GLOBAL CHANGE AND CONSERVATION ECOLOGY

Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming

N. Aberle · K. Lengfellner · U. Sommer

Abstract This study aimed at simulating different degrees of winter warming and at assessing its potential effects on ciliate succession and grazing-related patterns. By using indoor mesocosms filled with unfiltered water from Kiel Bight, natural light and four different temperature regimes, phytoplankton spring blooms were induced and the thermal responses of ciliates were quantified. Two distinct ciliate assemblages, a pre-spring and a spring bloom assemblage, could be detected, while their formation was strongly temperature-dependent. Both assemblages were dominated by Strobilidiids; the pre-spring bloom phase was dominated by the small Strobilidiids *Lohmaniella oviformis*, and the spring bloom was mainly dominated by large Strobilidiids of the genus *Strobilidium*. The numerical response of ciliates to increasing food concentrations showed a strong acceleration by temperature. Grazing rates of ciliates and copepods were low during the pre-spring bloom period and high during the bloom ranging from 0.06 (Δ0°C) to 0.23 day^{-1} (Δ4°C) for ciliates and 0.09 (Δ0°C) to 1.62 day^{-1} (Δ4°C) for copepods. During the spring bloom ciliates and copepods showed a strong dietary overlap characterized by a wide food spectrum consisting mainly of *Chrysochromulina* sp., diatom chains and large, single-celled diatoms.

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N. Aberle (✉) · K. Lengfellner · U. Sommer
IFM-GEOMAR Leibniz Institute of Marine Sciences,
Düsternbrooker Weg 20, 24116 Kiel, Germany
e-mail: naberle@awi-bremerhaven.de

Introduction

Recent studies have shown that climate change strongly influences aquatic communities on the global scale, thus affecting plankton community dynamics leading to regime shifts in the pelagic realm (Beaugrand et al. 2003; McGowan et al. 2003; Greve et al. 2004; Smol et al. 2005). The re-structuring of planktonic systems in response to global warming is one of the major topics in aquatic ecology at present, and there is much debate on the degree of climatic sensitivity of different trophic components (Walther et al. 2002; Hays et al. 2005; Winder and Schindler 2004). In this context, the microzooplankton is an important player as it is considered as the trophic link between the microbial components and higher trophic levels (Johansson et al. 2004; Sommer et al. 2005). Microzooplankton communities are generally regarded as being major consumers of planktonic primary producers, consuming as much as 60–70% depending on the species composition and the nutrient status of the environment (Landry and Calbet 2004). While traditional food-web models proposed a direct transfer of energy from phytoplankton to mesozooplankton (Cushing 1989), it has only relatively recently become clear that microzooplankton, and especially ciliates, can contribute considerably to the diets of mesozooplankters (Kleppel 1993). The trophic pathway through microzooplankton thus enables a rapid regeneration

and/or cycling of nutrients (Irigoien et al. 2005; Calbet and Saiz 2005).

In temperate regions, the seasonal succession of plankton is initiated by a spring bloom of phytoplankton. These blooms are triggered predominantly by increasing light and nutrient availabilities (Greve and Reiners 1995; Sommer 1996) and only indirectly by temperature, e.g., via the effects of thermal stratification and/or cloud cover (Sverdrup 1953; Wiltshire and Manly 2004). Growth and grazing of consumers are, however, strongly influenced by thermal conditions. The metabolism and production of zooplankton is known to increase with increasing temperature (Montagnes and Lessard 1999), and at identical food supply, zooplankton population growth will become faster the warmer the spring temperatures are. As hypothesized by Scheffer et al. (2001), such changes in thermal conditions might alter the timing and the extent of the clear-water phase with substantial consequences for phytoplankton biomass peaks in spring as well as for top-down effects on phytoplankton. Consequently, a rise in sea surface temperature will not only affect distinct trophic levels per se, but also the complex nature of trophodynamic interactions, leading to a temporal asynchrony between predators and their prey (match–mismatch hypothesis; Cushing 1975).

Especially in spring, ciliates are considered as key components of planktonic communities as they show a more rapid metabolism and production per unit weight than mesozooplankton (Fenchel and Finlay 1983; Mueller and Geller 1993; Montagnes and Lessard 1999), thus enabling an instantaneous response to increasing food availability during the phytoplankton spring bloom (Johansson et al. 2004). In addition, as over-wintering mesozooplankton populations are usually low at this time of the year, ciliates are still released from grazing pressure through secondary consumers. Previous studies on grazing preferences of ciliates have stressed the overall importance of ciliates as primary consumers in general and also the major role of certain ciliate species in consuming spring phytoplankton communities, especially in the Baltic Sea (Smetacek 1981; Kivi et al. 1993; Leppaenen and Bruun 1988; Johansson et al. 2004).

For north-central Europe, a pronounced winter warming is predicted (IPCC 2001), which could lead to an increase in the annual mean surface temperatures of 3–5°C and an increase in winter temperatures of even 5–10°C (prediction for 2070–2100 as compared to the reference period 1960–1990). In the light of these predictions, the motivation of this study was to address the question how the spring succession of plankton will change in response to the forecast climate changes at the beginning of the growth season. For this purpose, four different temperature regimes (+0, +2, +4, and +6°C) were chosen. It is hypothesized that increased temperatures will accelerate heterotrophic processes more strongly than light limited phytoplankton growth. As a consequence, this could lead to asynchronies between predators and their prey ("match–mismatch" hypothesis, Cushing 1975) with significant impacts on ecosystem stability.

In this study, we hypothesized that the different temperature regimes will lead to (1) an acceleration of ciliate growth by temperature, (2) higher amplitudes of ciliate biomass with increasing temperature, (3) an earlier initiation of the clear-water phase, (4) postponed and attenuated succession patterns of ciliate communities at lower temperature, and (5) higher grazing rates with increasing temperatures.

Materials and methods

Experimental set-up

The experimental set-up consisted of eight mesocosms in temperature-controlled culture rooms with an experimental period lasting from 4 February to 4 May 2005. The mesocosms consisted of a two-chamber system, with a 1,400-l plankton chamber and a smaller (300-l) benthos chamber, which served as a source for meroplanktonic larvae and of planktonic organisms germinating from benthic resting stages. Plankton was gently stirred by a propeller. There was a continuous, but small exchange (on average ca. 60 l day^{-1}) of the water between both chambers. Temperature and light regimes in both chambers were identical. The experiment was run as an almost closed system. Only the sample volume was replaced by unfiltered water from the Kiel Fjord. A detailed description of the set-up is given in Sommer et al. (2006). In this study, only samples from the plankton chamber are considered.

Four temperature regimes (+0, +2, +4, and +6°C; temperature difference to a baseline seasonal trend, each in duplicate) were established whereas temperature differences between treatments were 2°C until the end of February, and the differences were reduced by 0.25°C per month thereafter to mimic less pronounced warming later in the year. The +0°C temperature regime was defined as the decadal average 1993–2002 in the Kiel Bight. The light set-up allowed simulating daily triangular light curves with natural day lengths and preserved integrated light intensities; the timing of sunrise and sundown and the maximum light intensity was supplied daily by a computer program (GHL, Prometeus). Light

attenuation by the cloud cover was superimposed by a randomized cloud cover generator (Profilux II) assuming an average 80% cloud cover and a mean light intensity (I_{mix}) of a 12-m mixed water column with a vertical attenuation coefficient of 0.6 m^{-1}.

The mesocosms were filled with unfiltered water pumped directly from Kiel Bight in front of the IFM-GEOMAR pier (6-m water depth) containing the over-wintering populations of phytoplankton, bacteria and microzooplankton. The more sensitive copepod fraction was added from net catches at natural densities (ca. 16 ind l^{-1}) because a stocking of undamaged copepods via pumping could not be assured. For details on stocking the mesocosms with organisms and water exchange, see Sommer et al. (2006).

The in vivo fluorescence as a proxy for phytoplankton biomass was detected on workdays by a Turner Fluorometer 10 AU (Turner Designs, Sunnyvale, CA).

Ciliate sampling

Samples for ciliates were taken three times per week (Monday, Wednesday, and Friday) by sampling seawater from the mixed water column (30-cm water depth) with a bucket. A total of 250 ml of the sampled seawater was transferred to brown-glass bottles and fixed with Lugol's iodine (1% final concentration). A low concentration of Lugol's fixative was used in order to avoid a strong shrinkage of cells (see Setaelae and Kivi 2003). Of each sample, 100 ml was transferred to sedimentation chambers, and ciliates were counted by the inverted microscope method (Utermöhl 1958) at a 200× magnification with a Zeiss Axiovert 200. The whole area of the bottom plate was counted for each sample in order to guarantee a comparability of the counting both at periods of high and low ciliate abundance. The ciliates were identified to the lowest possible taxonomic level (some to the species, others to the genus level) according to Kahl (1932), Foissner et al. (1991, 1992, 1994, 1995) and Strüder-Kypke et al. (2002). Uncertain species were given scientific names after the ciliate species they most resembled (cf. indicates uncertain species names). Note that identification of ciliates in Lugol-preserved samples is in most cases uncertain below the genus level. A more precise determination of Lugol's fixed ciliates to the species level requires the use of specific staining methods and a laborious working-up of the samples. The present study was geared to determining morphospecies and changes in ciliate assemblages, and thus such complexity was not required. This is an accepted way to proceed in the literature (see: Setaelae and Kivi 2003; Gaedke and Wickham 2004; Johansson et al. 2004; Sommer et al. 2005; Berninger and Wickham 2005).

For biovolume calculations, 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).

Grazing experiments

The grazing experiments lasted for 48 h and were run twice during the whole experimental period (pre-spring bloom grazing experiment: 09–11 March 2005; spring bloom grazing experiment: 21–23 March 2005). A modified version of Landry and Hassett's (1982) dilution technique was used by replacing glass bottles by dialysis tubes of 300-ml volume (Medicell International Ltd., London) and a molecular weight cut-off of 12–14,000 Da (Wiltshire and Lampert 1999; Sommer et al. 2005). The dialysis membrane enabled the free exchange of nutrients between the interior of the bags and the surrounding water. At each temperature regime, one of the mesocosms was stocked with five dilution grades (20, 40, 60, 80, and 100% of unfiltered water), each receiving different mixtures of unfiltered water with the original plankton suspension (mesozooplankton removed by a 125-μm mesh) and 0.2 μm of filtered water from the mesocosms. The dialysis bags were placed close to the water surface within the mesocosms. For starting-point and end-point samples, 250 ml of water from the dilutions were transferred to brown glass bottles, preserved with Lugol's iodine solution, and 100 ml of each sample was transferred to sedimentation chambers. For the determination of the ciliates' biomass and taxonomic composition, see the details in the section Ciliate sampling. Phytoplankton >5 μm were counted under the inverted microscope and distinguished to the species or genus level. One hundred individuals per taxonomic unit were counted, which gave 95% confidence limits of ±20%; however, this standard could not be attained for rare species. Small phytoplankton and bacteria were counted by a flow cytometer (FACScalibur^{TM}, Becton Dickinson) and distinguished by the size and fluorescence of the pigments chlorophyll a, allophycocyanin and phycoerythrin. Three flow-cytometer categories of phytoplankton were matched to flagellate species identified microscopically: (1) *Chrysochromulina*, (2) autotrophic nanoflagellates (*Plagioselmis* sp., *Teleaulax* sp.) and (3) autotrophic picoplankton (APP).

Calculation of growth and grazing rates

Net growth rates (r; day^{-1}) in the mesocosms and the dialysis bags were calculated as:

$$r = (\ln N_1 - \ln N_2)/(t_2 - t_1). \tag{1}$$

Grazing rates by microzooplankton (γ_{micro}) in the mesocosms were calculated according to the method of Landry and Hassett (1982), where γ_{micro} can be calculated by a linear regression of r in the dialysis bags on the share of unfiltered water (x):

$$r = \mu - \gamma_{micro} \times x \tag{2}$$

(γ_{micro}, grazing mortality from slope; μ, growth rate from y-axis intercept; x, dilution factor).

Grazing rates by copepods (γ_{cop}) were calculated as the difference between net growth rates calculated from Eq. 2 for $x=1$ (r_1) and r in the mesocosms:

$$\gamma_{\mathrm{cop}} = r_1 - r_{\mathrm{meso}} \tag{3}$$

This assumes that phytoplankton in the mesocosms was only reduced by microzooplankton and copepod grazing and that other factors affecting phytoplankton mortality where equal between mesocosms and dialysis bags.

Total grazing rates of ciliates and copepods (γ_{tot}) were calculated from the sum of products of specific grazing rates for each algal species ($\gamma_{a,b,c,...}$) and the ratios between the carbon biomass of each algae ($B_{a,b,c,...}$) and the total algal carbon biomass (B_{tot}) ($a,b,c,... = B_{a,b,c,...}/B_{\mathrm{tot}}$).

$$\gamma_{\mathrm{tot}} = \gamma_a a + \gamma_b b + \gamma_c c + \cdots \tag{4}$$

Statistical analysis

To test for significant effects of the different temperature regimes (+0, +2, +4, and +6°C, each in duplicate) on the response variables of ciliates (timing of the ciliate biomass maxima, diversity), statistical tests using regression analysis were conducted. As independent factor ΔT (°C) and as dependent factors Julian day and H' were chosen using STATISTICA 6.0. Diversity was calculated using PRIMER 5.2 (2001 Primer-E Ltd.). Diversity was measured by the Shannon–Wiener function (H'; $\log_e$) (Shannon and Weaver 1963).

Results

Ciliate biomass

At the beginning of the experiment, ciliate carbon biomass increased in all mesocosms, leading to a pre-spring bloom ciliate maximum (PSCM) (Fig. 1a–d). During this period, carbon biomass increased more rapidly in the warmest mesocosms ($\Delta6$°C; PSCM = Julian day $47 + 54$), reaching values of 4.3 and 2.6 µg C l^{-1}, respectively (Fig. 1a). At the coldest temperature, ciliate biomass peaked on day 61 and 68, reaching maxima of 3.5 µg C l^{-1} (Fig. 1d). The timing of the pre-spring bloom ciliate maximum (t_{pscm}) showed a significant acceleration of 2.1 days per °C (Table 1).

After the PSCM, a decline in ciliate biomass was detected, followed by a transition phase characterized by fluctuating biomass. With the onset of the phytoplankton spring bloom, a significant increase in ciliate biomass was detected in all mesocosms (Fig. 1a–d). A more rapid increase was found at higher temperatures as the timing of the spring bloom ciliate maximum (t_{scm}) was accelerated by 2.0 days per °C (Table 1). The spring bloom ciliate maxima were: 17.3 µg C l^{-1} ($\Delta6$°C, Fig. 1a), 18.0 µg C l^{-1} ($\Delta4$°C, Fig. 1b), 16.0 µg C l^{-1} ($\Delta2$°C, Fig. 1c) and 6.3 µg C l^{-1} ($\Delta0$°C, Fig. 1d).

The biomass peaks were followed by a sharp decline within a few days, and minimum abundances were observed between Julian days 108–124.

Ciliate community structure

Size structure

During the pre-spring bloom period, the ciliate community was dominated by small ciliates (<25 µm), comprising a maximum of 74–98% of the total ciliate community (Fig. 2a–d). The proportions of large ciliates (>50 µm) were much smaller (4–23%), and medium size fractions (25–50 µm) were almost absent. With the onset of the phytoplankton spring bloom, the size structure changed considerably as a shift in size fractions towards larger ciliate taxa was observed. Especially in the warmest mesocosms ($\Delta6$, $\Delta4$°C), a dominance of large species (>50 µm) contributing up to 75% to the total ciliate community was found (Fig. 2a, b), whereas in the coldest mesocosms ($\Delta2$, $\Delta0$°C), similar proportions of medium- and large-sized taxa occurred (Fig. 2c, d).
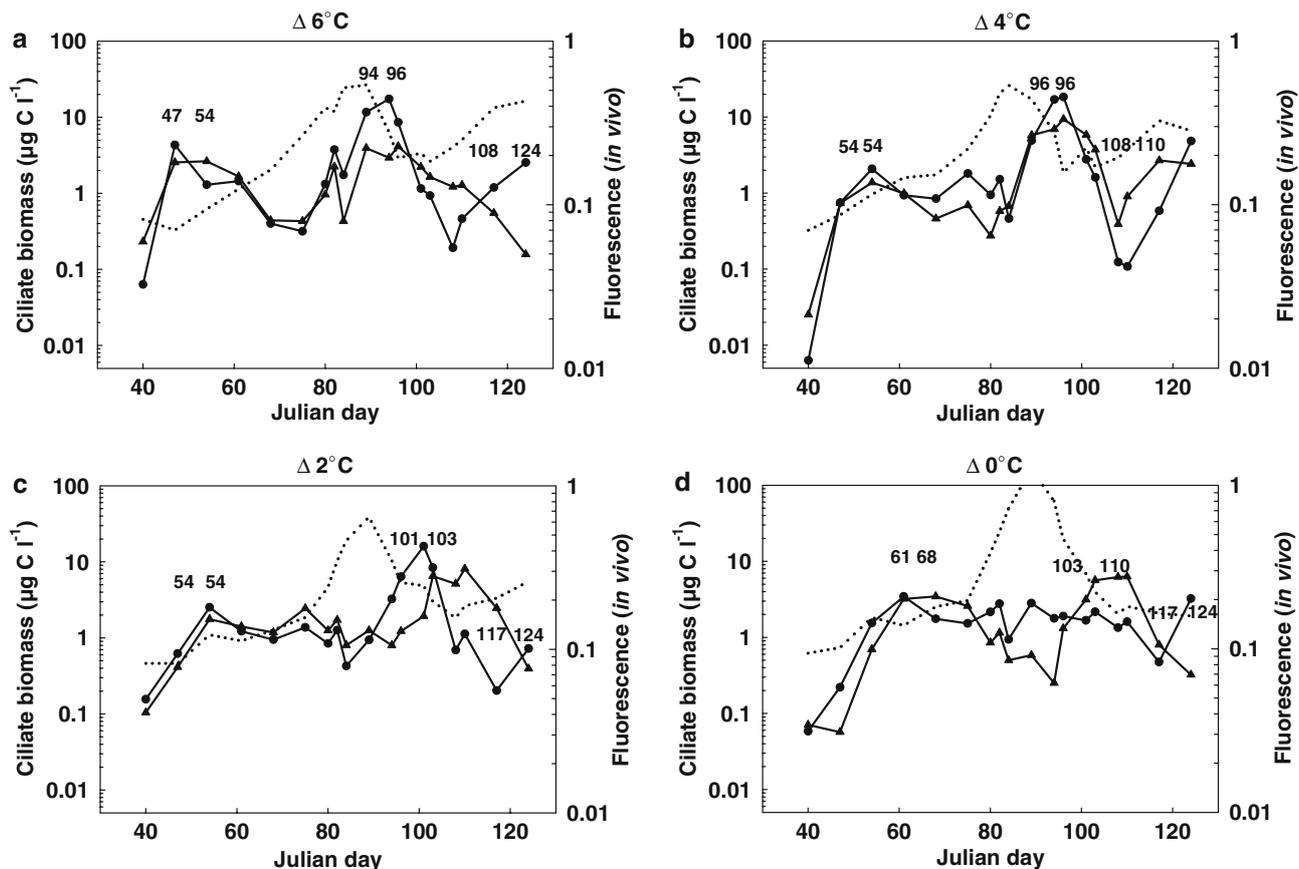
Fig. 1 Ciliate biomass (μg C l^{-1}) (*solid lines*) and in vivo fluorescence of phytoplankton (*dashed line*) in the mesocosms. *Numbers* indicate the day of the pre-spring bloom maximum, the spring bloom maximum and the biomass minimum after spring bloom; treatments: **a** Δ6°C; **b** Δ4°C; **c** Δ2°C; **d** Δ0°C. *Symbols* indicate the duplicate mesocosms: *triangles* (uneven mesocosm numbers), *circles* (even mesocosm numbers)

Table 1 Regressions of ciliate response variables on treatment intensity (ΔT in °C)

Variable	Unit	Equation	r^2	P
Time of pre-spring bloom ciliate maximum	Julian day	$t_{pscm} = 62.1 - 2.1\,\Delta T$	0.65	0.015
Time of spring-bloom ciliate maximum	Julian day	$t_{scm} = 106 - 2.0\,\Delta T$	0.81	0.0024
Ciliate diversity	H'	$d = 0.68 + 0.03\,\Delta T$	0.32	0.14
Time of clear-water phase	Julian day	$t_{cwp} = 119 - 4.25\,\Delta T$	0.80	0.0025

Taxonomic composition

At all temperature regimes the pre-spring bloom period was dominated by the Strobilidiid *Lohmaniella oviformis* showing biomass peaks ranging from 1.4 μg C l^{-1} (Δ4°C; Fig. 3b) to 3.2 μg C l^{-1} (Δ0°C; Fig. 3d). The dominance of *L. oviformis* persisted during the transition phase, while Scuticociliates made up only 0.3 μg C l^{-1} (Δ0, 2, 4°C) to 0.5 μg C l^{-1} (Δ6°C). The proportions of Strombidiids and other Strobilidiids were low prior to the spring bloom and increased rapidly shortly after the phytoplankton biomass started to increase. At warmer temperatures, the period of the spring bloom ciliate maximum was initiated by the appearance of *Balanion comatum*. This small Prostome occurred at high abundances at the very early start of the bloom, and its biomass reached values between 0.8 μg C l^{-1} (Δ2°C) and 1.7 μg C l^{-1} (Δ4°C) (Fig. 3a–c). Immediately after the *B. comatum* peak, the ciliates shifted towards a Strobilidiid-dominated community comprising of large ciliates, mostly of the *Strobilidium* species. Again, the peaks were most pronounced at elevated temperatures where the community was dominated by the species *Strobilidium*
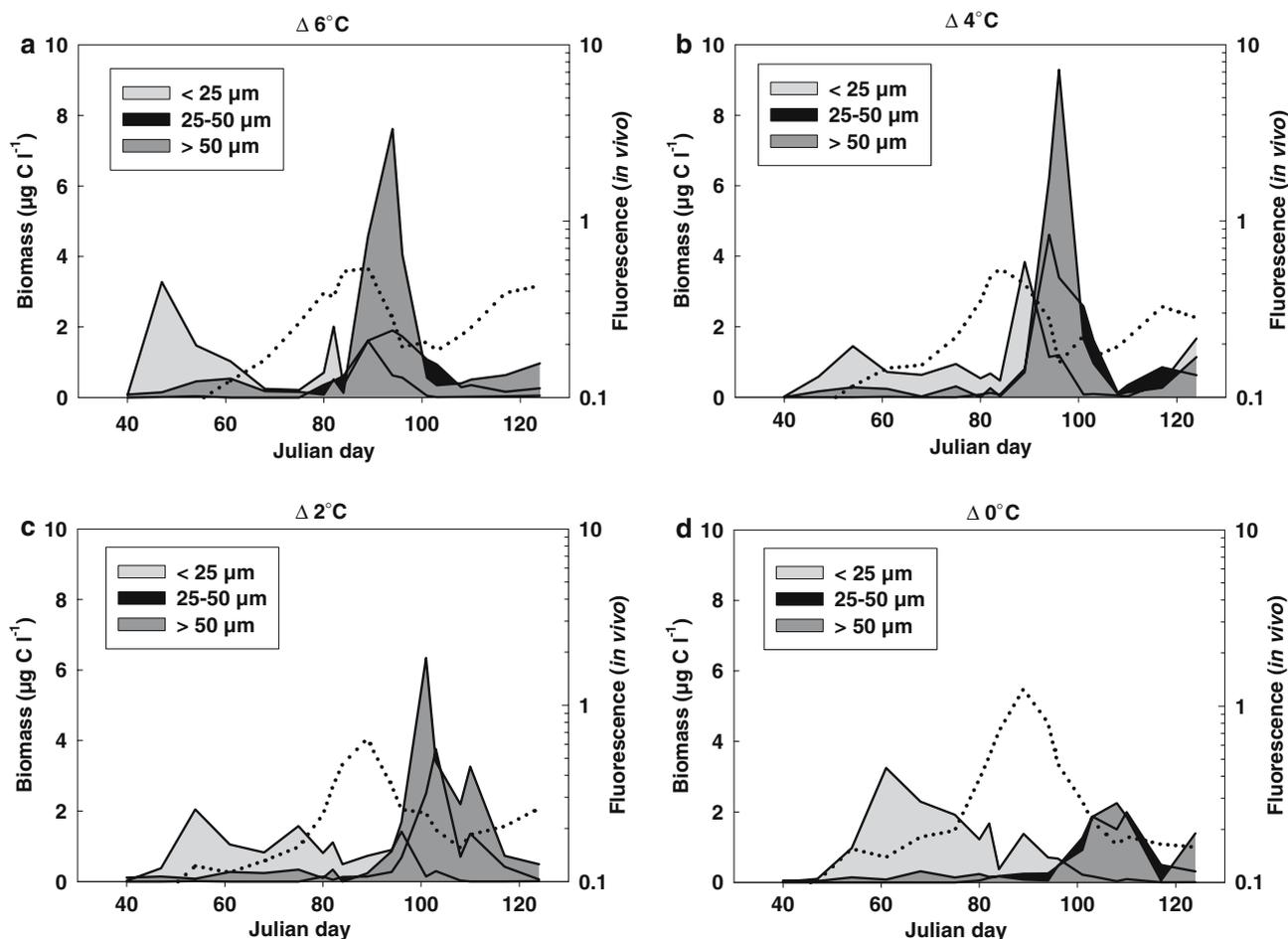
Fig. 2 Size class composition of ciliate biomass (µg C l^{-1}; <25 µm, 25–50 µm, >50 µm) as the mean of duplicate mesocosms and in vivo fluorescence (*dashed line*) in the mesocosms; treatments: **a** Δ6°C; **b** Δ4°C; **c** Δ2°C; **d** Δ0°C

caudatum, reaching biomass maxima of up to 8.8 µg C l^{-1} (Δ4°C). In addition, *Acineta* and *Euplotes* species occurred, although at low numbers. Heterotrophic dinoflagellates were of no importance in our mesocosms. At the coldest temperature (Δ0°C), the spring bloom ciliate community was also dominated by *S. caudatum* (Fig. 3d). However, compared to the warmer mesocosms, this species showed a much lower biomass of 2.2 µg C l^{-1} and other species, e.g., the *Strombidium conicum* and *Strobilidium longipes* appeared in low numbers.

Diversity

The diversity (H′) in the mesocosms showed higher values at elevated temperatures with a mean H′ between 0.9 (Δ6°C) and 0.7 (Δ0°C) (Fig. 4). Nevertheless, the correlation was weak, and the temperature dependence not significant (Table 1). The main reason

for the insignificance of this correlation was the low diversity in mesocosm 4 (Δ4°C), where especially *B. comatum* occurred at much lower abundances compared to its parallel mesocosm 3.
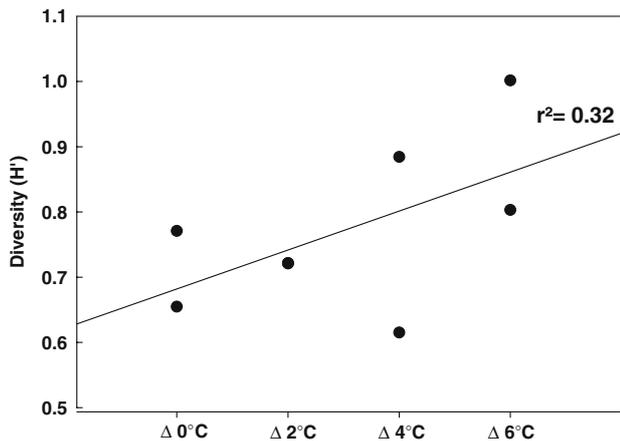
Ciliate grazing

Total grazing rates

During the pre-spring bloom period, total ciliate grazing rates showed a negative response to warming (Fig. 5a). Values at different temperatures ranged from 0.02 (7°C) to 0.11 day^{-1} (3°C). With the onset of the bloom, grazing rates showed a slight increase, with temperature and values ranging from 0.06 (4°C) to 0.23 day^{-1} (8°C).

During the pre-spring bloom period, copepods showed low grazing rates (0.003–0.14 day^{-1} at 3 and 6°C), and no clear trend in relation to temperature was
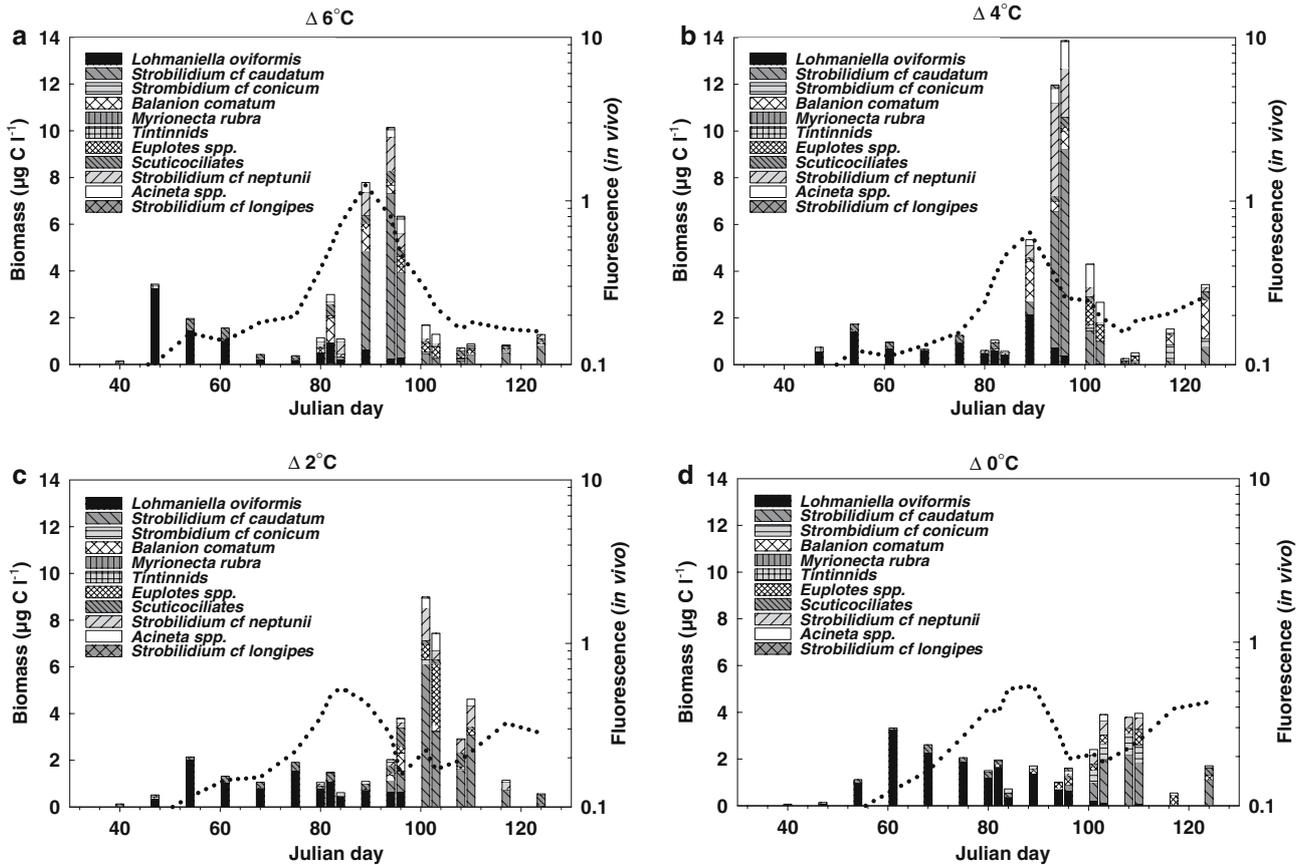
Fig. 3 Taxonomic composition of ciliates biomass (μg C l^{-1}) as the mean of duplicate mesocosms and in vivo fluorescence (*dashed line*) in the mesocosms; treatments: **a** Δ6°C; **b** Δ4°C; **c** Δ2°C; **d** Δ0°C. cf. indicates uncertain species names


Fig. 4 Diversity index (*H′*) of the ciliate communities in the mesocosms at Δ0, Δ2, Δ4, and Δ6°C. Details of the linear regression are shown in the *graph*

found (Fig. 5b). At the beginning of the spring bloom, grazing rates of copepods increased, showing values of 0.09–1.6 day^{-1} at 4 and 8°C. A trend of higher grazing rates of copepods at higher temperatures was observed.

Grazing selectivity

In general, no temperature-related effects on grazer selectivity were detected, and a strong overlap between the food sources used by ciliates and copepods was observed.

Due to the low grazing rates of ciliates and copepods during the pre-spring bloom period, the consideration of species-specific grazing by zooplankton was restricted to only a few phytoplankton taxa. For ciliates, grazing on *Chrysochromulina* sp. was detected in all treatments prior to the bloom, whereas diatoms (*Skeletonema costatum* and *Thalassionema nitzschioides*) were grazed in three out of four treatments (Fig. 6a). Data on bacteria grazing for this time frame are unfortunately not available since an analytical error occurred while measuring samples. Grazing of diatoms by ciliates was confirmed by microscopic observations showing diatoms within the ciliates' food vacuoles. Grazing upon autotrophic nanoflagellates and autotrophic picoplankton (APP) was negligible. At the beginning of the spring bloom ciliates showed high grazing rates when preying upon bacteria and diatoms
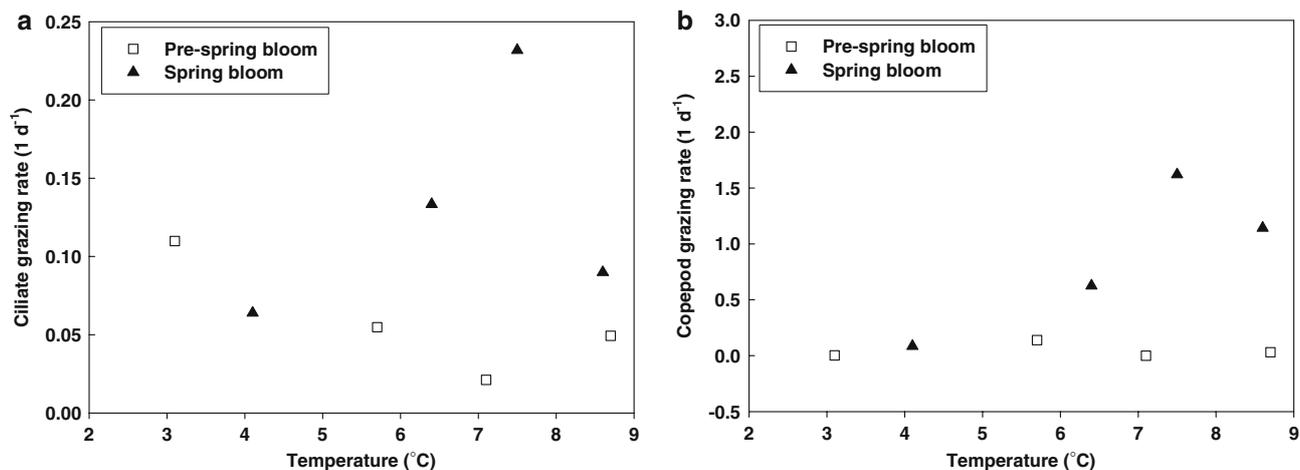
Fig. 5 Total grazing rates (1 day^{-1}) of ciliates (**a**) and of copepods (**b**) during the pre-spring bloom (*open squares*) and the spring bloom (*closed circles*) period in the mesocosms at actual temperatures (°C)

Fig. 6 Grazing rates (1 day^{-1}) of ciliates (**a**) and of copepods (**b**) during the pre-spring bloom period at Δ0, Δ2, Δ4, and Δ6°C; *APP*, autotrophic picoplankton; *Nanoflag*, nanoflagellates; *Chrysochrom*, *Chrysochromulina* sp.; *Tnem*, *Thalassionema nitzschioides*; *Skel*, *Skeletonema costatum*
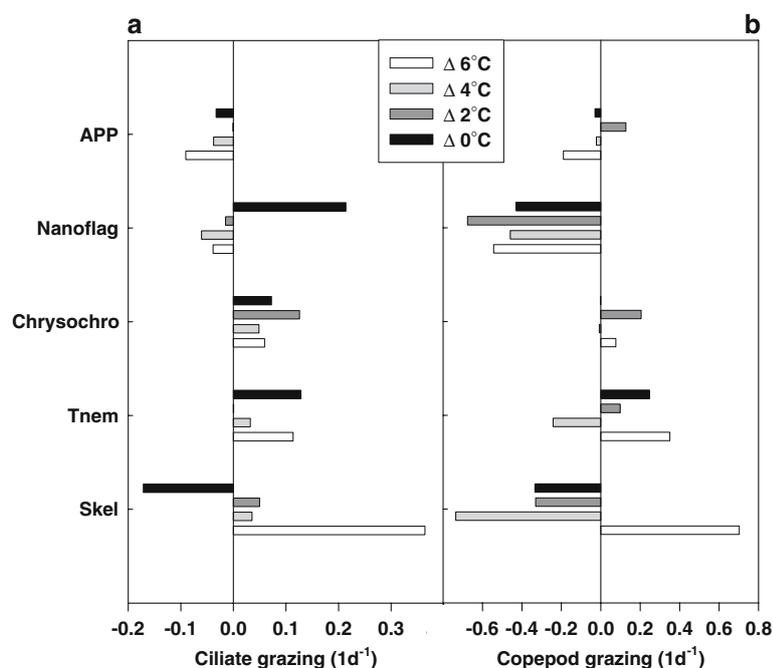
(*Nitzschia acicularis*, *Navicula* sp., *Tabularia fasciculata*), while *Chrysochromulina* sp. and the small diatom *S. costatum* were grazed at considerable amounts in the majority of treatments (Fig. 7a). Nanoflagellates and APP were of minor importance as prey for ciliates.

Copepods showed only a weak grazing during the pre-spring bloom period (Fig. 6b). Except for the Δ4°C treatment, the diatom *T. nitzschioides* was grazed to moderate degrees at all temperatures, whereas *Chrysochromulina* sp. and *S. costatum* were consumed only in some treatments. During the spring bloom the copepods showed a high consumption of several phytoplankton species no matter at which temperature

(*N. acicularis*, *Navicula* sp., *Chrysochromulina* sp. and *S. costatum*) (Fig. 7b). However, the diatom *T. fasciculata* was consumed only at elevated temperatures.

Discussion

The major aim of this study was to elucidate the impact of warming on ciliate communities during the winter-spring transition in the Baltic Sea. The hypotheses that higher temperatures will lead to accelerated growth and grazing rates, higher biomass and different succession patterns of ciliates were tested. Furthermore,

Fig. 7 Grazing rates (1 day^{-1}) of ciliates (**a**) and of copepods (**b**) during the spring bloom period at Δ0, Δ2, Δ4, and Δ6°C; *APP*, autotrophic picoplankton; *Chrysochrom*, *Chrysochromulina* sp.; *Nanoflag*, nanoflagellates; *Niac*, *Nitzschia acicularis*; *Navi*, *Navicula* sp.; *Tabu*, *Tabularia fasciculata*; *Skel*, *Skeletonema costatum*
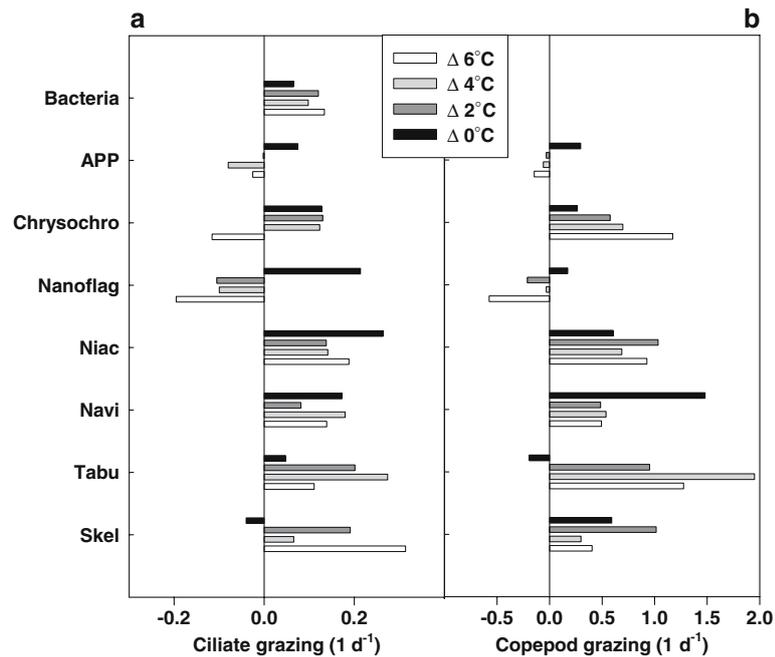
the coupling between phytoplankton, microzooplankton and mesozooplankton during spring succession, the ciliates' community dynamics and their trophic role were central focuses of the present study.

Ciliate biomass

The factors temperature and food supply are regarded as major triggers of short-term ciliate biomass maxima, especially during spring succession (Smetacek 1981; Johansson et al. 2004), and ciliate populations are known to be especially affected by the thermal conditions of a system (Weisse and Montagnes 1998; Montagnes and Lessard 1999; Johansson et al. 2004). Ciliates usually respond numerically and rapidly to increasing food availabilities, and their growth rates are considered to follow a linear rather than an exponential trend in response to temperature (Montagnes and Lessard 1999; Tillmann 2004). These general patterns of ciliate growth are supported by the findings from our mesocosm experiment.

In the light of a winter warming scenario for northern central Europe (IPCC 2001), with predicted increases in the sea surface temperature of 5–10°C during winter, an earlier onset of consumer pressure during the winter–spring transition is assumed since zooplankton growth is known to be highly affected by temperature, while light limited phytoplankton growth is not. Such a scenario could lead to temporal asynchronies between autotrophic production and heterotrophic consumption with substantial consequences for

the match or mismatch of planktonic organisms. During our experiment an acceleration of ciliate growth and higher biomass maxima at elevated temperatures were observed. Thus, our first two hypotheses that the ciliates' growth will be accelerated by temperature and that an enhanced growth of ciliates with increasing temperature will occur were confirmed.

Another good indication of climate-induced changes in the planktonic realm is the shift in timing of specific events during plankton succession, e.g., the timing of the clear-water phase. The initiation of the clear-water phase is, in general, attributed to heavy grazing, mainly by mesozooplankton, and several studies were able to link meteorological phenomena like the NAO index (North Atlantic Oscillation) to the timing of the clear-water phase (Straile and Adrian 2000; Scheffer et al. 2001). However, as already pointed out by Tirok and Gaedke (2006), the role of smaller zooplankton fractions, e.g., ciliates, on the timing of the clear-water phase have been mostly neglected, although their temperature response is well-documented in the literature (Mueller and Geller 1993, Montagnes and Weisse 2000; Weisse et al. 2001). In our experiment, we observed an earlier initiation of the clear-water phase at elevated temperatures and a shift in timing by 4 days per °C (Table 1). In addition, the timing of the ciliates' biomass maxima was accelerated by 2 days per °C, and thus, it seems likely that the rapid and more intense response of ciliate communities at elevated temperatures could be responsible for the earlier initiation of the clear-water phase in the warm set-ups.

Consequently, our hypothesis that an earlier initiation of the clear-water phase at elevated temperatures will occur could be confirmed. Similar to our experimental study, field data from Tirok and Gaedke (2006) point at a high grazing pressure by microzooplankton at times when mesozooplankton abundances are low. In their study, the clear-water phase was, however, only initiated when mesozooplankton populations grazing on large-sized algae developed. The discrepancies between their field data and the results from our mesocosm experiment might arise from the fact that a high proportion of ciliates in our mesocosms showed a preference for large diatom cells (see Discussion section on "Ciliate grazing and feeding preferences"). This enabled a predominately ciliate-induced initiation of the clear-water phase under warmer climatic conditions. Our results show that this small but important aspect— that, in response to warming, ciliates have a high potential to alter such distinct events as the timing of the clear-water phase— requires further attention.

However, blooming events of microzooplankton are not only bottom-up regulated. Several studies emphasized the role of ciliates as food source for mesozooplankton organisms (Stoecker and Capuzzo 1990; Nejstgaard et al. 2001; Granéli and Turner 2002). As in the field (Behrends 1996), copepod abundance showed a rapid decline with the duration of our experiment. The decline in predator abundance obviously released ciliates from grazing pressure through copepods in our mesocosms, a typical feature of reduced top-down control of ciliates in planktonic systems (Kivi et al. 1996; Granéli and Turner 2002; Calbet and Saiz 2005).

The degrees at which external forcing factors are responsible for the match or mismatch between organisms in the field usually remain uncertain. Our indoor mesocosm experiment provided new insights into the coupling between bottom-up and top-down control mechanisms in the light of warming trends and should thus stress the need for experimental approaches to meet the complexity of climate change research issues.

Ciliate community composition

Species composition, diversity and the peak amplitudes of single ciliate species were strongly affected by temperature in our study. An analysis of long-term plankton data in the North Sea showed similar patterns for mesozooplankton communities as shifts in species composition and increases in diversity were observed (Beaugrand 2004; Hays et al. 2005). However, Irigoien et al. (2004) characterized microzooplankton diversity predominantly as a unimodal function of phytoplankton

biomass, and ciliates are known to show a high species specificity regarding food concentrations, feeding preferences and temperature requirements (Mueller and Schlegel 1999; Weisse et al. 2001). Thus, it can be assumed that the combined effect of temperature, food supply and food composition might be responsible for the high diversity in the warmer set-ups.

In this study, the composition of ciliates during winter–spring succession was similar to the one documented by Smetacek (1981) and Johansson et al. (2004) for the Baltic Sea. Peaks of heterotrophic dinoflagellates, as observed by Smetacek (1981) during spring blooms in the Kiel Bight, could not be detected. Compared to ambient temperatures, the amplitudes of peak maxima of individual ciliate species showed a clear positive temperature response as, e.g., the small Strobilidiids *L. oviformis* showed a more rapid population growth in the warmer set-ups during the pre-spring bloom period. This species is known to occur mainly during winter or early spring when the temperatures and phytoplankton biomass are still relatively low (Johansson et al. 2004). Despite its natural thermal requirements, a strong temperature dependence of *L. oviformis* populations was detected. A similar trend was observed for the Prostome *B. comatum*, a species that dominated the ciliate community at the beginning of the spring bloom period and that is a typical representative of Prostomes in the Baltic Sea mainly during spring and summer (Johansson et al. 2004). Prostomes usually reach high biomass levels at intermediate phytoplankton biomass and high growth rates at moderate temperatures (Weisse et al. 2001). In our study, both intermediate food concentrations and increasing temperatures right at the beginning of the bloom seemed to favor the occurrence of this small Prostome species.

As proposed by Montagnes et al. (1988), clear spring assemblages with large-sized ciliates preying upon large phytoplankton size fractions are found, while summer, autumn and winter assemblages are usually dominated by small ciliates consuming small prey, e.g., bacterioplankton and flagellates (Kivi and Setaelae 1995; Setaelae and Kivi 2003). Our findings of composition changes and shifts towards larger ciliate size fractions during spring support Montagnes and co-workers' general concept on ciliate seasonal succession, a pattern which is additionally confirmed by field observations during spring succession in the Baltic Sea (Smetacek 1981; Johansson et al. 2004).

Nevertheless, the composition and succession patterns of ciliates in our indoor mesocosms were considerably affected by temperature. As hypothesized initially, we observed postponed and attenuated suc-

cession patterns of ciliate communities at lower temperatures; under elevated temperature regimes, large spring forms of the genera *Strobilidium* spp. and *Strombidium* spp. (>50 μm) increased rapidly and strongly when food concentrations increased, while their occurrence was delayed in the colder set-ups and their abundance remained low. A strong temperature response of the *Strobilidium* and *Strombidium* species has also been reported by Montagnes (1996), and thus, it can be speculated that an earlier and a more intense peak of large ciliate fractions could alter the timing and the duration of blooms. In the light of a winter warming scenario, the observed thermal sensitivity of large ciliate size fractions could have far-reaching consequences for the spring formation of phytoplankton blooms and the synchrony between planktonic organisms.

Ciliate grazing and feeding preferences

Numerous studies have emphasized the overall importance of micrograzers as dominant consumers of phytoplankton in oligotrophic and eutrophic oceans (Sherr et al. 1992). Traditionally, ciliates were considered as major grazers of microalgae, preying mainly upon nanoplankton size fractions (Jonsson 1986; Kivi and Setaelae 1995; Granéli and Turner 2002; Sommer et al. 2005; Berninger and Wickham 2005), whereas large phytoplankton size fractions like, e.g., diatoms are usually considered as the preferred food item of copepods (Kivi et al. 1996; Granéli and Turner 2002; Sommer et al. 2005). In addition, recent studies also point to the ciliates' importance as bacterivores and to their role as a trophic link between the microbial components in the food web and higher trophic levels (Posch et al. 1999; Simek et al. 2000). Several studies, however, emphasized that the potential food spectrum of ciliates is much larger than commonly believed, since, e.g., large-sized microzooplankton is not restricted to pico- and nanoplankton grazing (Smetacek 1981; Johansson et al. 2004; Tillmann 2004). This is especially true for non-loricate ciliates, which are known for their potential to capture and handle larger food particles with their feeding apparatus and to adapt their shape to that of the ingested particle, thus enabling the ingestion of cells that are as large as or even larger than their own size (Kahl 1932; Smetacek 1981; Montagnes et al. 1988; Jakobsen and Hansen 1997).

In our study, the transition phase was characterized by a low phytoplankton biomass dominated mainly by nanoflagellates in the elevated temperature regimes and diatoms in the +0° treatments, declining copepod abundances and a *L. oviformis* biomass that fluctuated. *L. oviformis* is considered as a selective feeder preying mainly upon bacterioplankton, heterotrophic nanoflagellates and small phytoplankton fractions and an optimum prey size of approximately 15% of their body length and prey items ranging from 2 to 15 μm (Jonsson 1986; Christaki et al. 1998). With its spherical diameter of 20 μm, *L. oviformis* might thus have most likely consumed prey items in the size range of bacterio- and nanoplankton. Unfortunately, data on bacteria and heterotrophic nanoflagellates (HNF) grazing during the pre-bloom period were not available; however, grazing on autotrophic picoplankton (APP) and nanoflagellates by ciliates could be ruled out. A consumption of bacterial and HNF fractions by *L. oviformis* seems thus most plausible. With the onset of the spring bloom, *L. oviformis* was displaced by *B. comatum*, and since data from the spring bloom period showed high grazing rates of ciliates preying upon bacteria, this might indicate a bacterivore feeding habit of *B. comatum*. Although this is in contrast to observations of *Balanion* spp. showing a preference for small cryptophytes with an optimal prey size of 8 μm (Jakobsen and Hansen 1997; Mueller et al. 1991; Weisse and Mueller 1998), a preference of *B. comatum* for picoplankton fractions seems likely due to its small size. Similar assumptions were drawn by Mueller (1989) on the potential prey items of a small Prostome in Lake Constance. In this context it can be speculated that, despite an overlap of trophic niches, both species, the cold-adapted *L. oviformis* and the warm-adapted *B. comatum*, are released from feeding competition due to their contrasting thermal requirements and their shifted occurrence during season.

In addition, a strong grazing pressure of ciliates on large phytoplankton size fractions was observed. Compared to the ciliates' body size (mainly >50 μm), large diatoms in the order of 30–180 μm (*Nitzschia acecularis*, *Navicula* sp. and *T. fasciculata*) seem to be exceptionally large prey items. However, this is a pattern commonly observed during phytoplankton blooms as, e.g., large Strobilidiid and Strombidiid ciliates have been shown to prey upon large diatoms or dinoflagellate species that are as large as or even larger than their own size (Kahl 1932; Smetacek 1981; Gifford 1985; Johansson et al. 2004). Our data on the grazing rates of large ciliate taxa support the findings of Strom et al. (2001) proposing that especially in highly productive, coastal areas, microzooplankton is one of the major heterotrophic components that directly consumes large-sized phytoplankton species, contributing to significant losses and a restructuring in phytoplankton biomass (Strom et al. 2001). Diatoms,

however, do not necessarily provide good food for microzooplankton, even if they are abundant, as some species are known for their grazing resistance. In this context, Irigoien et al. (2005) recently posed the hypothesis that phytoplankton blooms are a 'loophole in microzooplankton grazing' as blooming species are those that are capable of avoiding grazing by using special predation avoidance mechanisms (e.g., larger size, colony structure, and toxic components). In our mesocosm study, the bloom-forming diatom species were those that were consumed most by the zooplankton community, and a bloom formation of inedible phytoplankton could not be observed. However, predation avoidance mechanisms are often species-specific, and the degree varies in relation to biotic and abiotic conditions. The development of such 'loophole-like' bloom patterns can thus not be generalized. A good example is the consumption of *Chrysochromulina* spp. both by copepods and ciliates in our study. Some species of this genus are assumed to inhibit feeding by consumers due to chemical defence, especially during blooming events (Nielsen et al. 1990; John et al. 2002). In our mesocosms, a distinct bloom of *Chrysochromulina* spp. did not develop, and the grazing rates indicate that the species present in our study were a suitable food source for ciliates and copepods.

In our study, no clear temperature dependence of grazing was detected during the pre-spring bloom period, while during the spring bloom period, grazing rates were altered by temperature. Due to the contrasting results, the hypothesis that different grazing patterns and accelerated grazing rates might occur at higher temperatures was thus only confirmed to a limited extent. Multiple regression analyses on feeding rates of mesozooplankton published by Peters and Downing (1984) showed much clearer positive trends in response to temperature. Their findings are based on an extensive literature survey and the general statistical model aimed at indicating the extent of agreement among existing studies. Our small-scale approach using dilution experiments was, however, not powerful enough to evolve a clear trend for temperature-dependent grazing rates.

Grazing rates were at the upper end for copepods and at the lower end for ciliates when compared to a late summer situations in Norway (Nejstgaard et al. 2001; Sommer et al. 2005). However, it must be taken into account that during our experiment the cells grazed by ciliates were comprised mainly of large diatom cells with a much higher total biomass when compared to grazing rates that were calculated from nanoflagellate grazing in other mesocosm studies.

In our study, we found a strong dietary overlap in the food spectrum of ciliates and copepods as both groups showed a clear preference for the chains of *S. costatum*, large, single-celled diatoms, and *Chrysochromulina* sp. The chain-forming diatom *S. costatum* is known to be a suitable food source, especially for naupli and adult copepods (Olsson et al. 1992; Nejstgaard et al. 2001; Granéli and Turner 2002). Similar to our study, the results of Nejstgaard et al. (2001) also gave some indication for ciliate grazing on *S. costatum*.

In conclusion, the data presented here showed a clear temperature response of ciliate communities and their dynamics during winter–spring transition. Due to an acceleration of growth, high amplitudes of ciliate biomass and alterations of ciliate composition at elevated temperatures, our study points at potential asynchronies during the spring succession of plankton in the light of a winter warming scenario. At times when mesozooplankton grazing is still low, warming trends could open a loophole, especially for large-sized ciliate species, to evolve rapidly during spring bloom formation. The ability of large-sized ciliates to prey efficiently upon large phytoplankton fractions points at their potential to suppress phytoplankton blooms and furthermore to an enhanced resource competition between the heterotrophic components of the plankton due to a dietary overlap between ciliates and copepods.

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