DOY) where ΔT gives the temperature elevation and $I_0$ the percentage of sea surface irradiance

| ΔT | $I_0$ (%) | $D_{25}$ | $D_{50}$ | $D_{75}$ | $D_{max}$ |
|---|---|---|---|---|---|
| 0 °C | 49 | 65 | 72 | 79 | 67 |
| | | 69 | 74 | 79 | 81 |
| | 57 | 69 | 74 | 80 | 81 |
| | | 64 | 71 | 78 | 74 |
| | 62 | 62 | 70 | 77 | 67 |
| | | 64 | 70 | 74 | 74 |
| 6 °C | 49 | 56 | 59 | 62 | 60 |
| | | 56 | 60 | 64 | 60 |
| | 57 | 54 | 56 | 59 | 60 |
| | | 54 | 56 | 58 | 60 |
| | 62 | 55 | 57 | 59 | 60 |
| | | 55 | 57 | 59 | 60 |

The timing of cumulative biomass $D_{25}$, $D_{50}$, and $D_{75}$ as well as the timing of the microzooplankton biomass maximum ($D_{max}$) is given

Peak magnitudes of $D_{max}$ did not significantly differ between the two different temperatures and reached values between 7.3 (Δ0 °C, 62 % $I_0$) and 42.9 µg C l$^{-1}$ (Δ6 °C; 49 % $I_0$; Fig. 2a–f).

The growth rates of microzooplankton $\mu$ (day$^{-1}$) were significantly higher in the warm mesocosms (mean 0.25 day$^{-1}$ ± 0.03) than in the cold ones (0.12 day$^{-1}$ ± 0.03; Fig. 3).

### Phytoplankton and copepod biomass

Small phytoplankton had a higher initial biomass (~55 µg C l$^{-1}$) than medium-sized phytoplankton (~1 µg C l$^{-1}$), and a rapid increase in phytoplankton biomass was observed in all treatments (Fig. 4). Small phytoplankton reached their biomass peaks earlier in the warm mesocosms (Fig. 4a–c). Biomass maxima of small algae were similar at both temperatures but increased with increasing light intensities. In contrast, the mean biomass maxima of medium-sized phytoplankton was two times lower in warm (maxima of ~500 µg C l$^{-1}$, Fig. 4a–c) than in cold (maxima of ~1,100 µg C l$^{-1}$) mesocosms (Fig. 4d–f) and increased with increasing light intensities.

Copepod biomass in all twelve mesocosms started at 5 µg C l$^{-1}$ ‘(SD; Fig. 4). At the beginning of the experiment, an increase in copepod biomass was observed in all treatments except for the treatment Δ0 °C, 62 % $I_0$ (Fig. 4d) where biomass remained almost constant throughout the

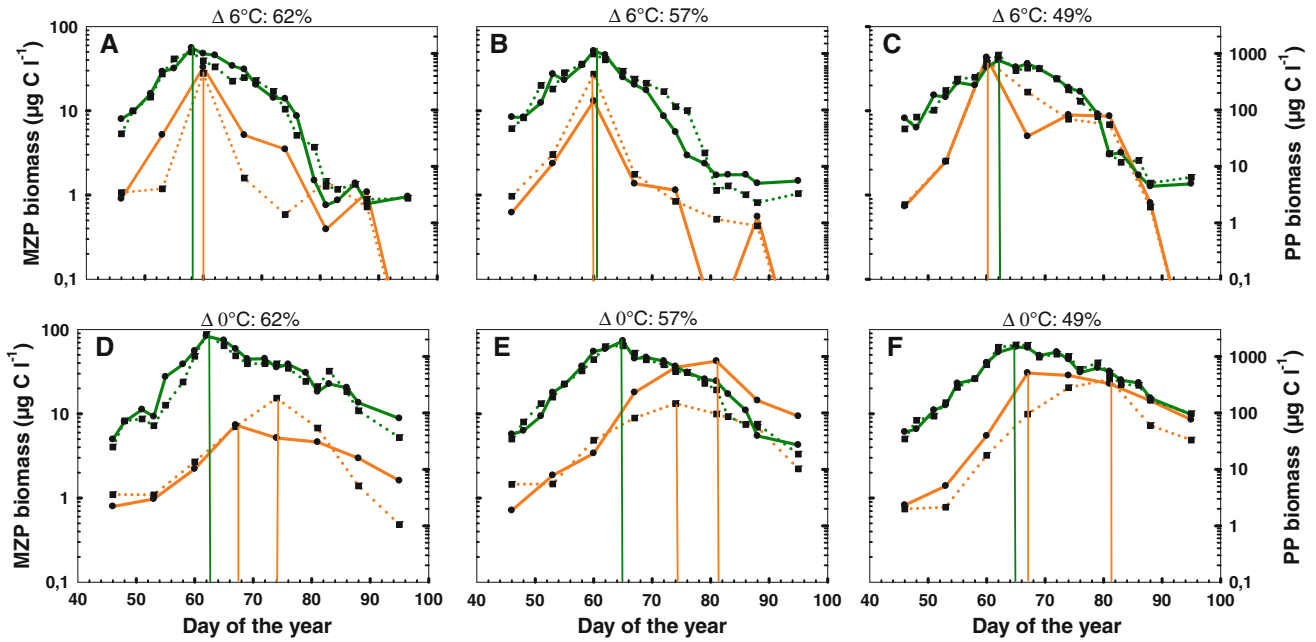


**Fig. 2** Microzooplankton (MZP) biomass (µg C $l^{-1}$) (*orange lines*; duplicate 1: *solid line*, duplicate 2: *dotted line*) and phytoplankton (PP) biomass (µg C $l^{-1}$) (*green lines*; duplicate 1: *solid line*, duplicate 2: *dotted line*) for each treatment. Factors temperature (°C) and light (%) of the different treatments: **a** Δ6 °C 62 %, **b** Δ6 °C 57 %, **c** Δ6 °C 49 %, **d** Δ0 °C 62 %, **e** Δ0 °C 57 %, **f** Δ0 °C 49 %. *Vertical lines* illustrate the reduced time-lags between phytoplankton biomass maxima (*green*) and microzooplankton biomass maxima (*orange*)

**Table 3** Impact of the factors light and temperature on the timing of microzooplankton biomass maxima ($D_{max}$)

| | *df* | MS | *F* ratio | *P* level |
|---|---|---|---|---|
| Temperature | 1 | 588.00 | 24.00 | 0.0027 |
| Light | 2 | 12.25 | 0.500 | 0.6297 |
| Temperature × light | 2 | 12.25 | 0.500 | 0.6297 |
| Error | 6 | 24.50 | | |

Results of a two-factorial ANOVA with 'temperature' (Δ0, Δ6 °C) and 'light' (49, 57, 62) as independent factors and 'timing of microzooplankton biomass maxima' ($D_{max}$) as dependent variable

experiment. The biomass increase was most pronounced in the warm mesocosms (Fig. 4a–c) where peak values of 29.1 (SD; Δ6 °C, 57 % $I_0$) and 112.8 µg C $l^{-1}$ (Δ6 °C, 49 % $I_0$) were reached. In contrast, peaks of copepod biomass remained lower in the cold mesocosms showing values of 18.1 (SD; Δ0 °C, 49 % $I_0$) and 20.2 µg C $l^{-1}$ (Δ0 °C, 57 % $I_0$).

## Microzooplankton community structure

### *Taxonomic composition*

While the initial microzooplankton community was dominated by dinoflagellates, ciliates increased during the phytoplankton spring bloom at high temperatures (Δ6 °C) followed by a rapid decline instantaneously after the bloom (Fig. 4a–c). The dominance of ciliates in the microzooplankton community lasted for approximately 1 week while dinoflagellates dominated during the post-bloom period. In the lower temperature treatments (Δ0 °C), similar succession patterns were observed as at elevated temperatures. However, succession happened much slower and ciliates dominated the community for almost 3 weeks and microzooplankton biomass declined only toward the end of the experiment (Fig. 4d–f). After the bloom, the microzooplankton community was dominated by dinoflagellates. The factor light played only a minor role in affecting microzooplankton succession patterns at both temperatures.

The initial taxonomic composition was similar in all twelve mesocosms (Table 4). At both temperatures, the pre-spring bloom period was dominated by the dinoflagellates *Protoperidinium* sp. (large; mean Ø 40 µm; 50–67 % of the total biomass) and *Gyrodinium spirale* (19–29 % of the total community) while *Gymnodinium* spp. occurred only at low biomass. In addition, the ciliates *Myrionecta rubra*, *Rimostrombidium* sp., *Euplotes* sp. and tintinnids contributed only low biomass to the overall community. Right after the beginning of the experiment, the relative proportion of the small choreotrichid ciliate *Lohmaniella oviformis* started to increase reaching its maximum already after 3 weeks in all mesocosms (73–88 % of the total community; Fig. 5a). At Δ6 °C, the relative shares of *L. oviformis* declined rapidly and right after the ciliate peak the community became dominated by *Protoperidinium bipes* (small; mean Ø 25 µm; 80–97 % of the total community,

Fig. 5b). In contrast, *L. oviformis* remained the dominant species over a period of 3 weeks in the cold mesocosms (Δ0 °C; Fig. 5a) and its relative biomass declined only during the last 2 weeks of the experiment when *P. bipes* dominated the community also at colder conditions (84–99 % of the total community; Fig. 5b).

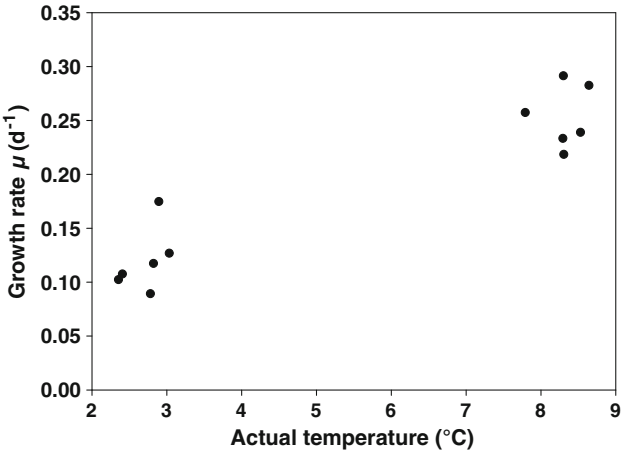


**Fig. 3** Relationship between the actual temperatures (°C) in the mesocosms and the growth rates $\mu$ (day$^{-1}$) of microzooplankton during the build-up of the phytoplankton bloom

## Predator–prey models with increasing temperature

In both, the tritrophic chain and 5-guild model, increasing $Q_{10}$ values in the cold treatments (Δ0 °C) did not result in substantially reduced time-lags between phytoplankton and grazers (copepods and protozoa). In the cold treatments, the temperature was ~2 °C which was close to our chosen reference temperature (2 °C). Thus, the time-regulation factor, *eT* (which represents the increase of grazing rates with temperature, see Methods: Predator–prey model), was 1 for all $Q_{10}$ values, resulting in the same grazing rates of predator and growth rate of algae regardless of $Q_{10}$ values. In contrast, time-lags in the warm treatments were strongly affected by the $Q_{10}$ values of the grazers and the food web structure (Figs. 6, 7). In the tritrophic food chain, warming led to a reduced time-lag between phytoplankton and copepods (Fig. 6a) as well as protozoa (Fig. 6b). With increasing $Q_{10}$ values of copepods and protozoa, this effect was enhanced (Fig. 6a + b).

In the 5-guild model, where specific predator and prey components were considered separately (Fig. 7), the effects of increasing $Q_{10}$ values of grazers on the phenology depended on their trophic position. Increasing $Q_{10}$ values of copepods decreased the time-lag between them and

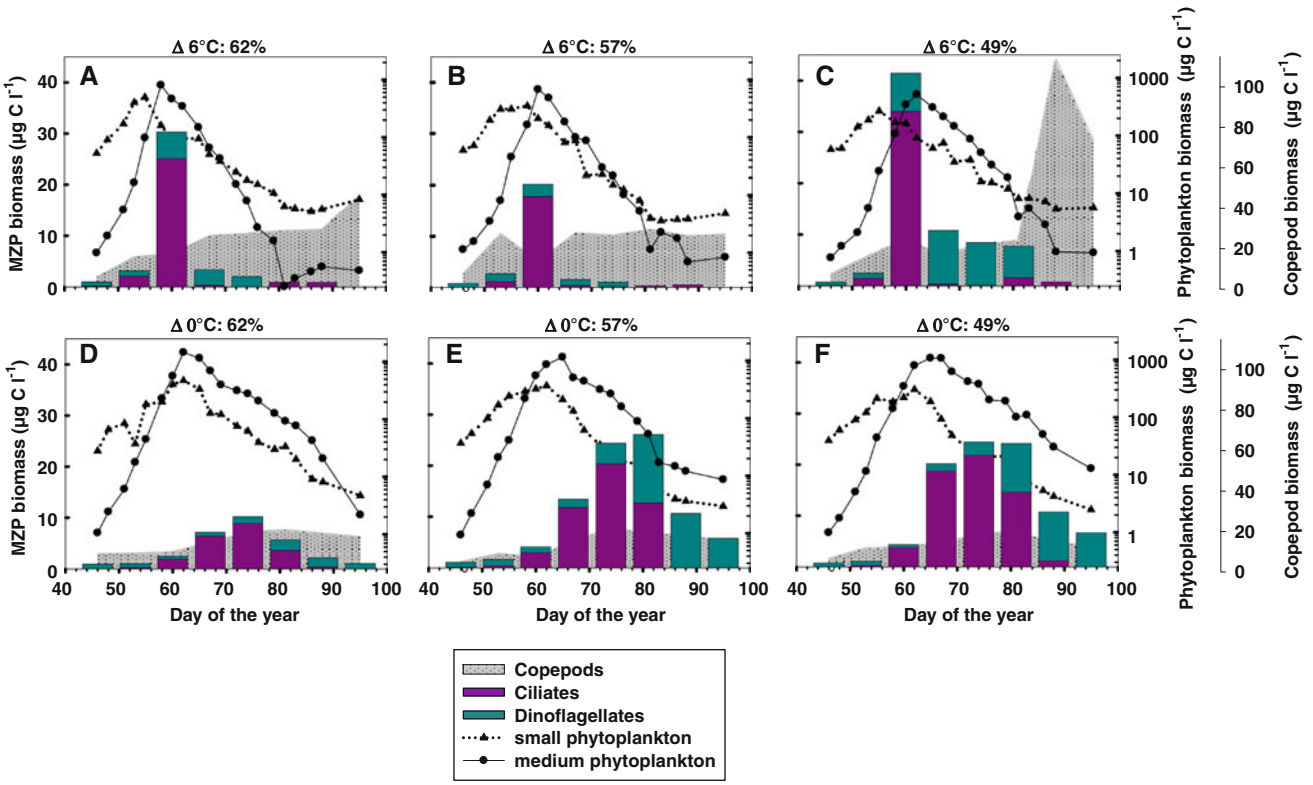


**Fig. 4** Microzooplankton (MZP) biomass (μg C l$^{-1}$) of ciliates and dinoflagellates (*blue*) as the mean of duplicate mesocosms, mean phytoplankton biomass (μg C l$^{-1}$) (*dashed line* small-sized phytoplankton; *solid line* medium-sized phytoplankton), and mean copepod biomass (μg C l$^{-1}$) (*gray areas*) for each treatment. Factors temperature (°C) and light (%) of the different treatments: **a** Δ6 °C 62 %, **b** Δ6 °C 57 %, **c** Δ6 °C 49 %, **d** Δ0 °C 62 %, **e** Δ0 °C 57 %, **f** Δ0 °C 49 %

**Table 4** Taxonomic composition of microzooplankton and biomass (μg C $l^{-1}$) of different species/genera during the course of the mesocosms experiment in the six different treatments (Δ6 °C: 64 %, Δ6 °C: 48 %, Δ6 °C: 32 %, Δ0 °C: 64 %, Δ0 °C: 48 %, and Δ0 °C: 32 %)

| | Day of the year (DOY) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 46 | 53 | 60 | 67 | 74 | 81 | 88 | 95 |
| Δ6 °C: 62 % | | | | | | | | |
| *Myrionecta rubra* | 0.06 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.01 | 1.99 | 25.13 | 0.26 | 0.02 | 0.00 | 0.00 | 0.00 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 5.00 | 3.07 | 2.02 | 0.08 | 0.00 | 0.00 |
| *Protoperidinium* sp. | 0.50 | 0.34 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.01 | 0.00 | 0.00 | 0.04 | 0.00 | 0.10 | 0.00 | 0.00 |
| *Gyrodinium cf. spirale* | 0.21 | 0.17 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.11 | 0.60 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.08 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.74 | 0.90 | 0.00 |
| Δ6 °C: 57 % | | | | | | | | |
| *Myrionecta rubra* | 0.02 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.01 | 0.92 | 17.77 | 0.17 | 0.09 | 0.00 | 0.00 | 0.00 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 2.33 | 1.25 | 0.90 | 0.01 | 0.00 | 0.00 |
| *Protoperidinium* sp. | 0.53 | 0.67 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.05 | 0.00 | 0.00 |
| *Gyrodinium cf. spirale* | 0.16 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.08 | 0.85 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.00 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.21 | 0.49 | 0.00 |
| Δ6 °C: 49 % | | | | | | | | |
| *Myrionecta rubra* | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.00 | 1.30 | 33.88 | 0.32 | 0.07 | 0.03 | 0.01 | 0.00 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 7.34 | 10.48 | 8.36 | 6.13 | 0.00 | 0.00 |
| *Protoperidinium* sp. | 0.39 | 0.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.00 | 0.00 | 0.10 | 0.02 | 0.00 | 0.72 | 0.00 | 0.00 |
| *Gyrodinium cf. spirale* | 0.21 | 0.21 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.08 | 0.45 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.00 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.86 | 0.76 | 0.00 |
| Δ0 °C: 62 % | | | | | | | | |
| *Myrionecta rubra* | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.00 | 0.20 | 1.94 | 6.41 | 8.84 | 3.49 | 0.27 | 0.01 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 0.07 | 0.43 | 1.35 | 2.11 | 1.83 | 1.01 |
| *Protoperidinium* sp. | 0.53 | 0.28 | 0.06 | 0.22 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.10 | 0.06 | 0.02 |
| *Gyrodinium cf. spirale* | 0.28 | 0.27 | 0.12 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.12 | 0.24 | 0.27 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 |
| Δ0 °C: 57 % | | | | | | | | |
| *Myrionecta rubra* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.00 | 0.32 | 2.99 | 11.78 | 20.07 | 11.85 | 0.02 | 0.01 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 0.12 | 1.04 | 4.05 | 13.42 | 10.60 | 5.73 |
| *Protoperidinium* sp. | 0.59 | 0.64 | 0.39 | 0.34 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.30 | 0.85 | 0.02 | 0.05 |

**Table 4** continued

| | Day of the year (DOY) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 46 | 53 | 60 | 67 | 74 | 81 | 88 | 95 |
| *Gyrodinium cf. spirale* | 0.28 | 0.33 | 0.02 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.09 | 0.25 | 0.59 | 0.19 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.12 | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Δ0 °C: 49 % | | | | | | | | |
| *Myrionecta rubra* | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Lohmaniella oviformis* | 0.00 | 0.24 | 3.83 | 18.78 | 21.39 | 14.10 | 1.21 | 0.01 |
| *Protoperidinium bipes* | 0.00 | 0.00 | 0.12 | 0.83 | 2.43 | 9.49 | 9.50 | 6.64 |
| *Protoperidinium* sp. | 0.45 | 0.48 | 0.20 | 0.22 | 0.11 | 0.00 | 0.00 | 0.00 |
| *Rimostrombidium* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 | 0.55 | 0.05 | 0.02 |
| *Gyrodinium cf. spirale* | 0.23 | 0.21 | 0.10 | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gymnodinium* spp. | 0.10 | 0.06 | 0.10 | 0.22 | 0.03 | 0.00 | 0.00 | 0.00 |
| *Tintinnids* | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euplotes* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

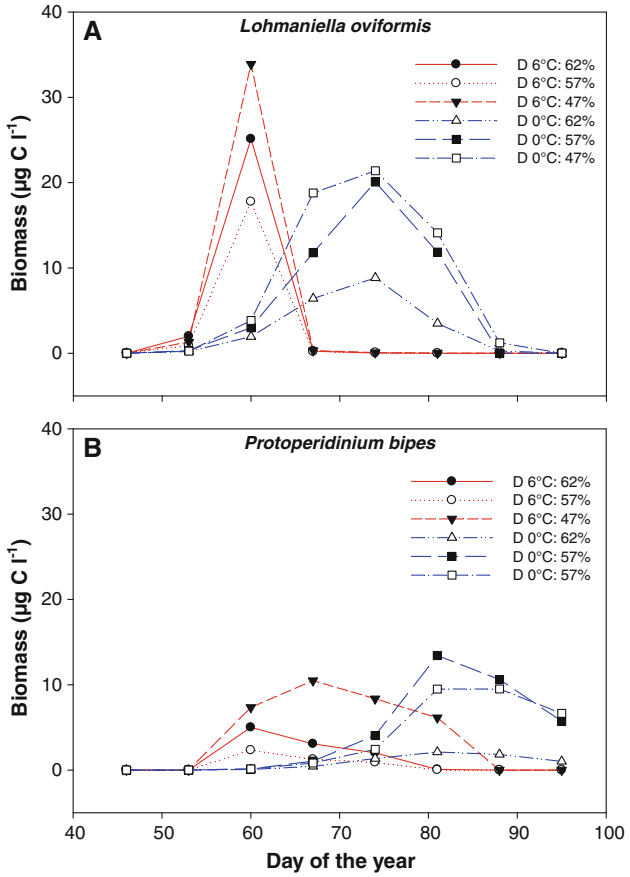


**Fig. 5** Temporal succession of the dominant ciliate *Lohmaniella oviformis* (**a**) and the dominant heterotrophic dinoflagellate *Protoperidinium bipes* (**b**) (both in the size range 20–30 µm) as the mean of duplicate mesocosms. Factors temperature (°C) and light (%) of the different treatments are given in the figure legend

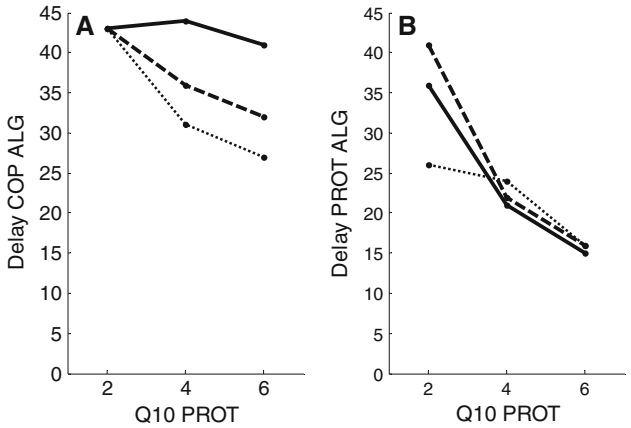


**Fig. 6** Difference between the day of the biomass peak of copepods, COP (**a**) or protozoans, PROT (**b**) and phytoplankton, ALG, in relation to the $Q_{10}$ value of protozoans assuming a $Q_{10}$ of 2 (*solid*), 4 (*dashed*) or 6 (*dotted line*) for copepods at Δ6 °C

medium-sized algae (Fig. 7a). The time-lag between copepods and medium-sized algae was slightly affected by the $Q_{10}$ values of protozoans. If the latter was 2, copepods suppressed both protozoans and medium-sized algae early, resulting in a relatively short time-lag between copepods and medium-sized algae. If the $Q_{10}$ of protozoans was 4, dinoflagellates terminated the bloom of medium-sized algae and the peak of copepods followed the peak of dinoflagellates; thus, the time-lag between copepods and medium-sized algae was longer. The bloom phenology was similar with a $Q_{10}$ value of 6 for the protozoans, but the dynamics was faster; thus, the time-lag between copepods and medium-sized algae reduced again. Increasing $Q_{10}$ values of

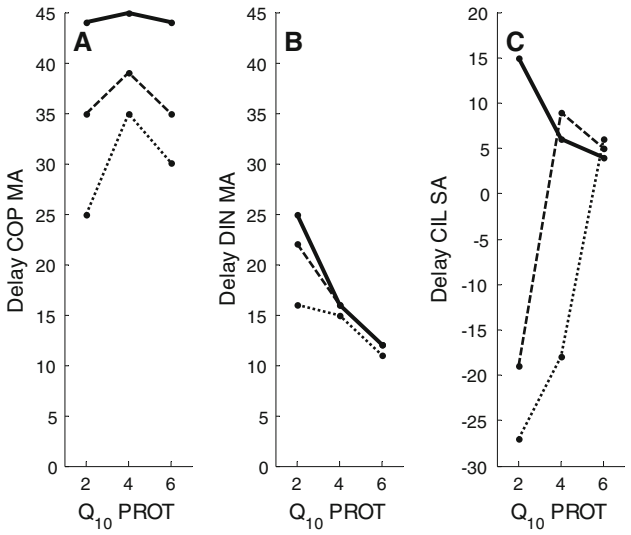


**Fig. 7** Difference between the day of the biomass peak of copepods, COP (**a**) or dinoflagellates, DIN (**b**) and medium-sized algae, MA, and between ciliates, CIL and small-sized algae, SA (**c**) in relation to the $Q_{10}$ value of protozoans, PROT, assuming a $Q_{10}$ of 2 (*solid*), 4 (*dashed*) or 6 (*dotted line*) for copepods at Δ6 °C. Please note the different scale of the *y* axis used in **c**

protozoans decreased the time-lag between dinoflagellates and medium-sized algae, irrespective of the $Q_{10}$ values of copepods (Fig. 7b). Increasing $Q_{10}$ values of protozoans decreased the time-lag between ciliates and small phytoplankton only if we assumed a lower or equal $Q_{10}$ value for copepods than for protozoans (Fig. 7c). If the $Q_{10}$ value of copepods was higher, they suppressed protozoans early, thus releasing small phytoplankton from ciliate grazing. Thus, small phytoplankton developed a bloom after the peaks of the grazers and of medium-sized algae, resulting in a 'negative' time-lag between them and ciliates (Fig. 7c).

## Discussion

### Acceleration of microzooplankton growth and species turnover with warming

Microzooplankton communities usually show a rapid numerical response to increasing food supply. Next to food availability, temperature is considered as a major controlling factor of microzooplankton (Weisse and Montagnes 1998; Rose and Caron 2007), especially during the spring succession of plankton (Johansson et al. 2004; Rose et al. 2009). In our mesocosm study, warming resulted in an earlier timing ($D_{max}$, $D_{25}$, $D_{50}$ and $D_{75}$) and higher growth rates of microzooplankton. Observations of an earlier timing of microzooplankton are similar to a previous mesocosm study on the effects of warming on spring microzooplankton communities (Aberle et al. 2007). Both an earlier timing and higher growth rates of microzooplankton are an expected phenomenon since the metabolism and production of microzooplankton is known to increase with increasing temperature (Montagnes et al. 2003; Rose and Caron 2007). In contrast to an earlier timing, peak magnitudes of $D_{max}$ were not significantly affected by warming. While this is supported by findings of Berger et al. (2010), it contrasts other experimental studies where peak magnitudes of spring microzooplankton were found to increase with warming (Aberle et al. 2007; Rose et al. 2009). While warming accelerated growth rates, this does not necessarily translate into a higher carrying capacity of microzooplankton which depends on resource availability. Only if a more efficient conversion of food into microzooplankton production had happened, higher peak magnitudes could be expected. As stated by Rose et al. (2009), the combination of both direct temperature effects and indirect bottom-up (due to changes in phytoplankton abundance and community composition) and top-down effects (due to grazer-induced phytoplankton community changes) affects microzooplankton dynamics thus pointing at the counteracting factors, food availability, grazing, and temperature in affecting microzooplankton in our mesocosms.

Furthermore, warming induced shifts in microzooplankton phenology resulting from a more rapid turnover of microzooplankton species. Such reduced time frames of microzooplankton were, for example, observed for ciliates where the dominance of *L. oviformis* lasted for only 1 week in the warm mesocosms while it dominated the cold mesocosms for 3 weeks. Shifts in the temporal occurrence of microzooplankton with warming have been scarcely investigated so far (Aberle et al. 2007; Rose et al. 2009). However, a faster species turnover at higher temperatures was shown for one-trophic level microalgal communities where its implications on community stability depended on the functional composition of the community (Hillebrand et al. 2011). In a multitrophic community, as the one studied here, it is even more complex to evaluate the consequences of faster species turnover. But it seems likely that a reduced temporal occurrence of microzooplankton might affect consumers' condition and reproductive success by increasing the probability of a temporal mismatch between microzooplankton, copepods, meroplanktonic larvae and fish larvae (Lasker 1981; Stoecker and Capuzzo 1990; Turner and Graneli 1992; Malzahn and Boersma 2009; Loeder et al. 2011).

Overall, our findings that warming accelerates microzooplankton growth and species turnover confirm hypothesis 1 of the present study and support predictions that microzooplankton might become a beneficiary of global warming.

### Reduced time-lags between autotrophs and heterotrophs in plankton communities: effects of warming and light availability

While warming accelerated $D_{max}$ of microzooplankton by 2.5 days per °C, phytoplankton peaks showed only an acceleration of 1 day $°C^{-1}$ (Lewandowska and Sommer 2010). This resulted in almost synchronous biomass peaks of phytoplankton and microzooplankton in the warm mesocosms while the time-lag in the colder mesocosms was on average 10 days. The observed patterns of a stronger thermal response of heterotrophic protists over autotrophic ones confirm our hypothesis 2. As stated by the MTE (Brown et al. 2004), the different temperature dependencies of autotrophic and heterotrophic processes result from different metabolic activation energies. Contrary to previous studies where a mismatch between predators and their prey was observed under warming conditions (Durant et al. 2007; Thackeray et al. 2010), the reduced time-lags between microzooplankton and autotrophic prey items resulted in an enhanced match situation for microzooplankton in our mesocosms.

One fundamental prerequisite for the development of phytoplankton spring blooms in temperate waters is, however, a delayed response of microzooplankton during winter–spring transition when growth of heterotrophs is restricted by low temperatures and phytoplankton growth exceeds grazing losses (Rose and Caron 2007). Then, a 'loophole' sensu Irigoien et al. (2005) opens thus enabling phytoplankton to form blooms. In light of a winter warming scenario for Northern-Central Europe (IPCC 2007), the combined effects of such an earlier timing of microzooplankton and reduced time-lags between autotrophs and heterotrophs might cause fundamental imbalances between growth and removal of phytoplankton thus affecting phytoplankton bloom dynamics (Wiltshire et al. 2008) and composition (Keller et al. 1999; Sommer and Lengfellner 2008).

Hypothesis 2 was also supported by our model results, which consistently predicted reduced time-lags between phytoplankton and its grazers with warming, especially when assuming high temperature sensitivity for the latter. A mismatch between primary producers and grazers depended on the dietary overlap between the two grazer groups and on their relative temperature sensitivities. It only occurred when temperature sensitivity of secondary consumers was higher than that of primary consumers. This assumption seems unrealistic for plankton.

Next to temperature, the factor light might alter the timing and biomass of phytoplankton and microzooplankton, since, for example, higher light intensities were shown to increase peak biomass of primary producers thus enhancing consumers' production due to enhanced food availability (Diehl et al. 2002; Tirok and Gaedke 2007). In our study, neither the timing nor the peak magnitudes of microzooplankton were affected by light, a pattern which was most likely related to the rather narrow range of light intensities applied. Due to the fact that all three treatments must be categorized as rather 'high light', our conclusions might have to be modified for strongly light limiting conditions.

### Top-down bloom control by microzooplankton and trophic interactions with mesozooplankton

The breakdown of a phytoplankton bloom can be attributed to an enhanced sedimentation as a result of nutrient depletion or grazing. Most likely the combination of both factors controlled the bloom in our mesocosms. The lower peak biomass of medium-sized phytoplankton at Δ6 °C might result from enhanced aggregation and thus sedimentation of diatom cells (Piontek et al. 2009) as well as from higher copepod densities and thus enhanced grazing at elevated temperatures. In the case of small algae, grazing was more likely to cause the breakdown of the bloom in the warm mesocosms. Here, we observed almost synchronous peaks of ciliates (dominated by *L. oviformis*) and small-sized phytoplankton, the preferred food items of *L. oviformis* (Jonsson 1986; Christaki et al. 1998). The reduced time-lag between autotrophs and heterotrophs resulted in a rapid depletion of small-sized phytoplankton followed by an instantaneous microzooplankton decline thereafter. The rapid overexploitation of food sources with warming points at an enhanced top-down control of small-sized phytoplankton by microzooplankton thus confirming the first part of hypothesis 3. In the second part, it was assumed that a stronger depletion of phytoplankton by microzooplankton with warming might enhance dietary competition with mesozooplankton due to an increased depletion of their common resource, that is, phytoplankton. Contrary to our expectations, we observed constantly high copepod densities in the warm mesocosms throughout the experiment while phytoplankton declined significantly. Thus, no direct negative effect of decreasing phytoplankton biomass on copepod densities was observed. Therefore, there was no indication for an enhanced dietary competition for the same resource between microzooplankton and copepods. This might be attributable to the predominance of small ciliates in the present study which prefer nano- and picophytoplankton (Jonsson 1986; Christaki et al. 1998). In contrast to large ciliates, which consume medium-sized phytoplankton (Aberle et al. 2007), small ciliates do not compete with copepods. The dominant copepods *Temora* sp., *Acartia* sp., and *Centropages* sp. in our mesocosms (Lewandowska and Sommer 2010) are categorized as omnivorous with the ability to catch motile heterotrophic

prey efficiently (Turner and Graneli 1992; Vincent and Hartmann 2001; Loeder et al. 2011). At times when microzooplankton occurred at high densities, the strategy of copepods to switch from suspension feeding to capturing motile prey might result in a twofold benefit for the consumers. First, it enables the exploitation of an additional, high quality food source which compensates stoichiometric imbalances at the primary producer level thus functioning as a trophic upgrader (Malzahn et al. 2010). Second, predation on microzooplankton by copepods suppresses a dietary competitor. Additional support for this assumption was generated by our models. These showed that small phytoplankton was only released from grazing by ciliates when an enhanced top-down control of microzooplankton by copepods occurred and that the suppression of ciliates was intensified with increasing $Q_{10}$ of the copepods. Thus, warming enhanced the top-down control of microzooplankton by copepods rather than enhancing dietary competition between micro- and mesozooplankton as initially hypothesized.

So far, most studies investigating the impact of climate warming on pelagic food webs focused on mesozooplankton (Edwards and Richardson 2004; Winder and Schindler 2004). The present study points at the necessity to consider both micro- and mesozooplankton grazers when addressing match–mismatch situations in the pelagic realm.

## Future implications

Our findings stress the relevance of the factors temperature combined with food supply and predation in altering phytoplankton–microzooplankton–mesoplankton interactions in the plankton (e.g., shifts in timing, species turnover, and time-lags). The present study adds to the current knowledge on warming-induced changes in the plankton by stressing the relevance of microzooplankton as a trophic intermediary and as key players regarding temperature sensitivity. Phenological changes and potential asynchronies between consumers and their prey in plankton communities were addressed in light of future climate change scenarios. Our findings suggest that indirect warming effects via enhanced microzooplankton grazing will not only alter phytoplankton bloom dynamics but might have major implications for the cycling of matter and energy through the microbial and traditional food webs with far reaching consequences for higher trophic levels, for example, fish stocks.

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