Experimental induction of a coastal spring bloom early in the year by intermittent high-light episodes

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ABSTRACT: Through the use of mesocosm experiments, we show that an unusually early spring phytoplankton bloom can be induced by intermittent high-light periods. We performed mesocosm experiments where plankton assemblages from Kiel Bight (Western Baltic Sea) received a light regime based on the natural seasonal irradiance dimmed to 43 % of surface irradiance of cloudless days, starting with irradiance levels of mid-January (6 mesocosms) and mid-February (6 mesocosms). After 6 d, half of the mesocosms received a ca. 2-fold increase in irradiance. In the January mesocosms, a phytoplankton bloom developed only in the treatments with the high-light episode, whereas in the February mesocosms a phytoplankton bloom also developed in the controls. Phytoplankton net growth rates, production:biomass ratios and biomass at the end of the high irradiance episodes were positively correlated to the daily light dose. The relative biomass of diatoms increased with increasing light, whereas the relative biomass of cryptophytes decreased. A bottom-up transmission to mesozooplankton (mainly copepods of the genera *Acartia* and *Oithona*) was evident by increased densities of copepod nauplii and egg production under higher light conditions, whereas copepodids and adults showed no responses during the experimental period. The taxonomic composition of the nauplii was shifted to the advantage of *Acartia*/*Centropages* (not distinguished at the naupliar stage) under higher light conditions.

KEY WORDS: Plankton · Spring bloom · Irradiance

INTRODUCTION

Although the importance of light for photo-autotrophic processes is beyond doubt, light has received little attention in the climate change literature on plankton systems. In the majority of correlative studies on the impact of climate change on plankton phenology, properties of the seasonal plankton cycle are related to temperature or to climate indices (Weyhenmeyer et al. 1999, Straile & Adrian 2000, Gerten & Adrian 2001, Edwards et al. 2002, Wiltshire et al. 2008). An exception are those studies that relate an earlier onset of the ice-free period or of thermal stratification with an improved light climate earlier in the year and thus an earlier onset of the phytoplankton spring bloom (Winder &

Schindler 2004, Peeters et al. 2007). The studies concentrating on stratification as the trigger of seasonal phytoplankton growth echo Sverdrup's (1953) critical depth concept, according to which mixing depth has to drop below a critical level in order to permit a sufficiently long residence of phytoplankton cells in the well-illuminated surface layer. This concept has been superseded by the critical turbulence concept (Huisman & Sommeijer 2002) because below a critical limit of turbulence, phytoplankton cells may remain long enough in the surface layer even when the depth of the isopycnal surface layer exceeds the critical depth.

An earlier onset of the spring bloom under warmer conditions is in agreement with the common expectation that biological spring events should be ad-

vanced temporally by warming (Walther et al. 2002, Cleland et al. 2007). However, data are far less clear for the plankton spring bloom (for an overview, see Ji et al. 2010), which is one of the most prominent features in the seasonal growth patterns of phytoplankton in temperate and cold oceans and lakes. At high latitudes and in nutrient-poor waters it is usually the single seasonal maximum of primary production, providing most of the energy and matter supply for zooplankton and fish production. A temporal advancement of the spring bloom under warming conditions has been reported in some cases (Weyhenmeyer et al. 1999, Gerten & Adrian 2001, Edwards et al. 2002), but there are also studies that found no warming effect (diatoms, Edwards & Richardson 2004; the entire phytoplankton community, Wiltshire et al. 2008) or even a retardation of the spring bloom under warmer conditions (Wiltshire & Manly 2004). Experimental studies with temperature-controlled mesocosms (Sommer et al. 2007, Sommer & Lengfellner 2008) have shown a slight advancement of the phytoplankton spring peak by ca. 1 d °C^{-1}, a shift that would remain unnoticed with the usual weekly sampling scheme. Wiltshire's et al. (2008) analysis of the Helgoland Straits time series (North Sea) is remarkable, because it showed both an insensitivity of the timing of the spring bloom to temperature and a strong interannual variability of up to 1.5 mo. Interannual differences in grazing pressure by overwintering zooplankton (mainly copepods) have been offered as a hypothetical explanation for the interannual variability, but an experimental study with a factorial combination of warming and a 7-fold gradient in the density of overwintering copepods showed no effect of copepod density on the timing of the phytoplankton spring bloom, whereas maximal biomass, size structure and taxonomic composition were significantly influenced by both temperature and copepod density (Sommer & Lewandowska 2011). Obviously, also light should be considered when explaining the interannual variability in the timing of the spring bloom. Siegel et al. (2002) found evidence that a compensation irradiance (calculated for the mixed water layer) of 1.3 mol photons m^{-2} d^{-1} (range 0.96 to 1.75 mol photons m^{-2} d^{-1}) had to be exceeded to initiate the spring bloom without apparent latitudinal variation. This compensation light level was also supported in the experimental study of Sommer & Lengfellner (2008). Although the onset of mixing is the dominant factor in deep water bodies, in more shallow ones, variability of surface irradiance at weekly time scales might be equally important. Day-to-day variability might be less important because it

usually takes 1 to 2 wk to build up a phytoplankton bloom (Sommer et al. 1986). Therefore, we used natural phytoplankton from the Baltic Sea subjected to simulated high-light episodes (2-fold increase over controls) of 10 d in mesocosms (operated in total for 5 wk) to answer the following questions: (1) Can a mid-latitudinal (Kiel Fjord, Northern Germany, 55° 33′ N) spring bloom be induced as early as January, a period when it usually does not occur? (2) Will such a high-light period further increase the biomass attained in a spring bloom later in the year? (3) How does light during the growth period of the spring bloom affect growth rates, primary production and biomass of phytoplankton and the performance of individual taxa? (4) Are light effects on phytoplankton transmitted to mesozooplankton, the most important trophic link between phytoplankton and fish production?

MATERIALS AND METHODS

Experimental design

Twelve mesocosms, each with a volume of 1400 l, were set up in temperature-controlled rooms (4.5°C, typical of moderately mild late winter seasons) and filled with natural, late-winter plankton communities from Kiel Fjord, Western Baltic Sea, on 23 January 2010 without sieving the water. Mesozooplankton was added from net catches at overwintering concentrations near the upper end of *in situ* interannual variation (Behrends 1996), targeted at ca. 15 to 20 ind. l^{-1}. The zooplankton community consisted mainly of the copepods *Acartia* and *Oithona*, with minor contributions of *Temora*, *Centropages* and *Pseudocalanus/ Paracalanus.* Other mesozooplankton (mainly meroplanktonic larvae of polychaetes) were approximately half as abundant as copepods. Gentle stirring by a propeller assured homogeneous distribution of the plankton without harming them, as shown in previous experiments using the same system (Sommer et al. 2007, Sommer & Lengfellner 2008).

Each mesocosm had a separate, programmable light unit (for details see Sommer et al. 2007). The surface irradiance for cloudless days (E_0) was programmed according to the astronomic model by Brock (1981), taking into account geographic latitude, season and daytime. The irradiance calculated according to this model was dimmed to 43% in order to make it similar to the mean mixed water irradiance (E_M; calculated according to Riley 1957) for sunny days at a halocline depth (z) of 10 m and a vertical

attenuation coefficient (k) of 0.2 m^{-1}, a value typical of late winter at the study site. For 6 of the mesocosms, the light program was started with the irradiance level of 13 January ('January mesocosms'); for the other 6 mesocosms, the start was set to 13 February ('February mesocosms'). The term 'day of year' in the subsequent text will refer to the light program, not the actual date. Five days after the start, light was doubled in half of the January and February mesocosms, while it remained at 43% E_0 in the control mesocosms (Fig. 1). The doubled light intensities were maintained for 10 d; thereafter they were reduced to the control levels again. In order to determine whether phytoplankton prevented from blooming by sustained low light levels could be stimulated to bloom without delay by an increase in light intensity, the January control mesocosms received a 10 d period of doubled light intensity starting at day of year (DOY) 33 (Fig. 1). In the following, the abbreviations JC (January control), JH (January high light), FC (February control) and FH (February high light) will be used for the mesocosms. For simplicity, the periods of doubled light will be called 'switch-on periods' in the following text ('switch-on period I' for JH and FH; 'switch-on period II' for JC).
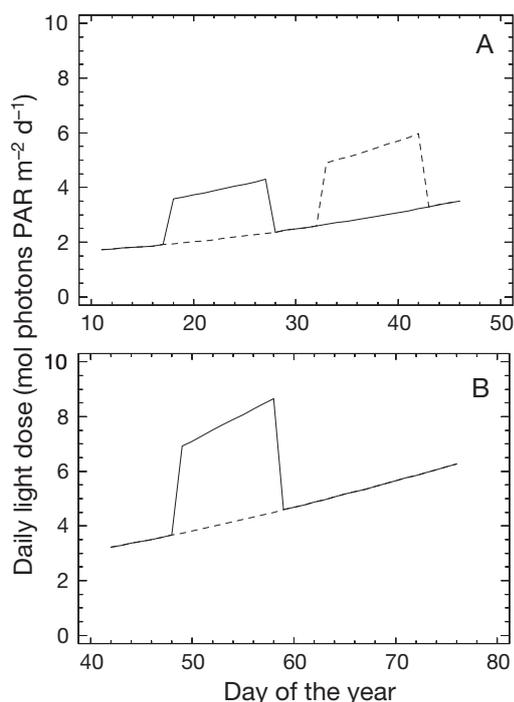

Fig 1. Time course of mesocosm light supply (daily light dose; mol photons photosynthetically active radiation [PAR] m^{-2} d^{-1}). Solid lines: high-light treatments; dashed lines: controls. (A) January mesocosms; (B) February mesocosms

Sampling

Phytoplankton were sampled 3 times per week (Monday, Wednesday and Friday). Phytoplankton >5 µm were counted by the inverted microscope method (Utermöhl 1958) and distinguished at the genus level in most cases. If possible, 100 individuals per taxonomic unit were counted in order to obtain 95% confidence limits of ±20%, but this was not possible with rare species. Small phytoplankton were counted using a flow cytometer (FACScalibur, Becton Dickinson) and distinguished by size and fluorescence of chlorophyll a and phycoerythrin. When flow-cytometer categories could be matched to phytoplankton in the microscopic counts (*Teleaulax* and *Plagioselmis*), we used the flow-cytometer data. Phytoplankton cell volumes were calculated from linear measurements after approximation to the nearest geometric standard solid (Hillebrand et al. 1999). Cell volume was converted to carbon after Menden-Deuer & Lessard (2000). However, for cells smaller than 180 µm^3 fixed carbon, volume conversion factors were used (0.108 pg C µm^{-3} for diatoms, 0.157 pg C µm^{-3} for the other species) because 180 µm^3 was the size of the smallest alga in the database of Menden-Deuer & Lessard (2000) and their non-linear models predict an unrealistically high carbon content for the smallest cells.

We sampled mesozooplankton for taxonomic analysis at weekly intervals by taking 3 vertical hauls with a small Apstein net (mesh size 64 µm, diameter 12 cm; Hydrobios). One additional haul served for egg production experiments. In total, this corresponds to an imposed artificial loss of 3% of the standing stock per week and was regarded as an appropriate sample size to avoid overfishing. Samples for taxonomic composition were fixed with Lugol's iodine solution or industrial alcohol and one subsample per mesocosm was analyzed under a stereo microscope (Zeiss Stereo Discovery V8 and Leica MZ 12.5). We distinguished meroplanktonic mesozooplankton larvae at the phylum or class level (e.g. Polychaeta, Bryozoa and Cirripedia) and copepods, the most abundant mesozooplankton component, at the genus level. However, young copepodids of *Paracalanus* and *Pseudocalanus* look very similar and were therefore merged into one group, though among older stages *Pseudocalanus* clearly dominated. Copepodids were staged (CIV to CVI were not distinguished) and nauplii were taxonomically identified 3 times during the experiment (start, middle and end). Because of morphological similarity, *Acartia* and *Centropages* nauplii had to be merged for analysis. For egg pro-

duction, adult females from the additional unfixed sample were sorted and individually kept for ~48 h in 6-well cell culture plates (filled with filtered seawater). Cell wells were checked every 8 to 14 h and freshly spawned eggs were counted and removed. Because of the small sample size we had to confine our egg production experiments to the dominant copepod genus *Acartia*. As egg production measurements are time consuming, we also had to confine measurements to one mesocosm per light treatment instead of measuring reproduction for all 3 replicate mesocosms per treatment block.

Primary production measurements

Primary production was measured by the ^{14}C incorporation method (4 µCi ^{14}C-bicarbonate per 30 ml sample) after Gargas (1975) in samples incubated inside the mesocosms at mid depth. Duplicate samples were incubated together with a blank (dark) sample during 3 to 4 h around noon. After incubation, samples were filtered through cellulose-nitrate membrane filters (0.2 µm pore size) to estimate the total primary production and polycarbonate membrane filters (10 µm pore size) to estimate production of phytoplankton >10 µm volume. The primary production of the size fraction >10 µm was measured separately, because these algae are grazed preferentially by copepods (Sommer & Sommer 2006). Filters were fumed with HCl, fixed with scintillation cocktail (Lumagel) and radio-assayed using a liquid scintillation counter (Tricarb counter, Packard). Primary production was calculated as µg C l^{-1} d^{-1} by assuming a linear relationship between production and light dose.

Data analysis

Net growth rates (*r*; d^{-1}) were calculated as the slope of a linear regression of ln-transformed abundance or biomass data over time. The analysis of the phytoplankton response focused mainly on the period when the light was doubled for the JH (DOY 18–27) and the FH mesocosms (DOY 39–41, switch-on period I). If biomass reached a peak before the end of the switch-on period, biomass data after the peak were excluded from calculating *r*. The phytoplankton response to the light doubling in the JC mesocosms (DOY 33–42; switch-on period II) was not included in the statistical analysis, but is shown for comparison in some of the graphs. The averaged phytoplankton response over the entire duration of the experiment was

mainly analyzed with a focus on the bottom-up transmission to mesozooplankton, which had to be analyzed at this longer time scale because of longer response times than the phytoplankton. The response of biological variables to experimental conditions was analyzed by regression analysis according to the best-fitting models, trying the linear and ln-transformed values of the independent and dependent variables. Although not being a mechanistic model like a Michaelis-Menten saturation curve, fitting of a linear regression with log-transformed *y* data does provide good fits of biological responses to light and robust estimates of threshold values with a minimal number of model parameters.

RESULTS

Phytoplankton response to high-light period

Phytoplankton biomass started to increase immediately in all mesocosms, but in the JC mesocosms, the initial increase was very slow until the light supply for these mesocosms was doubled on DOY 33
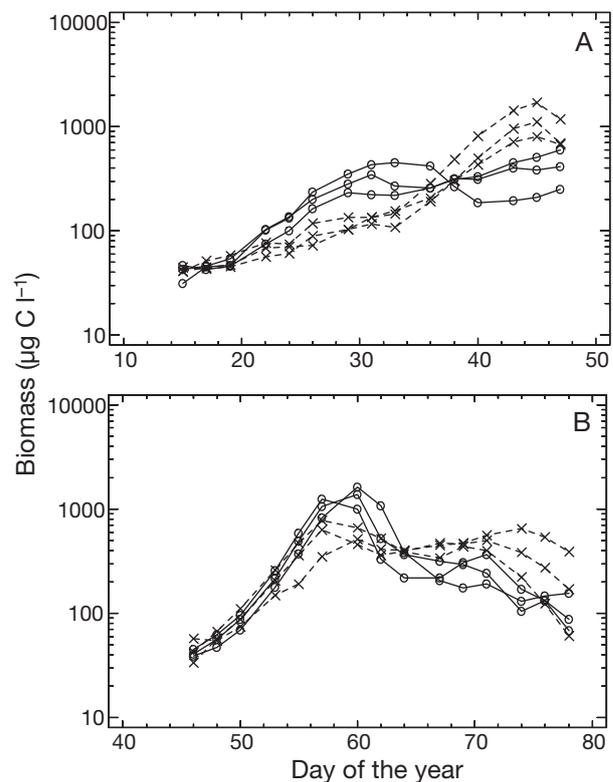

Fig. 2. Time course of phytoplankton biomass (mg C l^{-1}) in the mesocosms. Solid lines: high-light treatments; dashed lines: controls. (A) January mesocosms; (B) February mesocosms

Table 1. Response of phytoplankton net growth rates (r; d^{-1}), biomass at the end of switch-on period I (B; µg C l^{-1}), mean daily production (P; µg C l^{-1} d^{-1}) and mean P:B ratio (d^{-1}) to the mean daily light dose (LD; mol photons m^{-2} d^{-1}) during switch-on period I. Regression analysis was according to the model $y = a + bx$ or $y = a + b\ln x$ (n = 12)

y	x	a	b	R^2	p
r	$\ln LD$	−0.0782	0.217	0.92	<0.0001
B	LD	−282.6	171.1	0.80	0.0001
P	LD	−161.9	68.4	0.86	<0.0001
P:B	$\ln LD$	−0.0362	0.194	0.79	0.0001

(switch-on period II; Fig. 2). The highest peaks and the fastest growth were observed in the FH meso-cosms, followed by the FC mesocosms. The JH meso-cosms reached higher biomass levels than the JC mesocosms during the first period of light doubling, whereas the JC mesocosms surpassed them during the period when light was only doubled in the JC mesocosms (Fig. 2A). The timing of the biomass peak was controlled by the timing of the high-light period in the January mesocosms whereas the high-light period in the February mesocosms had no effect on the timing of the biomass peak (Fig. 2B).

In all cases, increasing the light intensity led to an immediate response of the growth rates. Phytoplankton net growth rates, biomass, mean daily production and production:biomass ratios during switch-on period I responded significantly to the mean daily light dose (Table 1). The phytoplankton in the JC mesocosms also showed a positive response to the light doubling during the period from DOY 33 to DOY 42, but this response was weaker than would have been predicted from the regressions in Table 1 (shown for the net growth rate in Fig. 3).

The growth rates of individual phytoplankton taxa also responded positively, with a significant (p < 0.05) response in 11 of 15 cases (Table 2). The 4 non-significant cases were rare taxa, whereas the taxa with significant responses made up >95% of phytoplankton biomass in all meso-cosms. The taxon-specific responses to light were unrelated to cell size and showed wide variability in the diatoms and the categories counted by flow cytometer, whereas the re-
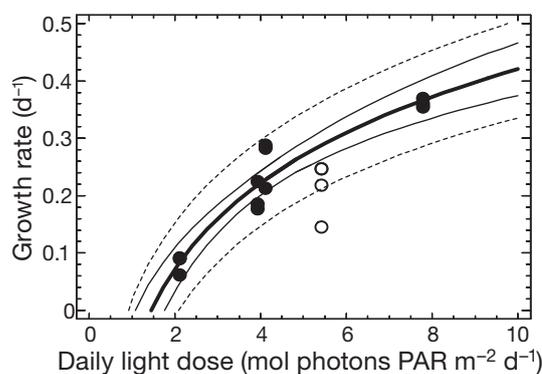

Fig. 3. Phytoplankton net growth rates (●, d^{-1}) during the switch-on period I (day of year 18–27 in the January meso-cosms; day of year 49–58 in the February mesocosms) as a function of mean daily light dose (mol photons PAR m^{-2} d^{-1}). Thick solid line: regression line (linear x, log y); thin solid lines: 95% confidence limits; broken lines: 95% prediction limits. January control mesocosm values for switch-on period II (day of year 33–42) are shown for comparison (○)

sponses of the cryptophytes and of the dinoflagel-lates were very similar to each other (Fig. 4).

Phytoplankton community composition also changed in response to the light treatments, as can be seen from the relative contribution of higher taxa

Table 2. Response net growth rates (r; d^{-1}) of individual phytoplankton taxa to the mean daily light dose (LD; mol photons m^{-2} d^{-1}) during switch-on period I. Regression analysis was according to the model $r = a + b\ln LD$ (n = 12)

Taxon	Cell carbon (pg C $cell^{-1}$)	a	b	R^2	p
Centric diatoms					
Rhizosolenia setigera	3382	−0.33	0.35	0.74	0.0004
Proboscia alata	1352	−0.38	0.10	0.09	0.35
Skeletonema costatum	15.9	−0.17	0.37	0.90	<0.0001
Pennate diatoms					
Thalassionema nitzschioides	126	−0.14	0.14	0.57	0.0043
Pseudonitzschia sp.	5.7	0.04	0.19	0.90	<0.0001
Cryptophytes					
Rhodomonas marina	155	0.07	0.07	0.39	0.029
Teleaulax amphioxeia	35	0.09	0.08	0.62	0.0022
Plagioselmis prolonga	6	0.06	0.06	0.67	0.0011
Dinoflagellates					
Heterocapsa rotundata	64	0.08	0.09	0.30	0.065
Gymnodinium sp.	29	0.07	0.09	0.23	0.11
Flow-cytometrically identified categories					
F1 & F2[a]	2.1	0.008	0.121	0.86	<0.0001
F4	33	−0.135	0.30	0.95	<0.0001
F7	9.2	−0.14	0.046	0.80	0.0001
F8	34	−0.16	0.14	0.24	0.13
F9	5.6	−0.22	0.097	0.45	0.017

[a]The initial categories F1 and F2 were lumped because of identical size and demarcation problems of the pigment signal in some samples
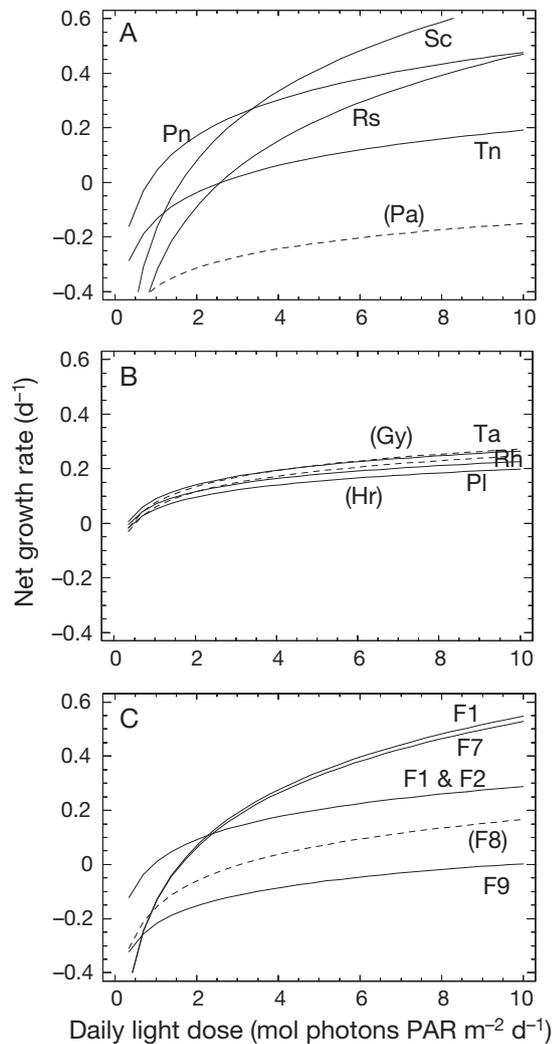
Fig. 4. Net growth rates (d^{-1}) of individual phytoplankton taxa during switch-on period I (day of year 18–27 in the January mesocosms; day of the year 49–58 in the February mesocosms) as a function of mean daily light dose (mol photons PAR m^{-2} d^{-1}). Solid lines: significant at $p < 0.05$; dashed lines and taxon code in brackets: not significant. (A) Diatoms. Pa: *Proboscia alata*; Pn: *Pseudonitzschia* sp.; Rs: *Rhizosolenia setigera*; Sc: *Skeletonema costatum*; Tn: *Thalassiosira nitzschioides*. (B) Cryptophytes and dinoflagellates. Gy: *Gymnodinium* sp.; Hr: *Heterocapsa rotundata*; Pl: *Plagioselmis prolonga*; Rh: *Rhodomonas marina*; Ta: *Teleaulax amphioxeia*. (C) Categories counted by flow cytometry; abbreviations as in Table 2
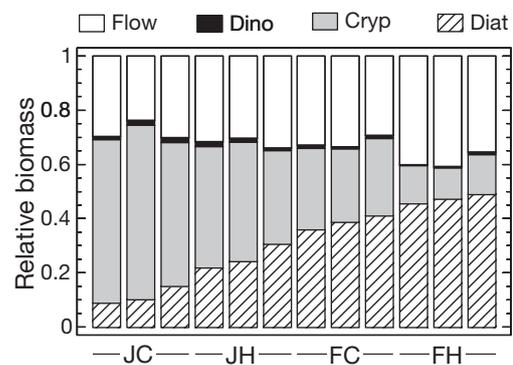

Fig. 5. Relative biomass of phytoplankton groups (calculated for the end of switch-on period I, i.e. day of year 18–27 in the January mesocosms, day of year 49–58 in the February mesocosms) in the different mesocosms. Each mesocosm was replicated three times (JC: January control; JH: January high light; FC: February control; FH: February high light). Cryp: Cryptophyta; Diat: diatoms; Dino: Dinophyta; Flow: flow-cytometrically counted taxa

Phytoplankton response over the entire experiment

The phytoplankton response averaged over the entire duration of the experiment was less pronounced than the response during the light elevation periods, but was still significant (p < 0.05; Table 3). The overall weaker response over the entire duration of the experiment was expected because total light supply over the entire experiment varied less (minimum:maximum light supply = 1:1.85) than during the switch-on periods (minimum:maximum light supply = 1:3.9). Moreover, the high maximal biomasses in the FH mesocosms were partially offset by a strong decline after the peak.

Zooplankton response

Densities of adult copepods and copepodids declined gradually at a mean (±SD) rate of $r = -0.023 \pm 0.08$ d^{-1} (Fig. 6). The negative growth rates showed

to total biomass (Fig. 5). The proportion of diatoms (strongly dominated by *Skeletonema costatum*) increased with light dose whereas the proportion of cryptophytes (dominated by *Rhodomonas marina*) decreased. The proportion of the flow-cytometrically determined small phytoplankton species showed no response to the different light treatments.

Table 3. Response of phytoplankton mean biomass (B; µg C l^{-1}), mean daily production (P; µg C l^{-1} d^{-1}) and mean P:B ratio (d^{-1}) to the light sum over the entire experiment (LS; mol photons m^{-2}). Regression analysis was according to the model $y = a + bx$, $y = a + b\ln x$ or $\ln y = a + b\ln x$ (n = 12)

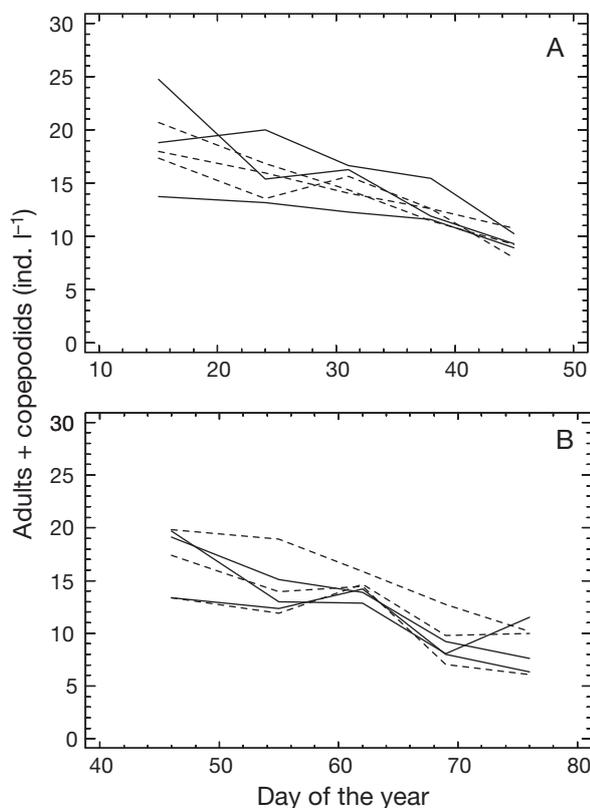| y	x	a	b	R^2	p
$\ln B$	$\ln LS$	3.306	0.49	0.39	0.0301
P	$\ln LS$	−295.5	69.57	0.55	0.006
P:B	$\ln LS$	−0.483	0.128	0.37	0.0394

Fig. 6. Time course of copepod (adults + copepodid stages) abundance. (A) January mesocosms; (B) February mesocosms. Solid lines: high light mesocosms; dashed lines: control mesocosms. n = 3 replicates per treatment

Table 4. Response of copepod nauplii (N; mean density, no. l^{-1}) to the light sum over the entire experiment (LS; mol photons m^{-2}), mean daily primary production (P; µg C l^{-1} d^{-1}) and mean daily primary production of phytoplankton >10 µm ($Ph_{>10}$; µg C l^{-1} d^{-1}). Regression analysis was according to the model $y = a + bx$ or $y = a + b\ln x$ (n = 12)

y	x	a	b	R^2	p
ln N	lnLS	−4.31	1.427	0.38	0.0342
N	P	2.81	0.298	0.49	0.0114
N	$Ph_{>10}$	4.44	0.615	0.57	0.0048

nauplii. Nauplii of *Acartia* and *Centropages* (not distinguished) dominated with 63 to 73% in the February light regimes; they contributed 24 to 40% to nauplii abundance in the JC mesocosms and 53 to 60% in the JH mesocosms (Fig. 7). Conversely, the nauplii of *Pseudocalanus/Paracalanus* and of *Oithona* had higher relative abundances in the January mesocosms. The relative abundances of *Acartia/Centropages* nauplii were positively correlated to the light sum of the entire experiment, whereas the relative abundances of *Pseudocalanus/Paracalanus* and *Oithona* nauplii showed the opposite correlation (Table 5).

DISCUSSION

The irradiance experienced by phytoplankton in a vertically mixed water column (E_M) was calculated according to Riley (1957):
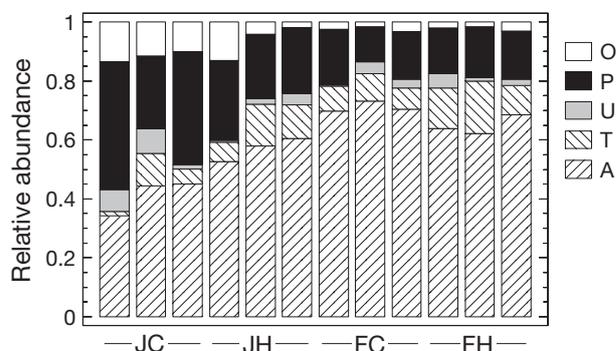
$$E_M = E_S(1 - e^{-kz})(kz)^{-1}$$

Fig. 7. Relative abundance of nauplii (calculated from means over entire experiment) in the different mesocosms. Each mesocosm was replicated three times (JC: January control; JH: January high light; FC: February control; FH: February high light). A: *Acartia/Centropages*; O: *Oithona*; P: *Pseudocalanus/Paracalanus*; T: *Temora*; U: unidentified

no correlation to the experimental conditions (R^2 = 0.06, p = 0.44). Other mesozooplankton (mainly polychaete larvae) were initially approximately half as abundant as copepods and declined at faster rates. The copepods were already in advanced stages (>90% CIV–CVI) at the beginning of the experiment. Therefore, no response of maturation to the experimental treatments could be assessed. At the end of the experiment, newly recruited CI stages were still too rare to obtain reliable counts. The mean density of nauplii showed a positive response to the light sum over the entire experiment, a correlation that became even tighter when mean primary production or primary production of the size fraction >10 µm were used as independent variables (Table 4). Mean daily egg production (P_{egg}; eggs l^{-1} d^{-1}) by *Acartia* was positively correlated to the light sum (LS): P_{egg} = −1.696 + 0.0225LS (R^2 = 0.96, p = 0.0179, n = 4).

Although species composition of copepodids and adults did not change very much over the experiment (*Acartia* and *Oithona* ca. 40% each, *Temora* ca. 10%, *Pseudocalanus/Paracalanus* ca. 8%, *Centropages* ca. 2%), there was a pronounced taxonomic response of

Table 5. Response of copepod nauplii genus composition (relative abundance; $p_i = N_i/N_{tot}$, calculated for mean abundances over entire experiment) to the light sum over the entire experiment (LS; mol photons m^{-2}). Regression was according to the model $\arcsin\sqrt{p_i} = a + b\ln LS$ (n = 12)

Taxon	a	b	R^2	p
Acartia and *Centropages*	−40.3	18.24	0.46	0.0151
Pseudocalanus/Paracalanus	108.1	−16.17	0.47	0.0133
Oithona	84.45	−14.47	0.45	0.0171
Temora		No correlation		

where E_S is the surface light intensity (under any light conditions, as opposed to E_0 for cloudless days), z is the mixing depth (m) and k is the vertical attenuation coefficient (m^{-1}). We derived 2 characteristic values of the daily light dose from the saturation curve in Fig. 3 and the assumption that phytoplankton received 90.6% of the surface irradiance due to vertical mixing in mesocosms: 1.3 mol photons photosynthetically active radiation (PAR) m^{-2} d^{-1} as a threshold for positive growth, and 2.8 mol photons PAR m^{-2} d^{-1} as the daily light dose required for a 10-fold increase within 2 wk (i.e. $r = 0.164$ d^{-1}), our operational definition for 'bloom'.

For comparison with *in situ* conditions, we assumed a mixing depth of 10 m (depth of the halocline at our study site) and a vertical attenuation coefficient of 0.2 m^{-1}. The following critical dates can be calculated
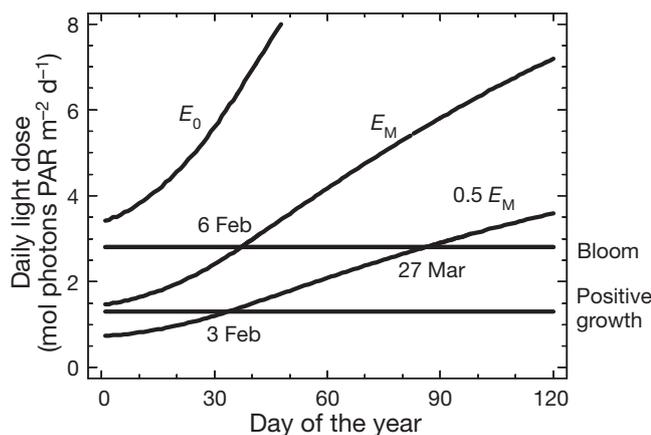

Fig. 8. Change of irradiance during the first 120 d of the year (ascending lines) compared with the demand (horizontal lines) for positive phytoplankton growth and bloom development, defined as a 10-fold increase during 2 wk (both in mol photons PAR m^{-2} d^{-1}). E_0: surface irradiance on sunny days; E_M: mixed layer irradiance at a depth of 10 m and a vertical attenuation coefficient of 0.2 d^{-1}; 0.5 E_M: mixed layer depth with a 50% light reduction by clouds. Dates are given for intersections between the horizontal lines for positive growth and bloom development and the line for E_M and 0.5 E_M

(Fig. 8). Surface irradiance at cloudless days (E_0) and E_M at cloudless days always exceed the threshold daily light dose for positive phytoplankton growth. Under 50% light reduction by clouds ($E_S = 0.5E_0$), this threshold is surpassed on 3 February. The daily light dose required for bloom-like growth is exceeded by E_0 throughout the year, by E_M on sunny days on 6 February, and by E_M on days with 50% irradiance reduction by clouds on 27 March. Sverdrup's (1953) classic concept of the critical mixing depth assumes that phytoplankton spring growth would not occur as long as E_M is too low. However, phytoplankton growth has been observed under conditions of a pycnocline below the critical mixing depth, if calm, windless conditions permit a sufficiently long residence of phytoplankton near the well-lit surface, as shown in a modelling study by Huisman & Sommeijer (2002) and also empirically for deep Lake Constance (Tirok & Gaedke 2007).

Our experiments have confirmed that solar irradiance in coastal North Central Europe and other regions of similar latitude can be sufficient to induce phytoplankton blooms as early as in January under calm conditions and at the beginning of February under sunny but vertically mixed conditions if mixing is restricted to ca. 10 m by the sea bottom or a halocline. Such early blooms have been reported from coastal seas, e.g. Narragansett Bay (Borkman & Smayda 2009) and Bay of Biscay (Labry et al. 2001). However, they are not commonly found in the Baltic Sea or in the shallow German Bight of the North Sea, where the first annual bloom does not occur before mid-February (Wiltshire et al. 2008). Wiltshire et al. (2008) emphasized the importance of top-down control for the timing of the spring bloom: the more grazing, the higher the light requirements for achieving a phytoplankton growth rate in excess of the losses. Similarly, Oviatt et al. (2002) explained the absence of the winter–spring bloom in Narragansett Bay in a warm El Niño winter by elevated grazing under warmer conditions.

However, we argue that the early timing of the spring bloom in our experiment could not have been caused by a less stringent top-down control by zooplankton, because our copepod densities were 10 times higher than the overwintering densities in the German Bight (0.3 to 1.6 ind. l^{-1}). Our copepod densities were at the upper end of the range of variation for the Western Baltic Sea (Behrends 1996) and thus represent a high-grazing scenario. Thus we conclude that the frequent absence of mid-latitude phytoplankton blooms in January is not caused by a lack of solar irradiance above clouds or by

excessive grazing, but by atmospheric (clouds) and underwater (mixing depth, attenuation coefficient) light attenuation.

In the January mesocosms, the timing of a relatively modest high-light period (doubling of light) of 10 d was sufficient to induce a temporal shift of the spring peak of phytoplankton. In the JC mesocosms, which received the high-light period 15 d later than the JH mesocosms, the biomass maximum occurred ca. 2 wk later. Although positive net growth of phytoplankton could already be detected before the doubling of light, both growth rates and biomass were far below the levels that would usually be called a bloom (usually a 10-fold increase of biomass within 2 wk and a biomass peak level >200 µg C l⁻¹ in the study region). In the February mesocosms, however, the phytoplankton biomass maximum occurred almost at the same time in all mesocosms, independent of an intermittent high-light period. However, the high-light period led to higher growth rates, higher production rates and a higher peak biomass in the FH mesocosms. This means that the sensitivity of peak timing to intermittent high-light periods decreases with increasing background light, i.e. later in the late winter/early spring season. The decreased sensitivity later in the year agrees with the results from an experiment in the same mesocosms system, where the factors light and temperature were combined in an orthogonal factorial design (Lewandowska & Sommer 2010). In those experiments, the 3 light scenarios (32, 48 and 64 % of surface irradiance on sunny days) started in February. Consequently, the effect of light on the timing of the spring bloom was small. In water bodies with stronger light attenuation in late winter, e.g. because of deeper mixing, or at higher latitudes (Eilertsen & Frantzen 2007), the sensitive phase should extend further into the spring season.

It should be noted that our light increases were a relatively 'soft' manipulation compared with the light increase when thermal stratification starts in a deep circulating water body. At realistic values of k and z, the term e^{-kz} becomes almost negligible and E_M/E_S becomes inversely proportional to k and z. In deep water bodies (mixing depth in the order of 10^2 m), the onset of stratification leads to an order-of-magnitude increase in E_M. However, a 2-fold increase in light intensity at this temporal scale is quite substantial, if it is compared with natural changes in surface irradiance. We analyzed a 7 yr database (1998–2004; Meteorology Department, GEOMAR) for sea-surface irradiance at Kiel and calculated the irradiance ratios between subsequent calendar weeks during the first quarter of the year. The maximal ratio between 'darker' and 'brighter' weeks following each other was 2.75, the 90th percentile was 2.11 and the 75th percentile was 1.68.

Our threshold value for positive phytoplankton growth of 1.3 mol photons PAR m⁻² d⁻¹ agrees with the threshold values found previously in the same experimental system (1.34 mol photons PAR m⁻² d⁻¹, range = 1.14 to 1.63; Sommer & Lengfellner 2008) and by an analysis of remote sensing data for the North Atlantic Ocean (1.3 mol photons PAR m⁻² d⁻¹, range = 0.96 to 1.75; Siegel et al. 2002). This light threshold is not the compensation point of usual photosynthesis–irradiance curves, i.e. a compensation point for phytoplankton photosynthesis and respiration. It can be viewed as a 'community compensation point' because it is calculated for net growth rates, i.e. it describes the light requirement for a growth rate at least in balance with the losses, e.g. grazing. The same applies to the taxon-specific light response curves in Table 2 and Fig. 4. We may assume that losses were relatively similar across treatments because of similar copepod densities. Therefore, between-taxon differences would influence parameter a of the regressions (height of the curves), whereas the exponent b would characterize their response to limiting light.

Phytoplankton in our experiments was co-dominated by *Skeletonema costatum*, the cryptophyte *Rhodomonas marina* and the small algae (<5 µm) counted by flow cytometer. The latter category of algae often remains unreported or under-reported in field studies based on microscopic counts alone, in spite of the generally acknowledged importance of picoplankton and small nanophytoplankton. *Skeletonema* '*costatum*' is a ubiquitous aggregate of several cryptic species (Kooistra et al. 2008) and is frequently dominant during winter–spring blooms at mid latitudes (Borkman & Smayda 2009) and during high-latitude blooms (Eilertsen & Degerlund 2010). It is also a regularly occurring and often dominant component of the Baltic Sea spring bloom, although earlier in the 20th century it was more typical in summer and fall (Wasmund et al. 2008). Wasmund et al. (2008) speculated about a taxonomic shift from *S. costatum* sensu stricto to S. *marinoi*. *S. costatum* sensu lato was already been one of the dominant species in the inoculums of our experiment, and its strong response to light (Fig. 5) was driving the positive response of diatoms to light. In the experiment of Lewandowska & Sommer (2010), *S. costatum* benefited significantly from cold conditions and showed a slight though insignificant trend to increase in abun-

dance with light. However, the light levels in their experiment were not as low as in the January treatments here. The flow-cytometric categories F1 & F2 and F7 (see Table 2) responded similarly to light, but were too rare initially to lead to a significant aggregate response of the algae counted by flow cytometer. The flat response of *R. marina* and the other cryptophytes to light can be explained either by an unusually early onset of light saturation or by supplementary heterotrophy of these mixotrophic flagellates (Jones 2000) at low light conditions (Sanders et al. 1990, Gervais 1997).

We could not find a response of copepodids and adult copepods to the experimental conditions. The starting copepod populations were obviously too mature (>90% CIV to CVI) and the developmental times at our low temperatures too long to find such an effect within the duration of the experiment. However, a clear bottom up-transmission of effects was found at the level of nauplii, which responded positively to phytoplankton production and daily light dose. The bottom-up transmission occurred in spite of a rather moderate manipulation of the basal resource light (1.9-fold difference in light sums over the entire experiment). Because of the positive correlation between total primary production and primary production of phytoplankton >10 μm, it cannot be stated with certainty which of the 2 was decisive. However, the better correlation of naupliar abundance with phytoplankton >10 μm is in line with the preference of copepods for larger algae (Katechakis et al. 2002, Sommer & Sommer 2006).

The taxonomic shifts in the copepod nauplii resemble long-term taxonomic trends in Baltic Sea zooplankton (Möllmann et al. 2000, Alheit et al. 2005). *Acartia* and *Centropages* tend to increase, while *Pseudocalanus* tends to decrease. In contrast to our experimental results, the taxonomic shifts *in situ* have not been ascribed to changes in food availability but to hydrographic changes, *Acartia* and *Centropages* profiting mainly from increased temperatures and *Pseudocalanus* suffering from decreased salinity, whereas in our experiments the shift in favor of *Acartia/Centropages* was brought about by high light and thus improved food conditions. However, it should be kept in mind that surface warming usually decreases mixing depth and thus increases mean light intensity in the mixed water layer, if solar irradiance and underwater light attenuation remain unchanged.

Our results re-focus the attention on light as an important regulating factor of the spring bloom. Although the focus on light has never been lost in basic research (e.g. Eilertsen & Frantzen 2007, Álvarez et

al. 2009), there has been a lack of attention to light in most of the literature on shifts in plankton seasonality due to climate change (Gerten & Adrian 2001, Wiltshire et al. 2008). This may just be a minor problem in deep water bodies (e.g. Peeters et al. 2007), where early season temperature and effective underwater light are tightly coupled via the onset of thermal stratification, but it is a serious omission for studies in shallow and moderately deep water bodies, where the start of the spring bloom does not depend on the onset of stratification. Here, changes in solar irradiance may play an important role, as shown by Nixon et al. (2009), who explained the long-term decrease of the spring bloom in Narragansett Bay by an increase of cloudiness in the course of climate warming. Because of the week-to-week changes in cloud cover and its effect on surface irradiance, the timing of the spring bloom in shallow or moderately deep waters might be more influenced by the actual weather conditions than by long-term climatic trends.

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