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Temperature effects on phytoplankton diversity — The zooplankton link

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ABSTRACT

Recent climate warming is expected to affect phytoplankton biomass and diversity in marine ecosystems. Temperature can act directly on phytoplankton (e.g. rendering physiological processes) or indirectly due to changes in zooplankton grazing activity. We tested experimentally the impact of increased temperature on natural phytoplankton and zooplankton communities using indoor mesocosms and combined the results from different experimental years applying a meta-analytic approach. We divided our analysis into three bloom phases to define the strength of temperature and zooplankton impacts on phytoplankton in different stages of bloom development. Within the constraints of an experiment, our results suggest that increased temperature and zooplankton grazing have similar effects on phytoplankton diversity, which are most apparent in the post-bloom phase, when zooplankton abundances reach the highest values. Moreover, we observed changes in zooplankton composition in response to warming and initial conditions, which can additionally affect phytoplankton diversity, because changing feeding preferences of zooplankton can affect phytoplankton community structure. We conclude that phytoplankton diversity is indirectly affected by temperature in the post-bloom phase through changing zooplankton composition and grazing activities. Before and during the bloom, however, these effects seem to be overruled by temperature enhanced bottom-up processes such as phytoplankton nutrient uptake.

1. Introduction

Current global warming pits us with the necessity to understand and predict the impact of rising temperatures on ecosystems. During the last two decades, ecological sciences have therefore put more focus on this important issue, for example to gain insight into how temperature affects properties and functioning of food webs. Recent marine studies revealed that temperature impacts marine organisms on different trophic levels and alters species interactions between and within trophic levels (Kordas et al., 2011; O'Connor, 2009; O'Connor et al., 2011).

Phytoplankton generally forms the base of the pelagic food web and hence merits special attention. Although increased temperature speeds up metabolic processes of phytoplankton and might increase primary production in certain regions (Chavez et al., 2011; Doney, 2006), global phytoplankton decline with climate warming has been reported (Boyce et al., 2010; Moran et al., 2010). Two major processes were defined to be responsible for this decline: i) increasing resource limitations as a consequence of stronger water column stratification in the warmed ocean and ii) increasing top-down control of phytoplankton by zooplankton with rising temperature.

Phytoplankton diversity is also expected to be altered by climate change but this link is less well understood. Recent studies draw different pictures: whereas controlled laboratory experiments reported more rapid competitive exclusion resulting in a loss of species richness at higher temperature (Burgmer et al., 2011), field studies found an increasing number of species (richness) by immigrating warm-adapted species (Beaugrand et al., 2010). It seems, however, that irrespective of the net effect on richness, higher temperatures are strongly associated to higher species turnover (Hillebrand et al., 2012). Before species go extinct, rising temperatures will alter species dominance. Therefore, phytoplankton evenness (a measure of how equitable species are distributed within the community) is expected to be even more responsive to rising temperatures than richness (Hillebrand et al., 2008).

Mesozooplankton can strongly reduce the biomass of microalgae and affect phytoplankton diversity (richness and evenness). Generally zooplankton can reduce the number of phytoplankton species by increasing phytoplankton mortality or can increase richness by feeding on dominant algae taxa and thus releasing rare species from interspecific competition. With respect to evenness, consumers predominantly have a positive effect as they reduce the proportion of the dominant species (Hillebrand et al., 2007). However, zooplankton can also decrease phytoplankton evenness if the dominant algal species are not included in the zooplankton food spectrum. Thus, the consumer effect on phytoplankton evenness depends on consumer quantity as well as on its identity and feeding preferences. Moreover, it depends on the quality of phytoplankton itself in terms of nutritional value and essential compounds (Hall et al., 2007).

The impact of temperature on phytoplankton depends on its successional stage (Thackeray et al., 2008). Prior the peak in biomass, positive

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effects of temperature on the phytoplankton growth rates prevail (Reynolds, 2006). After the peak in biomass, loss rates exceed the growth rates and temperature acts on phytoplankton mainly indirectly modifying grazing activity of consumers. One can suspect that the phytoplankton diversity will change over entire time of the phytoplankton bloom and its response to increased temperature might also vary with the bloom development.

In this study we hypothesised i) that phytoplankton biomass and diversity responses to increased temperature differ depending on the bloom phase and ii) that the temperature effects are mediated by increased zooplankton grazing activity under warmer conditions. Previously published results have shown a decline of phytoplankton biomass and size at the bloom maximum in response to increased temperature and copepod density (Sommer and Lewandowska, 2011). However, the periods before and after the bloom maximum have not been analysed yet. Thus, our present analysis extends previous analyses of the mesocosm experiments not only by its topical focus (on diversity) but also by paying attention to different phases of the bloom development.

2. Material and methods

2.1. Experimental setup and laboratory techniques

Eight (experiments 2006 and 2007) or twelve (experiments 2008 and 2009) mesocosms (1400 L volume, 1 m depth) were set up in temperature regulated climate rooms. Sea water containing the natural late winter plankton community (phytoplankton, bacteria and protozoa) from the Kiel Fjord, Baltic Sea, was pumped into a distribution tank and gravitationally transferred to the experimental units. The mesocosms were filled simultaneously to assure homogenous distribution of plankton. Mesozooplankton was added from net catches at appropriate concentrations for each experiment (Table 1) as it did not pass through the pumping system. The water column was gently mixed by a propeller. Temperature and light conditions simulated natural daily and seasonal patterns. There were two temperature scenarios tested in the experiments 2008 and 2009: a baseline corresponding to the decadal mean (1993–2002) of sea surface temperature in Kiel Fjord starting from 15th of February ($\Delta T = 0$ °C) and a warming scenario where the temperature was elevated 6 °C above the baseline ($\Delta T = 6$ °C) according to the most drastic warming scenario predicted by the Intergovernmental Panel on Climate Change (IPCC, 2007). In the experiment 2008 the factor temperature was combined with the factor light intensity with three levels of the initial surface irradiance (4.8, 5.7 and 6.5 mol quanta m^{-2} d^{-1}) and in the experiment 2009 the factor temperature was combined with the factor initial copepod density with three start abundances (1.5, 4 and 10 ind. L^{-1}), resulting in two replicates of each factor combination in each experiment (Lewandowska and Sommer, 2010; Sommer and Lewandowska, 2011). In the experiments 2006 and 2007 four temperature regimes: $\Delta T = 0$ °C, $\Delta T = 2$ °C, $\Delta T = 4$ °C and $\Delta T = 6$ °C were tested whereby each regime was replicated twice (Sommer and Lengfellner, 2008). For straight comparison between experiments we used only data for $\Delta T = 0$ °C and $\Delta T = 6$ °C.

Phytoplankton was sampled three times per week, preserved with Lugol's iodine and counted using the inverted microscope technique according to Utermöhl (1958) for species >5 μm. Flow cytometry technique (FACScalibur, Becton Dickinson) was used to count smaller species (Sommer and Lengfellner, 2008). Phytoplankton biomass was defined as carbon content calculated from cell volumes (Menden-Deuer et al., 2000) after an approximation of cell volumes to geometric standards (Hillebrand et al., 1999). Zooplankton was sampled once a week with a net (12 cm diameter, 64 μm mesh size), shock frozen with liquid nitrogen (experiments 2006 and 2007) or fixed with Lugol's iodine (experiments 2008 and 2009) and counted with a stereomicroscope. Copepods were specified to the genus level, *Temora* sp. and rare *Eurytemora* sp., as well as *Pseudocalanus* sp. and rare *Paracalanus* sp. were paired together, because their early copepodid stages are difficult to distinguish. Copepod biomass was estimated as a carbon content using species and stage specific conversion factors (Lengfellner, 2008). More details on the experimental setup and sampling procedure for each experiment can be found elsewhere (Lewandowska and Sommer, 2010; Sommer and Lengfellner, 2008; Sommer and Lewandowska, 2011).

2.2. Diversity parameters and statistics

We defined three phases of the phytoplankton bloom and performed separate analyses for each of them. The period before the bloom was characterised by the mean biomass values from the beginning of the experiment to the phytoplankton total biomass maximum and represents the phase of exponential growth. Bloom period was characterised as a point of the phytoplankton total biomass maximum (a proxy for phytoplankton carrying capacity). The post-bloom phase was characterised by the mean values from the phytoplankton total biomass maximum to the end of the experiment and represents the phase, in which loss processes overrule phytoplankton growth.

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

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

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

We calculated the magnitude of the effect of temperature on phytoplankton richness, evenness and biomass for each experiment, using log response ratios (LRR):

$$LRR = \ln \frac{X_{6^\circ C}}{X_{0^\circ C}}$$

where $X_{6\,^\circ C}$ is phytoplankton richness, evenness or biomass under high temperature ($\Delta T = 6$ °C) and $X_{0\,^\circ C}$ is phytoplankton richness, evenness or biomass under low temperature ($\Delta T = 0$ °C) accordingly.

Table 1
Experimental design of mesocosm experiments. Temperature elevation (ΔT), initial light intensities (I), initial copepod densities (ICD) and dominant copepod species.

Experiment	ΔT (°C)	I (mol quanta m^{-2} d^{-1})	ICD (ind. L^{-1})	Bloom forming algae (% phytoplankton biomass)	References
2009	0, 6	5.7	1.5, 4, 10 (*Acartia*)	Diatoms (93 ± 6% SD)	Sommer and Lewandowska, 2011
2008	0, 6	4.8, 5.7, 6.5	8 (*Oithona*)	Diatoms (97 ± 6% SD)	Lewandowska and Sommer, 2010
2007	0, 2, 4, 6	1.9	4.5 (*Pseudocalanus*)	Silicoflagellate (42 ± 38% SD)	Sommer and Lengfellner, 2008
2006	0, 2, 4, 6	3.9	8.5 (*Pseudocalanus*)	diatoms (95 ± 2% SD)	