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The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach

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Abstract The response of the Baltic Sea spring bloom was studied in mesocosm experiments, where temperatures were elevated up to 6°C above the present-day sea surface temperature of the spring bloom season. Four of the seven experiments were carried out at different light levels (32–202 Wh m^{-2} at the start of the experiments) in the different experimental years. In one further experiment, the factors light and temperature were crossed, and in one experiment, the factors density of overwintering zooplankton and temperature were crossed. Overall, there was a slight temporal acceleration of the phytoplankton spring bloom, a decline of peak biomass and a decline of mean cell size with warming. The temperature influence on phytoplankton bloom timing, biomass and size structure was qualitatively highly robust across experiments. The dependence of timing, biomass, and size structure on initial conditions was tested by multiple regression analysis of the y-temperature regressions with the candidate independent variables initial light, initial phytoplankton biomass, initial microzooplankton biomass, and initial mesozooplankton (=copepod) biomass. The bloom timing predicted for mean temperatures (5.28°C) depended on light. The peak biomass showed a strong positive dependence on light and a weaker negative dependence on initial copepod density. Mean phytoplankton cell size predicted for the mean temperature responded positively to light and negatively to copepod density. The anticipated mismatch between phytoplankton supply and food demand by newly hatched copepod nauplii occurred only under the combination of low light and warm temperatures. The analysis presented here confirms earlier conclusions about temperature responses that are based on subsets of our experimental series. However, only the comprehensive analysis across all experiments highlights the importance of the factor light.

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Introduction

Phytoplankton accounts for about one half of global primary productivity and forms the trophic basis of the pelagic food web and consequently for pelagic fisheries. Therefore, it is no surprise that the response of phytoplankton to climate warming has become one of the foci of global change ecology. Recently, Boyce et al. (2010) reported a global decline of phytoplankton biomass in response to global warming. Moran et al. (2010) have reported a decline of overall phytoplankton biomass in the North Atlantic Ocean, while the biomass of pico-phytoplankton (<2 μm) increased. This trend toward smaller body size under warming conditions has also been reported for other groups of organisms (Daufresne et al. 2009), whereas its universal applicability is still controversial (Gardner et al. 2011). A further line of research has focused on the effects of climate warming on the seasonal wax and wane of phytoplankton, often with an emphasis on the spring bloom. The spring bloom is a repeated, annual feature of phytoplankton

seasonality in fresh and marine waters. In many cases, it is the most important annual pulse of primary production in the pelagic system and the dominant input of energy into the food web. In line with similar predictions for other ecosystems (e.g., Walther et al. 2002; Cleland et al. 2007), an earlier onset of the spring bloom under warmer conditions has been reported by several studies (Weyhenmeyer et al. 1999; Gerten and Adrian 2001; Weyhenmeyer 2001; Edwards et al. 2002; Stenseth et al. 2002), whereas also retardations of the spring bloom (Wiltshire and Manly 2004) or high interannual variations in timing without a strong relationship to the warming trend after 1975 (Wiltshire et al. 2008) have been reported. Wiltshire and Manly (2004) explained the reversal of the usual response to warming by zooplankton grazing. If overwintering zooplankton are more active under warmer conditions, phytoplankton might need more light and a longer day length to achieve growth rates exceeding the grazing losses. In order to disentangle the effects of temperature, light, and grazing, we have conducted a series of mesocosm experiments with natural late winter plankton from the western Baltic Sea during the period 2005–2009. While an analysis of individual experiments (Aberle et al. 2007; Hoppe et al. 2008; Sommer et al. 2007; Sommer and Lewandowska 2011; Wohlers et al. 2009) or a comparative analysis of some of the experiments (Sommer and Lengfellner 2008) have been published, a synthesis analysis of all experiments has been reserved for this special issue of Marine Biology. This article will focus on an overarching analysis of aggregated phytoplankton responses (biomass, bloom timing, size structure) to warming, light and zooplankton. In addition we will analyze the potential impact of different starting conditions in the different years caused by interannual variations of the natural plankton communities.

The mechanistic basis for our working hypotheses presented below lies in the widespread observation that heterotrophic processes are more strongly accelerated by warming than autotrophic ones: Light limited photosynthesis is insensitive to temperature above 0°C (Tilzer et al. 1986) and the Q_{10}-value (factor, by which a rate is increased by 10°C warming) of light-saturated phytoplankton growth (1.88, Eppley 1972) is lower than most Q_{10}-values reported for heterotrophic processes [microalgal respiration, 2.6–5.2 (Hancke and Glud 2004); zooplankton respiration, 1.8–6.0 (Ivleva 1980; Ikeda et al. 2001, Isla et al. 2008); zooplankton filtration rates, 2–3 (Prosser 1973); initial slope of *Pseudocalanus,* an overwintering copepod of the Baltic Sea, functional response, 5.4 (Isla et al. 2008); bacterial respiration, 3.3 (Sand-Jensen et al. 2007)]. In addition, an attempt was made to apply Cushing's (1990) match–mismatch hypothesis to the trophic link phytoplankton–copepod nauplii. A change in the relative timing of phytoplankton food and naupliar food demand might result, if first feeding of nauplii (2nd or 3rd instar) occurs at a time of low food availability. This risk emerges if hatching of nauplii produced by the overwintering generation of copepods is more controlled by maternal conditions and temperature signals than by actual feeding conditions. Nauplii are the bottleneck in the food transfer between phytoplankton and copepods, because they are far more sensitive to starvation than later developmental stages. Our specific working hypotheses about the effect of temperature, light, and overwintering copepods on the spring peak of phytoplankton were as follows:

1. Magnitude of the phytoplankton spring peak
   a. Warming will reduce phytoplankton peak biomass because of increased heterotrophic losses.
   b. More light will increase phytoplankton peak biomass because of enhanced autotrophic production.
   c. More overwintering copepods will lead to a lower phytoplankton peak biomass because of enhanced grazing.
2. Mean phytoplankton cell size
   a. Warming will lead to a reduced cell size because of preferential grazing of copepods on large algae.
   b. Less light will lead to a smaller cell size, because the selective advantage of smaller size (higher optical cross-section : volume ratio) increases with increasing light limitation (Reynolds 1989).
   c. More copepods will lead to a smaller mean cell size because of preferential grazing on the larger algae.
3. Timing of the phytoplankton spring peak:
   a. Warming will cause an earlier spring peak because of higher phytoplankton growth rates.
   b. More light will cause an earlier spring peak because of higher phytoplankton growth rates.
   c. More overwintering copepods will lead to an earlier spring peak because the break-even point between declining phytoplankton growth rates (resource limitation) and grazing rates will be reached earlier.
4. Temporal mismatch in the phytoplankton-nauplii trophic link:
   a. A negative offset in the timing of phytoplankton and nauplii (nauplii too early) is expected under conditions of low light (late phytoplankton growth) and warm temperature (early hatching of nauplii).
   b. A positive offset (nauplii too late) is expected under conditions of high light (early phytoplankton growth) and cold temperature (late hatching of nauplii).

We will not provide an analysis of primary production to the experimental conditions here, because such an analysis is being published elsewhere (Lewandowska et al. 2011).

Methods

In this article, we will only provide a brief overview about the experimental methodology (Table 1), because the details have been published previously (Lewandowska and Sommer 2010; Sommer et al. 2007; Sommer and Lewandowska 2011).

Experimental design

The experiments consisted of 8 (2005–2007) or 12 (2008–2009) 1.4 m^3-mesocosms in temperature controlled rooms of the GEOMAR at Kiel, Germany. During the first 4 experiments (2005, 2006-1, 2006-2, 2007), 4 temperature levels were applied within each experiment and light supply was similar among treatments, but varied between experiments. The experiment 2008 consisted of a factorial combination of two temperature levels and 3 light levels, the experiment 2009 of a factorial combination of two temperature levels and 3 mesozooplankton (copepod) levels. Mesocosms were filled with near surface water from the Kiel Fjord, containing the natural assemblage of phytoplankton, heterotrophic protists and bacteria. Mesozooplankton (mainly copepods) were added from net catches. Initially, it was planned to add the same amount of mesozooplankton each year (except 2009), but for practical reasons, the target density could not be achieved in all years, thus adding a further dimension of interannual variability in the experimental conditions. The temperature regime was programmed according to the decadal mean 1993–2002 of local sea surface temperatures of the spring–winter transition and elevated by 0, 2, 4, and 6°C for the different treatments. There were some temperature differences between replicate mesocosms, therefore actual temperatures instead of planned ones are used for data analysis. Similarly, a seasonal pattern of light supply was employed. Irradiance was calculated according to astronomic models (Brock 1981) and dimmed to a defined fraction for each experiment (3 levels in 2008, 1 level in each other experiment) in order to account for clouds and underwater light attenuation. Seasonal light and temperature programs started on a virtual 4 February in the experiments 2005-7 and on a virtual 15 February in the experiments 2008 and 2009. Actual starting dates differed from that. Experiments lasted for 5½ to 12 weeks, well beyond the peak of phytoplankton biomass. However, after the phytoplankton peak, communities in the mesocosms began to denature because of wall growth. Therefore, the analysis presented here is restricted to the data until the peak was reached.

Samples

Phytoplankton samples were taken 3 times per week, zooplankton samples once per week. Phytoplankton >5 µm and microzooplankton were counted microscopically, cell volumes were estimated after microscopic measurements (Hillebrand et al. 1999) and converted to carbon biomass according to Menden-Deuer and Lessard (2000) and Putt and Stoecker (1989). Abundance and biomass of phytoplankton <5 µm was measured by flow-cytometry (FACScalibur, Becton–Dickinson), and volume calculation was done assuming a spherical shape. For calculating biomass and mean cell size, the microscopic and the flow cytometric data sets were merged. Zooplankton samples were taken once per week by a plankton net (64 µm mesh size), but in

Table 1 Summary of experimental conditions

Exp	Δt	L	C	M	B_0	S_0	NO_3	NH_4	PO_4	Si	Progr. start	Actual start
2005	0, 2, 4, 6	32.27	16.24	0.09	17.16	6.25	21.5	2.2	0.8	24.5	04.02	04.02
2006-1	0, 2, 4, 6	201.6	5.47	1.284	3.58	3.24	21.1	5.6	0.9	20.4	04.02	06.01
2006-2	0, 2, 4, 6	129.1	9.13	0.124	74.85	5.71	8.7	1.7	0.7	18.9	04.02	17.02
2007	0, 2, 4, 6	64.54	4.03	1.97	9.56	1.46	31.9	4.4	1.1	32.5	04.02	17.02
2008-hL	0, 6	381	8.5	0.963	6.0	51.28	10.6	1.3	0.9	30.2	15.02	06.02
2008-mL	0, 6	317.6	7.14	0.938	6.34	51.36	10.6	1.3	0.9	30.2	15.02	06.02
2008-lL	0, 6	265.2	7.53	0.908	5.88	53.39	10.6	1.3	0.9	30.2	15.02	06.02
2009-lC	0, 6	317.6	1.38	3.785	37.95	3.89	13.7	3.0	0.9	30.5	15.02	09.01
2009-mC	0, 6	317.6	3.91	7.87	38.61	3.94	13.7	3.0	0.9	30.5	15.02	09.01
2009-hC	0, 6	317.6	11.11	11.73	40.1	4.02	13.7	3.0	0.9	30.5	15.02	09.01

Δt planned elevation of temperature above seasonal pattern of sea surface temperature mean 1993–2002 (°C), L daily light dose at start of experiments (Wh m^{-2} PAR), C copepod abundance at start (ind l^{-1}), M microzooplankton biomass at start (µg C l^{-1}), B_0 phytoplankton biomass at start, S_0 mean phytoplankton cell size at start (pg $cell^{-1}$), *nutrients* dissolved concentration (µmol l^{-1})

this article, we will focus on copepod nauplii because of their relevance for the match–mismatch hypothesis.

Summary analysis

Time series of phytoplankton variables were smoothed by 3-pt running means to reduce the influence of short-term scatter along temporal trends. Response variables were as follows:

- Total phytoplankton biomass at the biomass peak (B; in µg C l^{-1})
- Duration from the start of the experiments to the peak of phytoplankton biomass (D; in days)
- Mean phytoplankton cell size at the biomass peak, calculated by dividing total biomass by total cell number (S; in pg $cell^{-1}$)
- Temporal offset between the timing of the phytoplankton biomass peak (D_P) and the timing of the peak of naupliar biomass (D_N) ($O = D_N - D_P$; in days)

Independent variables were as follows:

- Temperature (t; in °C)
- Light at the start of the experiment, expressed as daily light dose (L; in Wh m^{-2})
- Copepod abundance at the start of the experiments, only adults and copepodites, nauplii not included (C; in ind l^{-1})
- Microzooplankton biomass at the start of the experiments (M in µg C l^{-1})
- Phytoplankton biomass at the start of the experiments (B_0; in µg C l^{-1})
- Mean phytoplankton cell size at the start of the experiments (S_0; in pg $cell^{-1}$)

First, the single experiments were analyzed for the response to temperature. In the experiments 2008 and 2009, separate analyses were performed for the different light (2008) and zooplankton (2009) levels (hereafter called sub-experiments). The analysis was performed by regression analysis according to the models $y = a + b(t - 5.28)$ for D or $\ln y = a + b(t - 5.28)$ for biomass and cell size because log-transformation resulted in linear plots. $t - 5.28$ was taken instead of t, because this way the height of the regression line (a) was characterized by the response to the grand mean of the experimental temperatures.

The comparative analysis across all experiments was performed using the values of a and b, denoted with a subscript for the appropriate dependent variable. As a first step, a multiple regression with stepwise variable selection (backward procedure, F-to-remove = 4) with the candidate independent variables $\ln L$, $\ln C$, $\ln M$, $\ln B_0$, $\ln S_0$ was performed.

If the multiple regression indicated a dominant influence of light, also a saturation curve of the Michaelis–Menten-type

$$y = (y_{\max} x)(k + x)^{-1}$$

was fitted to the data. This was done by a double reciprocal regression analysis of the type

$$y^{-1} = a + bx^{-1}$$

from which the asymptotic value of y could be calculated as $y_{\max} = 1/a$ and the half-saturation constant as $k = by_{\max}$.

Results

Phytoplankton peak biomass

Figure 1 shows the temporal pattern of phytoplankton for the extreme conditions (lowest and highest temperature, lowest and highest light). The magnitude of the biomass peak increased with light and decreased with temperature. The analysis of the entire data set confirmed this response. Phytoplankton peak biomass responded negatively to temperature in all experiments. Regressions were significant ($p < 0.05$), except for the medium and high-copepod sub-experiments in 2009 (Table 2, Fig. 2). However, a previous multiple regression analysis (Sommer and Lewandowska 2011) with temperature and copepods as independent variables had shown a significantly negative temperature response and a significantly negative response to initial copepod density.

The final model of the multiple regression analysis showed a significant positive response of a_B to light and a significant Ó:

$$a_B = 0.90 \pm 0.52 + 1.11 \pm 0.075 \ln L - 0.36 \pm 0.09 \ln C + 0.15 \pm 0.06 \ln B_0$$

$$r^2 = 0.97;\ p_L < 0.0001;\ p_C = 0.0072;\ p_{B_0} = 0.034;\ p_{\text{model}} < 0.0001$$

while there was no significant influence of the other independent variables. The Michaelis–Menten-model with light as the only independent variable provided a similarly good fit (Fig. 3):

$$a_B^{-1} = 0.13 \pm 0.003 + 3.71 \pm 0.244\,\text{L}^{-1};\quad r^2 = 0.97;\ p < 0.0001$$

which permits the calculation of a asymptotic biomass of ca. 2,200 µg C l^{-1}.

No significant model could be found for the slopes of the biomass–temperature regression, which was no surprise,

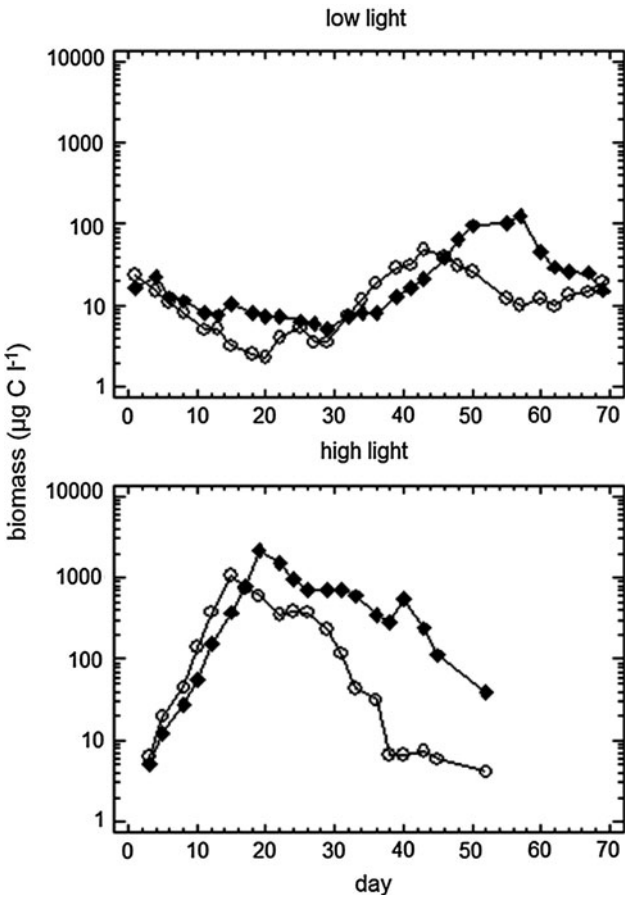

Fig. 1 Examples for the time course of phytoplankton biomass in µg C l^{-1}. *Top* low light experiment 2005, *bottom* highest light level of the experiment 2008, *full diamonds* coldest mesocosm, *empty diamonds* warmest mesocosm

because slopes were relatively uniform, except for the much steeper slope in the 2007 experiment (Fig. 2). For the other experiments, the mean of the slope equals −0.115 ± 0.029 (SD) which translates to a ca. 11% decrease in biomass per °C.

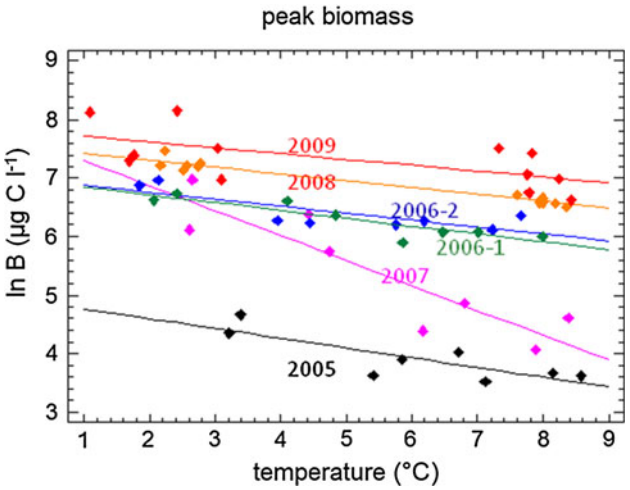

Fig. 2 Regression of ln phytoplankton biomass during the spring peak (µg C l^{-1}) versus temperature for the different experiments shown by different *color codes*. Contrary to Table 2, the subexperiments of 2008 and of 2009 were pooled

Phytoplankton cell size

Mean phytoplankton cell size at the biomass peak responded negatively to temperature, all regressions being significant at $p < 0.05$, except for the high-light subexperiment in 2008 and the high-copepod sub-experiment in 2009 (Table 3, Fig. 4). Slope and elevation of the regression lines varied considerable between experiments. The cell size predicted for 5.28°C responded positively to light and negatively to copepod density:

$$a_S = -0.575 \pm 0.64 + 0.763 \pm 0.099 \ln L - 0.261 \pm 0.123 \ln C; r^2 = 0.91; p_L = 0.001; p_c = 0.071, p_{\text{model}} = 0.0001.$$

The slopes of the size–temperature regressions (b_s) responded positively to light and initial phytoplankton

Table 2 Log phytoplankton mean biomass (ln B in µg C l^{-1}; 3-pt running mean) as a function of experimental temperature (t in °C) analyzed according to the model $y = a + b(t + 5.28)$, where 5.28 is the grand mean of all temperatures

Exp	a	b	r^2	p_a	p_b	n
2005	4.05 ± 0.097	−0.167 ± 0.048	0.67	<0.0001	0.013	8
2006-1	6.27 ± 0.055	−0.135 ± 0.027	0.80	<0.0001	0.0026	8
2006-2	6.37 ± 0.074	−0.118 ± 0.035	0.65	<0.0001	0.016	8
2007	5.47 ± 0.18	−0.426 ± 0.085	0.81	<0.0001	0.0024	8
2008-hL	6.98 ± 0.07	−0.116 ± 0.023	0.93	0.0001	0.038	4
2008-mL	6.88 ± 0.025	−0.109 ± 0.009	0.99	<0.0001	0.0071	4
2008-lL	6.91 ± 0.019	−0.125 ± 0.007	0.99	<0.0001	0.0028	4
2009-lC	7.74 ± 0.044	−0.111 ± 0.015	0.97	<0.0001	0.017	4
2009-mC	7.22 ± 0.075	−0.051 ± 0.026	0.73	0.0001	0.14	4
2009-hC	6.93 ± 0.097	−0.094 ± 0.027	0.86	0.0001	0.073	4

biomass, which in this case means a less negative slope at higher levels of the independent variable:

$$b_s = -1.506 \pm 0.177 + 0.22 \pm 0.031 \ln L + 0.054 \pm 0.024 \ln B_0; r^2 = 0.85; p_L = 0.0002; p_{B_0} = 0.059; p_{\text{model}} = 0.0005.$$

Timing of spring peak

The duration until the peak of phytoplankton biomass was reached responded negatively to temperature throughout all experiments (Table 4, Fig. 5), though four of the regressions did not meet the $p < 0.05$ significance criterion. The predicted duration at 5.28°C (a_D) was only related to light, as shown by the fact that all other independent variables were eliminated in the stepwise selection procedure. The Michaelis–Menten fit was performed by taking the linear value of D as dependent variable, that is, by assuming that D^{-1} should show a saturating response to light:

$$a_D = 10.02 \pm 2.87 + 1437.7 \pm 247.4\,L^{-1}; \quad r^2 = 0.81; p = 0.0004$$

which indicates a duration of ca. 10 days at saturating light levels and mean temperatures.

The slopes of the duration–temperature regressions showed no relationship to the candidate independent variables and varied little between experiments. The values indicated an advancement of the spring peak by 1.01 ± 0.45 (SD) days °C^{-1}.

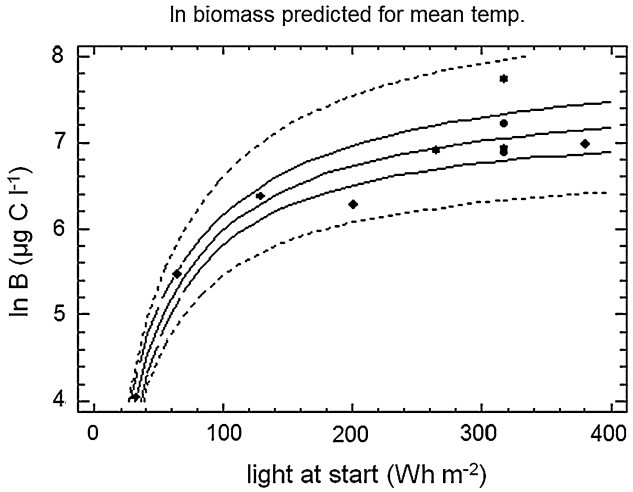

Fig. 3 Double reciprocal regression of ln phytoplankton biomass (µg C l^{-1}) predicted for 5.28°C (grand mean temperatures) versus light at the start of the experiments (Wh m^{-2}). *Central line* regression, *inner lines* 95% confidence limits for regression, *outer lines* 95% prediction limits for individual points

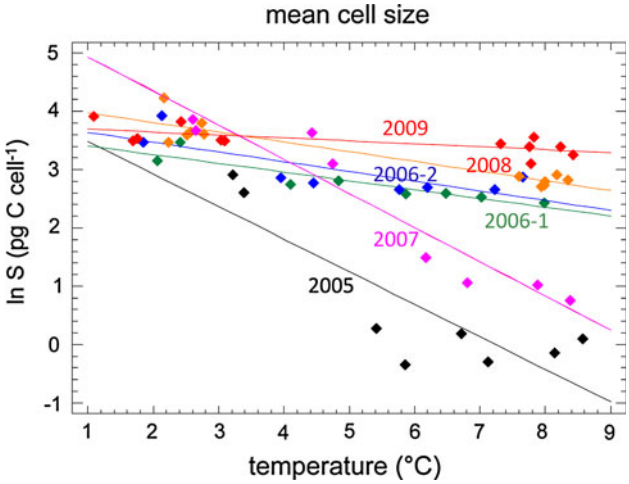

Fig. 4 Regression of ln phytoplankton mean cell size during the spring peak (pg C cell^{-1}) versus temperature for the different experiments shown by different *color codes*. Contrary to Table 3, the subexperiments of 2008 and of 2009 were pooled

Table 3 Mean log cell (ln S in pg C cell^{-1}) of phytoplankton at the spring peak (D in days) as a function of experimental temperature (t in °C) analyzed according to the model $y = a + b(t + 5.28)$, where 5.28 is the grand mean of all temperatures

Exp	a	b	r^2	p_a	p_b	n
2005	1.094 ± 0.289	−0,558 ± 0.143	0.72	0.009	0.008	8
2006-1	2.766 ± 0.053	−0.151 ± 0.026	0.85	<0.0001	0.0012	8
2006-2	2.926 ± 0.109	−0.166 ± 0.052	0.63	<0.0001	0.019	8
2007	2.428 ± 0.156	−0.585 ± 0.075	0.91	<0.0001	0.0002	8
2008-hL	3.279 ± 0.191	−0.187 ± 0.068	0.79	0.0034	0.11	4
2008-mL	3.263 ± 0.087	−0.161 ± 0.032	0.93	0.0067	0.037	4
2008-lL	3.24 ± 0.019	−0.149 ± 0.007	0.995	<0.0001	0.0022	4
2009-lC	3.65 ± 0.037	−0.062 ± 0.012	0.93	0.0001	0.038	4
2009-mC	3.45 ± 0.011	−0.02 ± 0.004	0.92	<0.0001	0.039	4
2009-hC	3.35 ± 0.056	−0.056 ± 0.017	0.84	0.0002	0.084	4

Table 4 Duration until phytoplankton peak (D in days) as a function of experimental temperature (t in °C) analyzed according to the model $y = a + b(t + 5.28)$, where 5.28 is the grand mean of all temperatures

Exp	a	b	r^2	p_a	p_b	n
2005	51.62 ± 0.97	−1.608 ± 0.748	0.67	<0.0001	0.075	8
2006-1	14.97 ± 0.56	−1.506 ± 0.877	0.83	<0.0001	0.0016	8
2006-2	7.91 ± 0.59	−1.238 ± 0.285	0.76	0.0001	0.0049	8
2007	44.08 ± 0.88	−1.12 ± 0.414	0.55	<0.0001	0.034	8
2008-hL	16.12 ± 0.89	−0.454 ± 0.316	0.51	0.03	0.286	4
2008-mL	16.28 ± 0.90	−0.463 ± 0.324	0.50	0.03	0.295	4
2008-lL	20.05 ± 0.036	−0.362 ± 0.013	0.997	<0.0001	0.013	4
2009-lC	13.99 ± 0.309	−0.835 ± 0.102	0.97	0.0005	0.015	4
2009-mC	14.37 ± 0.362	−1.259 ± 0.127	0.98	0.006	0.010	4
2009-hC	13.22 ± 0.88	−1.206 ± 0.304	0.89	0.0044	0.058	4

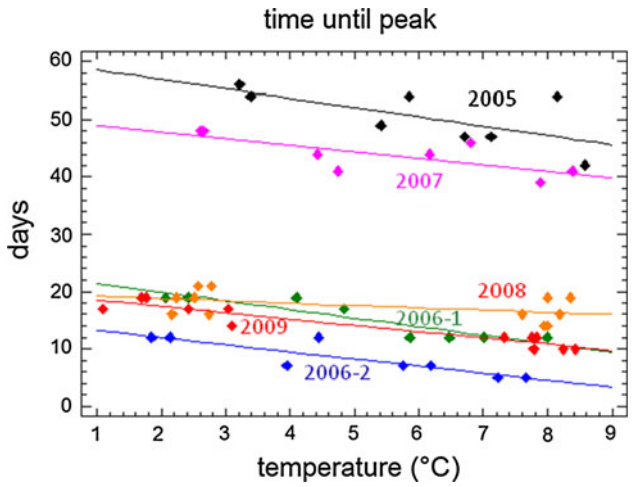

Fig. 5 Regression of the time from the start of experiments until the phytoplankton biomass peak (days) versus temperature for the different experiments shown by different *color codes*. Contrary to Table 4, the subexperiments of 2008 and of 2009 were pooled

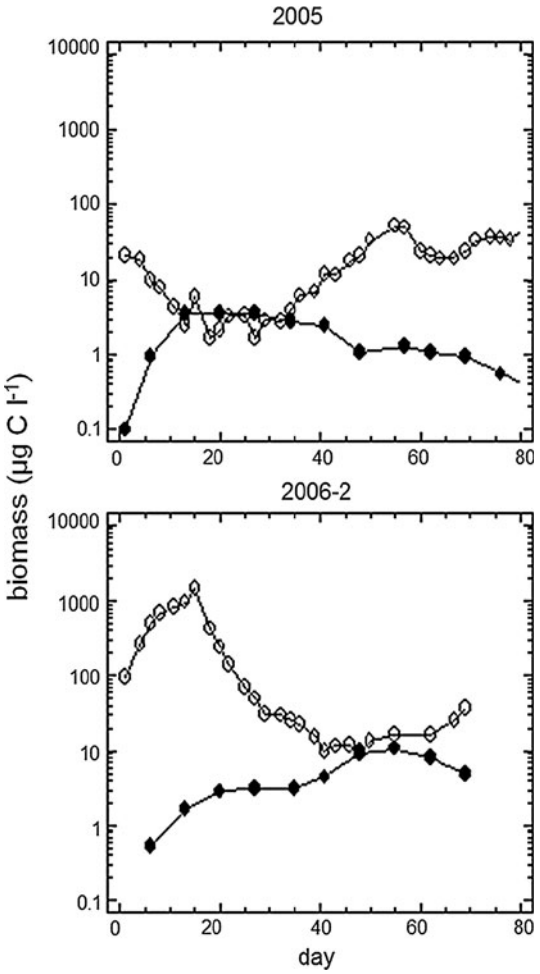

Fig. 6 Examples for a temporal mismatch between phytoplankton and nauplii biomass (µg C l^{-1}), *top* warmest mesocosm of the 2005 experiment (nauplii too early) and coldest mesocosms of the 2006-2 experiment (nauplii too late), *open symbols* phytoplankton, *full symbols* nauplii

Temporal offset between nauplii and phytoplankton

Figure 6 shows two extreme cases of a negative and a positive offset. In the low-light experiment 2005, nauplii hatched before the phytoplankton biomass peak in the warm mesocosms. This was due to strong acceleration of naupliar hatching by temperature (9 days $°C^{-1}$; Sommer et al. 2007) which strongly exceeded the acceleration of the phytoplankton peak. In the experiment 2006-2, phytoplankton bloomed very early and well before the nauplii hatched in the cold mesocoms. However, no such extreme case of positive offset was found in the experiments with even higher irradiance. The temporal offset responded negatively to temperature in all experiments except for the high-light sub-experiment in 2008, where the response was not significantly different from zero (Table 5). In the experiment 2006-1, the relationship between the temporal density of nauplii-sampling and experimental duration was insufficient to warrant such an analysis.

Table 5 Temporal offset between phytoplankton and naupliar biomass peak (O in days) as a function of experimental temperature (t in °C) analyzed according to the model $y = a + b(t + 5.28)$, where 5.28 is the grand mean of all temperatures

Exp	a	b	r^2	p_a	p_b	n
2005	−9.85 ± 4.45	−8.41 ± 2.2	0.71	0.069	0.0088	8
2006-1	Insufficient temporal resolution of nauplii					
2006-2	13.13 ± 1.78	−3.96 ± 0.86	0.78	0.0003	0.0036	8
2007	5.73 ± 1.6	−1.96 ± 0.77	0.52	0.012	0.043	8
2008-hL	21.51 ± 0.86	−0.86 ± 2.17	0.07	0.073	0.73	4
2008-mL	23.67 ± 0.9	−2.78 ± 0.33	0.97	0.0015	0.014	4
2008-lL	27.33 ± 1.41	−4.12 ± 0.51	0.97	0.026	0.015	4
2009-lC	7.77 ± 0.74	−2.00 ± 0.25	0.97	0.009	0.015	4
2009-mC	8.83 ± 1.28	−1.66 ± 0.45	0.87	0.021	0.066	4
2009-hC	10.22 ± 1.86	−1.68 ± 0.67	0.77	0.032	0.12	4

The offset predicted for the mean temperature responded positively to light

$$a_O = -37.8 \pm 7.3 + 9.54 \pm 3.3 \ln L;\ r^2 = 0.48;$$
$$p = 0.0223$$

while the slope responded negatively to initial copepod density

$$b_O = -3.26 \pm 0.53 + 1.04 \pm 0.33 \ln C;\ r^2 = 0.52;$$
$$p = 0.018.$$

We also calculated the "optimal temperature," that is, the temperature where zero offset would be predicted from the equations in Table 5. The optimal temperature showed no relationship to any of the candidate independent variables.

Discussion

Phytoplankton peak biomass

Hypothesis 1a (reduction by warming), 1b (increase by more light), and 1c (reduction by more copepods) were confirmed. The support for the light hypothesis is no surprise, because of the light's role as limiting resource for photo-autotrophic growth. For the temperature effect, we can exclude a simple physiological explanation, that is, warming exceeding temperature optima. The experiments were conducted in a temperature range well below the temperature optimum for most phytoplankton species, except some obligate Antarctic ones (Jacques 1983). The physiological explanation can also be excluded, because a metaanalysis of primary production : biomass ratios in our experiments showed a positive temperature effect (Lewandowska et al. 2011), that is, biomass should have grown faster under warmer conditions in the absence of losses. Therefore, the reduced biomass accumulation under higher temperatures has to be explained by intensified grazing or other removal processes of primary production (e.g., cell lysis, sinking). This effect was also found in other locations, for example, in coastal ecosystems of South Carolina (O'Connor et al. 2009) and in the northern Baltic Sea (Müren et al. 2005). Copepod grazing as a component of the heterotrophic losses also had a negative effect on phytoplankton peak biomass, but the importance of this factor should not be overestimated: The multiple regression with three variables (ln L, ln C, ln B_0) explained just as much of the total variance as the Michaelis–Menten-model with light alone ($r^2 = 0.97$). A strong copepod effect on total phytoplankton biomass could not be expected a priori, because copepods are not broad-spectrum filter feeders like *Daphnia* spp. in lakes. Instead, they pick food particles quite selectively from a size range from ca. 5–10 µm to several 100 µm length. By feeding also on heterotrophic protists, they release phytoplankton below their food size spectrum from protist predation thus diminishing the impact on total phytoplankton biomass (Sommer and Sommer 2006). Thus, the observed biomass effect depends on the dominance of medium-sized phytoplankton, often diatoms, which is common for the spring bloom in temperate and boreal seas (Smetacek 1999; Tilstone et al. 2000; Wasmund et al. 2008; Wiltshire et al. 2008). In other seasons, small phytoplankton may benefit from the suppression of an intermediate trophic level (often ciliates) and may compensate or even over-compensate the losses of diatoms (Stibor et al. 2004; Sommer and Sommer 2006).

Boyce et al. (2010) have tentatively explained the global decline of oceanic chlorophyll as a proxy of phytoplankton biomass by strengthened stratification and a thereby reduced vertical nutrient transport to the surface ocean, while not considering a potentially changed balance between autotrophic and heterotrophic processes, which we show to have an important impact on the phytoplankton standing biomass.

Phytoplankton cell size

Hypotheses 2a (size decrease by warming), 2b (size increase by more light), and 2c (size decrease by more copepods) were confirmed by the response of a_S to temperature, light, and copepods. A decrease in average cell size is the typical footprint of copepod grazing (Sommer and Sommer 2006), except for the rare cases where biomass is dominated by algae being too large for ingestion (e.g., *Coscinodiscus* spp.). Under such circumstances, removal of the medium to large, but not extremely large species shifts mean size upwards, but this was not the case in our experiments. It seems plausible that the temperature effect was due to increased copepod per capita grazing rates at higher temperatures, because direct physiological temperature effects predicted by the "temperature size rule" (Atkinson et al. 2003) are far too small to explain the observed effect (2.5% shrinkage per °C). Copepod grazing as the main driver of the negative effect of warming on phytoplankton size has also been discussed in detail (incl. species specific information) in the analysis of the 2009 experiment, where the factors copepod density and temperature had been crossed in a factorial design (Sommer and Lewandowska 2011).

For the response of the slope of the size–temperature regression to light and initial phytoplankton biomass we can only offer a tentative explanation. The slope became less negative with increasing light and initial biomass, which means less divergence of phytoplankton communities along the temperature gradient because of less time for divergence (earlier bloom under higher light, see above) and a smaller difference between starting biomass and carrying capacity.

Timing of the spring bloom

Hypothesis 3a (earlier peak by warming) and 3b (earlier peak by more light) could be confirmed, while hypothesis 3c (earlier peak by more overwintering copepods) was not supported. The latter result agrees with the experiment 2009, where 2 temperature levels were crossed with 3 copepod levels in a factorial design (Sommer and Lewandowska 2011). In this study, increasing copepod density decreased phytoplankton biomass and mean cell size, but had no effect on the timing of the spring bloom. The temperature effect was consistent across all experiments with little difference in the slopes. However, the temperature effect is only moderate in intensity (ca. 1 days $°C^{-1}$), which amounts to slightly less than 1 week for a range of 6°C warming, that is, a shift of one sampling interval of high-resolution sampling programs over the entire range from today to the most pessimistic IPCC scenarios for 2100 (IPCC 2007). Shifts by 1 week are also much less than the natural interannual variability in the timing of the phytoplankton spring peak, which might amount to 1 or 1½ months (Wiltshire et al. 2008). The light effect can be seen in the inter-experiment comparison. The times needed until the phytoplankton peak was reached differed by slightly more than 1 month between the lowest and high-light treatments. A much weaker light effect was found in the 2008 experiment, where the factors light and temperature were crossed (Lewandowska and Sommer 2010), but the light gradient encompassed only the upper third of the different light levels across all experiments.

Temporal offset between phytoplankton and nauplii

Hypothesis 4a (nauplii too early under warm and low-light conditions) was supported by a single experiment (2005) and the seeming support of hypothesis 4b (phytoplankton too early under cold and high light) by experiment 2006-2 could not be upheld by the later experiments. A temporal mismatch between supply and demand in food chains is one the major ecological concerns about global change (Visser et al. 1998), and its analysis has been one of the motivations for our experiments. The importance of the phytoplankton–nauplii link is based on the fact that copepod nauplii are the most important food for first feeding fish larvae and therefore of utmost importance for the energy and carbon transfer from primary production to pelagic fish production. We have to conclude that the risk of a mismatch between phytoplankton and nauplii is most probably restricted to warm and cloudy late winter and early spring conditions. Such conditions might become more common in the course of climate warming, because warming will increase the content of water vapor in the atmosphere and thereby increase cloudiness in many regions (Ruprecht et al. 2002; Zhang et al. 2007).

Effects of overwintering plankton

Ideally, all experiments would have been performed at the same time, and thus, the influence of all factors which were not manipulated intentionally would have been excluded. However, the number of mesocosms needed for that was not available. On the other hand, performing the experiments with different natural inocula each year also offered some valuable insights, for example, the robustness of the negative temperature effect on phytoplankton bloom biomass and cell size irrespective of different initial conditions. The quantitative comparison of the temperature effects (elevation and slopes of regression lines) across experiments also provided strong hints on the importance of the intentionally varied factor light and the factors related to the plankton community at the start: phytoplankton biomass and mean size, microzooplankton biomass and mesozooplankton

biomass. Light obviously played an outstanding strong role and the biomass of overwintering mesozooplankton was the most important inoculum factor. Plankton ecologists have usually assumed that winter resets plankton communities almost to zero and that they are reassembled each year from bottom-up, that is, primary producer growth preceding the built-up of consumer stocks (Sommer et al. 1986; Sommer 1996; Smetacek 1999). However, memory effects from 1 year to the next have been found in a multiannual modeling study (Huisman et al. 2005) and in a model based on our experiment 2005 (Gaedke et al. 2010). Obviously, the strongest priority effect in our experiments was exerted by the guild with the slowest response time, the copepods as dominant component of the mesozooplankton. Resulting from the slow response, there was a strong positive correlation between log mean copepod biomass and log start copepod biomass across all mesocosms ($r = 0.86$; $p < 0.0001$), while no such correlation was found for phytoplankton and microzooplankton biomass. They rather responded to the experimental conditions, while copepods were almost an independent variable at the time scale of our experiments.

Coupling of light and temperature in situ

Having demonstrated the dominant influence of the factors light and temperature, it seems adequate to discuss to which extent they are coupled or independent of each other in situ. Thermal stratification and the extent of vertical mixing form the most obvious link between temperature and the light experienced by phytoplankton. The mean light intensity in a mixed water body (I_{mix}) can be calculated as

$$I_{\mathrm{mix}} = I_0(1 - \mathrm{e}^{-kz})(kz)^{-1}$$

(Riley 1957) where I_0 is surface light intensity, k the vertical attenuation coefficient (m^{-1}) and m the mixing depth (m). At realistic values of k and m, the term e^{-kz} becomes negligible, thus making the ratio of I_{mix}/I_0 an inverse function of k and z. The onset of stratification in deep, stratifying water bodies often leads to a fast order of magnitude decrease in mixing depth and thus to a similarly fast increase in I_{mix} which by far exceeds the light changes between cloudy and sunny periods. Therefore, spring warming has traditionally been considered as a kind of light switch for the spring growth of phytoplankton. This trigger mechanism was been formally postulated by Sverdrup's (1953) critical depth concept, according to which mixing depth has to drop below a critical level in order to retain phytoplankton cells long enough in the well-illuminated surface layer. Meanwhile, the critical depth concept has been superseded by the critical turbulence concept (Huisman and Sommeijer 2002; Tirok and Gaedke 2007) because below a critical limit of turbulence phytoplankton cells may stay long enough in the surface layer even when the depth of the isopycnal surface layer exceeds the critical depth. However, phytoplankton blooms starting under such circumstances are expected to be unstable, because any wind event would destroy such a bloom. Therefore, the tendency toward increased storminess in a warming climate (IPCC 2007) will make phytoplankton blooms less common under conditions of a deep pycnocline but calm surface conditions.

In shallow water bodies where either the bottom or a halocline (like in the Kiel Fjord) restrict mixing depth to values below Sverdrup's critical limit, the factors light and temperature are not as tightly coupled. Here, the phytoplankton spring bloom can start before the onset of thermal stratification. In shallow waters changes in cloud cover (leading to variation in I_0), changes in turbidity by suspended sediments or by suspended matter from the catchment (both increasing k) become decisive components of the underwater light supply experienced by phytoplankton. Increased cloud cover, resuspension of sediments and floods in the catchment are often predicted to become more common in a warming climate, but all three phenomena are more episodic in time and more regional in space than the general warming trend. Therefore, the impact of climate change on the spring bloom in shallow waters might be more strongly characterized by an increasing variability than by a tendency of the mean.

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