



# Climate warming and heat waves alter harmful cyanobacterial blooms along the benthic–pelagic interface

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**Abstract.** In addition to a rise in mean air and water temperatures, more frequent and intense extreme climate events (such as heat waves) have been recorded around the globe during the past decades. These environmental changes are projected to intensify further in the future, and we still know little about how they will affect ecological processes driving harmful cyanobacterial bloom formation. Therefore, we conducted a long-term experiment in 400-L shallow freshwater mesocosms, where we evaluated the effects of a constant +4°C increase in mean water temperatures and compared it with a fluctuating warming scenario ranging from 0 to +8°C (i.e., including heat waves) but with the same +4°C long-term elevation in mean water temperatures. We focused on investigating not only warming effects on cyanobacterial pelagic dynamics (phenology and biomass levels), but also on their recruitment from sediments—which are a fundamental part of their life history for which the response to warming remains largely unexplored. Our results demonstrate that (1) a warmer environment not only induces a seasonal advancement and boosts biomass levels of specific cyanobacterial species in the pelagic environment, but also increases their recruitment rates from the sediments, and (2) these species-specific benthic and pelagic processes respond differently depending on whether climate warming is expressed only as an increase in mean water temperatures or, in addition, through an increased warming variability (including heat waves). These results are important because they show, for the first time, that climate warming can affect cyanobacterial dynamics at different life-history stages, all the way from benthic recruitment up to their establishment in the pelagic community. Furthermore, it also highlights that both cyanobacterial benthic recruitment and pelagic biomass dynamics may be different as a result of changes in the variability of warming conditions. We argue that these findings are a critical first step to further our understanding of the relative importance of increased recruitment rates for harmful cyanobacterial bloom formation under different climate change scenarios.

**Key words:** climate change; climate warming; cyanobacteria; cyanobacterial blooms; heat waves; lakes; mesocosms; recruitment.

## INTRODUCTION

Globally, mean air and water temperatures have been rising at an unprecedented rate since the past century (IPCC 2013, O'Reilly et al. 2015). In addition, the incidence of extreme climate events, such as heat waves, has also dramatically increased during past decades and is projected to further intensify in the future (Easterling

et al. 2000, IPCC 2013, Seneviratne et al. 2014). Cyanobacteria, the primary taxa causing toxic freshwater algal blooms, are thought to be favored in an increasingly warmer environment (Paerl and Huisman 2008, Brooks and Carey et al. 2011). This notion has been corroborated by observational as well as experimental studies, showing a positive relationship between elevated mean water temperatures and cyanobacterial biomass levels (Kosten et al. 2012, Ekvall et al. 2013, Hansson et al. 2013, Urrutia-Cordero et al. 2016). In addition, a few observational and modeling studies have shown positive responses of cyanobacterial growth to heat waves (Jöhnk et al. 2008, Huber et al. 2012, Anneville et al.

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2015). However, it remains unknown whether cyanobacterial bloom formation responds differently to a climate scenario with just elevated mean water temperatures or to another including warming variability below and above mean warming conditions, thus resulting in an increased frequency of heat waves (IPCC 2013). This is important because the impacts of extreme climate events on the ecological dynamics of biological communities may be just as strong as long-term changes in temperatures (Lawson et al. 2015).

The occurrence of cyanobacterial blooms in eutrophic freshwaters is especially troublesome for both societal recreation and drinking water supply (Hudnell 2008), specifically because many cyanobacterial taxa produce potent toxins affecting human and animal health (Codd 1995, Falconer 1999, Mantzouki et al. 2018a, b). In addition, their mass proliferation is often followed by anoxic events, negatively affecting ecosystem functioning and biodiversity, such as the impairment of fish stocks or benthic primary and secondary production (Falconer 1999, Codd et al. 2005).

In temperate lakes, the onset of cyanobacterial blooms in the pelagic environment generally starts with their recruitment from dormant stages (i.e., life stages with reduced metabolic activity in the form of akinetes or vegetative cells) laying at the sediment surface (Hansson 1996, Verspagen et al. 2005, Carey et al. 2014). Dormancy is a common feature shared by many planktonic organisms and is an efficient way to escape temporally from harsh environmental conditions (e.g., in winter; Reynolds 2006, Zhang et al. 2015, 2018). When light and water temperature become favorable again in spring and summer, these benthic populations can become active, grow at the sediment surface, and subsequently migrate into the water column, thereby providing a constant source for surface growth and biomass development (Hansson 1996, Verspagen et al. 2005, Carey et al. 2014). However, no study has actually tested how recruitment rates of different bloom-forming cyanobacterial species are affected in connection to their pelagic dynamics, under neither an increased mean water temperature scenario, nor a climate scenario with the same long-term elevation in mean water temperatures, but including short-term warming variability (below and above mean warming conditions), thus resulting in an increased incidence of heat waves.

Previous studies have noted differences among cyanobacterial species with respect to their growth response to increased water temperature (Carey et al. 2012, Lüring et al. 2013, Paerl 2014). For example, species from the genus *Microcystis* generally display a very high rate of growth acceleration ( $Q_{10}$ ), which is the acceleration of the growth rate over a 10°C step (Reynolds et al. 2006, Carey et al. 2012, Lüring et al. 2013). In contrast, increased water temperature has generally weaker positive effects on the growth rate of species from other bloom-forming cyanobacterial genera, such as *Aphanizomenon*, *Dolichospermum*, or *Limnithrix*

(Reynolds et al. 2006). Assessing specific-specific responses in growth and/or biomass production to climate warming is therefore highly important because some species may be favored over others, which can have consequences for overall community structure patterns. Furthermore, climate warming is likely to favor the recruitment of cyanobacterial species differently. There is generally a lag-phase that can last up to weeks prior to recruitment of akinete-forming cyanobacteria (e.g., from the Nostocales order) in response to increased water temperatures, as the akinetes must germinate and mature before migrating into the water column (Barbiero 1993, Karlsson-Elfgren et al. 2004). In contrast, physiologically resting vegetative cells of some phytoplankton species may activate even within a day after temperature increases (Sicko-Goad et al. 1986), which may also be the case for many cyanobacterial species that do not form akinetes. It is then plausible that non-akinete-forming cyanobacterial species also show high recruitment sensitivity in response to increases in water temperature (e.g., like *Microcystis* spp.; Carey et al. 2012). Hence, generating knowledge on species-specific responses of recruitment and surface biomass to climate warming would considerably improve predictions of future climate-change-induced trends in the development and composition of cyanobacterial blooms, as well as to pinpoint critical aspects of their life history that are prone to change in response to climate change.

Our study is focused on shallow systems (around 1 m deep), which are especially common in periurban and agricultural areas and are the most abundant water bodies worldwide (Downing et al. 2006). Shallow aquatic ecosystems are predominantly mixed, so the indirect effects of elevated temperatures through enhanced water column stratification on cyanobacterial dynamics are much less pronounced compared to deep systems (Scheffer 1998). Instead, cyanobacteria in shallow water bodies are expected to be mainly favored by the direct effects of elevated water temperature that create optimum conditions for their recruitment and growth (Reynolds et al. 2006, Paerl and Huisman 2008, Brookes and Carey 2011, Paerl et al. 2011, Paerl 2014).

The aim of this study was to address two major research gaps: (1) do cyanobacterial species-specific recruitment rates and surface biomass both increase similarly to elevated water temperature, or is the response isolated to just increases in surface biomass? (2) How do the effects of a constant rise in mean water temperatures on recruitment rates and surface biomass differ from those of a projected climate scenario including warming variability below and above mean warming conditions? To answer these questions, we conducted a long-term mesocosm experiment where we evaluated the response of dominant bloom-forming species from a natural cyanobacterial community to two climate warming scenarios: one with a constant elevation in water temperatures (mimicking a rise in mean water temperatures), and another with the same long-term water temperature

elevation, but including short-term decreases and increases in water temperature below and above mean warming conditions. Hence, the second climate scenario captured predicted climate warming variability according to climate change models, where increases above mean warming conditions reflect a greater incidence of heat waves (IPCC 2013). We hypothesized that:

**H1:** Overall, increased water temperatures in the two heated treatments would result in a shift to an earlier onset of the cyanobacterial bloom and higher cyanobacteria biomass at the community level relative to ambient water temperatures.

**H2:** Overall elevated water temperatures in the two heated treatments will increase both the rate of benthic recruitment and pelagic biomass of specific cyanobacterial species, as well as reduce the time it takes for them to reach their peak biomass during the growing season compared to ambient temperatures. We predict cyanobacterial taxa undergoing dormancy as physiologically resting vegetative cells (e.g., *Microcystis* spp.) to show greater positive response in recruitment rates to elevated water temperatures compared to akinete-forming cyanobacteria. We also expect *Microcystis* spp. to show stronger positive responses to warming in surface biomass development compared to other cyanobacterial species due to their high growth sensitivity to water temperature increases (Reynolds et al. 2006, Carey et al. 2012).

**H3:** Increased warming variability can either increase or decrease benthic recruitment rates and pelagic biomass of specific cyanobacterial species compared to a constant elevation in water temperatures. Extreme temperature fluctuations from mean warming conditions can considerably alter population growth rates, and thereby standing biomass dynamics (Thompson et al. 2012, Lawson et al. 2015), where the exact direction of the response (positive or negative) is strongly determined by the shape of the temperature–growth performance curve of each species (Reynolds et al. 2006, Lüring et al. 2013, Paerl et al. 2014). Because cyanobacterial migration from the benthic to the pelagic environment is generally preceded by their activation, maturation, and growth from resting stages at the sediment surface (Hansson 1996, Verspagen et al. 2005, Carey et al. 2014), we also expect a similar response in recruitment rates.

## MATERIALS AND METHODS

### Experimental design and maintenance

Our mesocosms were established outdoors at Lund University (55°42'46" N, 13°12'26" E), and lasted between May 2014 and October 2015. This study, however, mainly focused on describing patterns of both cyanobacterial recruitment rates and pelagic dynamics on the second growing season, that is, between February and October 2015. The reasons for this design are that

many cyanobacteria start recruiting from sediments before May (Verspagen et al. 2005, Reynolds et al. 2006) and the early start in February 2015 allowed us to cover an entire growing season over nine consecutive months.

The experiment consisted of 24 insulated, cylindrical, polyethylene enclosures (diameter = 0.7 m; height = 1 m) with a total volume of 400 L. The enclosures were placed in a randomized design, so all enclosures were exposed to the same natural variation in the light climate. Three experimental treatments ( $n = 8$  replicates per treatment) consisted of (1) ambient environmental conditions (C), (2) a constant elevation of 4°C above the ambient water temperature (T), and (3) a treatment with fluctuating warming—ranging from 0 to +8°C from ambient conditions (F). This latter treatment mimicked a predicted climate scenario of more frequent and intense temperature variations in the future based on model simulations from IPCC and the Swedish Meteorological and Hydrological Institute (SMHI) for a climate scenario during the period 2071–2100, that is, about 50–75 yr into the future when heat waves are predicted to become more frequent (IPCC 2013). In total, the model scenario in the F treatment allowed for a total cumulative time of 14 weeks with water temperature increases above the T treatment (i.e., ranging between +5 and +8°C above ambient temperature). These heat waves occurred during different seasonal periods (February–March, April–May, and July and September 2015) and lasted from 2–5 weeks (Fig. 1; see background colors in Figs. 2, and 4). It should be noted that the yearly mean temperatures were +4°C higher than at present in both T and F treatments. Hence, any differences in response among organisms between those two treatments were due to the way temperature was distributed (as a mean increase [T] or as fluctuating warming including heat

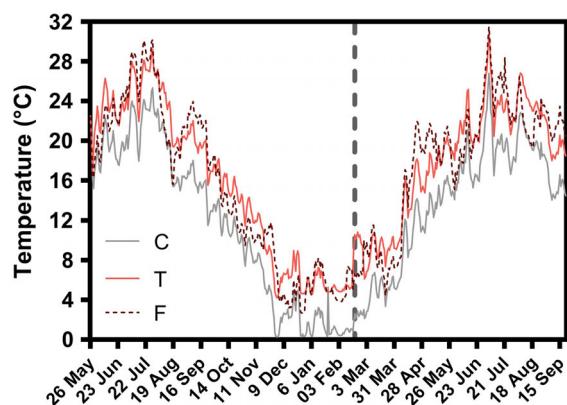


FIG. 1. Temperature recorded during the experiment, including the previous experimental year. Values represent ambient, daily mean temperature (°C) in the control (C; gray line), constant-heated treatment (+4°C above control; T; red line), and fluctuating-heated treatment (+0–8°C above control; F; dark-red broken line). The dashed vertical line represents the time when the monitoring of both cyanobacterial recruitment rates and pelagic biomass started.

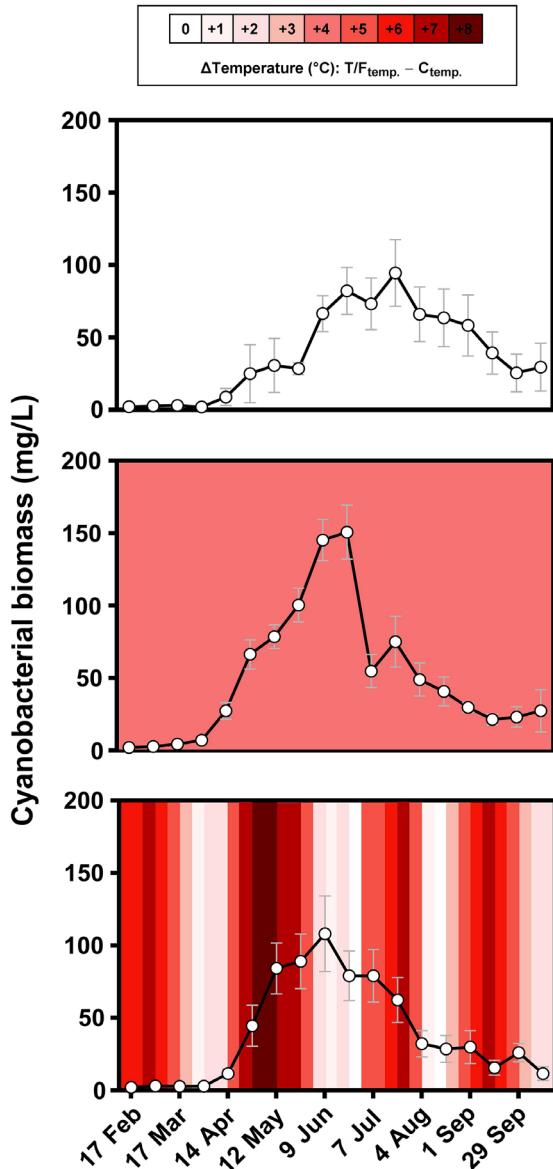


FIG. 2. Temporal dynamics of the total cyanobacterial biomass (mg/L). The three rows show time-series development (means  $\pm$  SE) at ambient temperatures (upper row; C-treatment), constant-heated treatment (middle row; T-treatment) and fluctuating-heated treatment (bottom row; F-treatment). The temperature experienced in the heated treatments (T and F) with respect to the control (C) is represented by the increase in red intensity (i.e.,  $\Delta$ Temperature ranging from +0–8°C).

waves [F], respectively), and not a result of differences in the long-term elevation in mean temperatures. This experimental design therefore allowed testing the potential effects that a mean temperature increase will have on species-specific recruitment rates and pelagic dynamics in comparison to a scenario incorporating predicted patterns of more frequent and intense extreme climatic events in the future.

The sediment and water were collected from Lake Krankesjön (55°42'27" N, 13° 27'58" E; mean depth, 1.5 m), a lake in southern Sweden. We chose Lake Krankesjön because it is a mesotrophic to eutrophic lake, where cyanobacteria constitute an important component of the phytoplankton community and where monitoring data are available (Appendix S1: Table S1). To initiate the experiment in May 2014, we placed mixed lake sediment in a plastic tray (40  $\times$  30  $\times$  12 cm) at the bottom of the enclosures and then filled the mesocosms with 400 L of unfiltered lake water. The sediment was collected from the top few centimeters of the lake sediment with hand nets and placed in dark boxes for transportation to the experimental facilities at Lund University. The water temperature in the mesocosms was controlled by a computerized system using real-time temperature sensors and heaters (Hansson et al. 2013). The ambient temperature changes in the control treatments were mirrored at a specified, elevated temperature level in the heated treatments (Fig. 1). The volume of the mesocosms was adjusted every week by adding distilled water to compensate for evaporation losses. The walls of the containers were scrubbed weekly to minimize the growth of periphytic algae and minimize enclosure effects.

Our mesocosms mimicked natural eutrophic lake ecosystems by having both high levels of nutrient supply and limited zooplankton herbivory, bottom-up and top-down conditions that are known to favor the occurrence of harmful cyanobacterial blooms (Urrutia-Cordero et al. 2015, Ger et al. 2016). To achieve this, all mesocosms contained juvenile fish from the start of the experiment (approximate length 50 mm). Two *Pungitius pungitius* were added initially (May 2014), and one *Carassius carassius* was added to each mesocosm in July 2014. Both fish species are common in southern Sweden and are known to exert a strong top-down control on zooplankton in outdoor mesocosms (Urrutia-Cordero et al. 2016, 2017). In addition, all enclosures received the same amount of nutrients every second week, so any difference among treatments in a response variable cannot be attributed to changes in nutrient supply. The nutrient additions consisted of 1 mL of commercially available plant nutrients (Blomstra växtnäring, Cederroth, Upplands Väsby, Sweden; solution concentration of nitrogen and phosphorus of 50.1 and 10.0 g/L, respectively).

#### Sample collection and analysis

We sampled both cyanobacterial recruitment and pelagic biomass every second week from 17 February 2015 to 13 October 2015. During samplings, the sediment trays were gently lifted to the water surface by strings, and traps with an area of 0.008 m<sup>2</sup> were set at the top of the sediment to quantify cyanobacterial recruitment (hereafter denoted as “recruitment”). The traps consisted of a jar and a funnel attached to a plastic frame with two 10- $\mu$ m-mesh windows to allow

circulation and exchange of water between the trap and the surroundings (Stahl-Delbanco et al. 2003; Zhang et al. 2015, 2018). Hence, the traps were set at the top of the sediments with the funnel facing downwards. To avoid contamination by plankton from the water column, the traps were filled with dechlorinated tap water before setting. Traps were retrieved after 24 h by again gently lifting the sediment trays, and the samples were preserved with Lugol's solution and stored at 4°C. With this controlled procedure we minimized any intrusion of organisms from the water column, as well as any resuspension of the sediment; that is, only organisms actively recruiting from the sediment were caught in the traps and sediment disturbance effects during the process of trap setting and retrieval were minimal.

The day after the recruitment traps were deployed (i.e., the same day when the recruitment traps were retrieved), samples from the water column (hereafter denoted as "establishment") were taken from the surface to 0.1 m above the bottom using a Plexiglas™ tube (length: 1 m; diameter: 70 mm). We took samples from the water column before retrieving the recruitment traps. Three samples were taken across the diameter of each enclosure and were pooled in a bucket (10 L). Subsamples were then taken for phytoplankton counts (100 mL) and immediately preserved in Lugol's solution and stored at 4°C. In order to characterize the trophic status of our mesocosms, we also collected subsamples (50 mL sterile falcon tubes) for nutrient analyses in three of the samplings (at 17 February, 13 June, and 13 October of 2015). These nutrient samples were immediately stored at -20°C until further analyses. In addition, we collected zooplankton samples (every second week) in order to determine the overall effectiveness of the fish additions in controlling the composition of the zooplankton community. From the remaining water in the 10-L bucket, we filtered 5 L of water through a nylon mesh (50-µm pore size). The animals in the mesh were collected in a 100-mL glass bottle by flushing them with tap water. The zooplankton samples were immediately preserved in Lugol's solution and stored at 4°C.

For the phytoplankton samples taken from the recruitment traps and the water column, cyanobacteria and other algal groups were determined to the species and genus level, respectively, by using tubular chambers and an inverted microscope (Olympus IX53; magnification: 400, 200, and 100 magnification for taxa <20 µm, 20–50 µm, and >50 µm, respectively). Phytoplankton biomass of the different taxa was estimated according to Ekvall et al. (2014). Recruitment rates were calculated based on the area of the recruitment traps (0.008 m<sup>2</sup>), the time that the traps were deployed (24 h), and the cyanobacterial biomass counted in each sample. The nutrient samples were analyzed for total phosphorous and total nitrogen concentrations following Swedish standards methods (SS-EN ISO 6878:2005) by the Swedish Standards Institute at a certified laboratory (Synlab, Malmö, Sweden). For the

zooplankton samples, we counted the animals on a stereoscopic microscope (Olympus SZ40) at ×20 magnification, and biomasses were estimated using length–weight regressions according to (Dumont et al. 1975, Bottrell et al. 1976).

To provide a proxy of the cyanobacterial biomass dynamics in the water column since the establishment of the mesocosms, we also monitored the pelagic biomass of cyanobacteria every second week during both years (from May 2014 until October 2015) based on photosynthetically derived fluorescence data. Samples were taken using the same procedure as the phytoplankton samples described above, except that they were not fixed in Lugol's solution. We then measured in these samples the chlorophyll-a concentrations attributed to the cyanobacterial community immediately after sampling on a fluorometer in the laboratory (AlgaeLabAnalyser fluorometer, bbe moldaenke, Preetzer Chaussee, Germany).

#### *Data analyses*

We were primarily interested in determining whether there were changes among treatments in cyanobacterial recruitment rates and pelagic biomass levels across the entire experimental period. In addition, we were interested in determining whether there were changes among treatments in the phenology of recruitment and pelagic biomass dynamics. We assessed these changes at both species and community level. First, we created individual time series for each mesocosm with GraphPad Prism 6.0, where the response variable (cyanobacterial recruitment rate or pelagic biomass) was plotted against experimental time. For each time series, we then calculated the area under the curve (hereafter denoted as AUC) as a measure of the overall level of recruitment rate and pelagic biomass across the entire experimental period, after a similar approach in Frenken et al. (2015). The calculation of the AUC was done with GraphPad Prism 6.0. In addition, we identified in each time series the experimental week of the recruitment rate peak and pelagic biomass peak (Appendix S1: Table S2). Hence, a change in the timing of the recruitment rate peak or pelagic biomass peak (hereafter denoted as TP) among treatments would explicitly indicate whether there is a change in phenology (Zhang et al. 2015). To evaluate treatment differences in our response variables (the AUC and TP for both recruitment rates and pelagic biomass) we used one-way ANOVA analyses with R (version R-3.4.4.; 'stats' package, 'aov' function). We then used Tukey's multiple comparison test to identify which treatments differed from one another (version R-3.4.4.; 'stats' package, 'TukeyHSD' function). If a statistical analysis did not meet assumptions for parametric tests, we log-transformed the response variable. Recruitment samples of one replicate from treatment F were unavailable from 23 June 2015 and onwards; therefore

this replicate was excluded from all analyses of recruitment data.

Finally, we used effect sizes as supporting information in order to assess the overall direction of cyanobacterial recruitment rates and pelagic biomass levels in response to the two warming treatments relative to the controls. Temporal effect sizes (i.e., means calculated from all sampling occasions;  $n = 18$  samplings) were calculated according to Cohen (1988), where large differences in mean values between control and treatment in combination with low variances provide a high effect size. Small differences in mean values in combination with high variances result in a low effect size. Effect sizes larger than 0.5 are generally considered strong (Cohen 1988). Hence, this statistical method is suitable for illustrating overall changes and also provides a graphical representation of their direction relative to the control, where positive and negative effect sizes indicate an increase or decrease in a response variables compared to the control. All final graphs were created with GraphPad Prism 6.0.

## RESULTS

### *Bottom-up and top-down conditions during the experiment*

Total phosphorus concentrations seasonally ranged from 30 to 75 g/L on average across treatments, which indicates that our experimental conditions successfully mimicked nutrient levels typically found in eutrophic lakes (Appendix S1: Fig. S1). In addition, the presence of fish resulted in a zooplankton community dominated across all mesocosms by inefficient small-bodied *Bosmina* spp. (89% of the total zooplankton biomass) and cyclopoid copepods (9% of the total zooplankton biomass), which indicates that the top-down control of cyanobacteria by the zooplankton community was weak (Ger et al. 2016).

### *Cyanobacterial community responses*

We did not find differences among treatments in the total cyanobacterial biomass based on photosynthetically derived fluorescence data during the first year the mesocosms were established (Appendix S1: Fig. S2). During the study period (February 2015 to October 2015), the total cyanobacterial biomass started to increase substantially in all treatments by March–April (Fig. 2). After reaching peaks in June–July, they then showed a gradual decline until the end of the experiment in October (Fig. 2). Constant warming (T) increased the total cyanobacterial biomass compared to the control (C) and fluctuating warming (F) across all the experiment (Fig. 2; Table 1, one-way ANOVA, AUC, significant treatment effect,  $P = 0.019$ ; Tukey post hoc,  $P < 0.05$  for C–T comparison). This is also indicated by the strong positive effect size relative to the control (Fig. 3). The timing of the biomass peak was significantly affected by both constant (T) and fluctuating warming (F; Fig. 2; Table 1, one-way ANOVA,

significant main treatment effect,  $P = 0.007$ ; Tukey post hoc,  $P < 0.05$  for both C–T and C–F comparisons), occurring about 4 and 6 weeks earlier (24 and 9 June, respectively) than the control (22 July), respectively (Fig. 2). Fluctuating warming (F) had no significant effects on the total cyanobacterial biomass (Table 1), although there was a slight tendency for higher total cyanobacterial biomass as revealed by effect size analyses (Fig. 3). Overall, the phytoplankton community was dominated by cyanobacteria (about 88% across all treatments) throughout most of the experiment (Appendix S1: Fig. S3).

### *Cyanobacterial species responses*

The cyanobacterial community was dominated by the taxa *Limnothrix redekei* (67%), *Aphanizomenon gracile* (17%), and *Microcystis* spp. (7%) over the entire experiment and across all mesocosms (Fig. 4). However, the relative contribution of *Microcystis* spp. to the total cyanobacterial biomass increased during late summer and fall, with a contribution of nearly 40% to the total cyanobacterial biomass and with maximum dominance peaks of up to 76% in mid-September (Fig. 4). *Limnothrix redekei* showed high recruitment rates in all treatments already in the beginning of the season, which together with *A. gracile*, was among the first to establish in the water column during spring and the beginning of summer (Fig. 4a, b).

We found tendencies for higher *L. redekei* recruitment rates under constant warming (T) than at ambient control conditions (C) and fluctuating warming (F; Fig. 4a; Table 1, one-way ANOVA, AUC, marginally significant treatment effect,  $P < 0.073$ ). Effect-size analyses confirmed the positive effect of constant warming (T) on the recruitment rate of *L. redekei* (Fig. 5). Similarly, *L. redekei* showed stronger establishment in the water column under constant warming (T) compared to the controls (C) and fluctuating warming (F; Fig. 4a; Table 1, one-way ANOVA, AUC, significant treatment effect,  $P = 0.041$ ; Tukey post hoc,  $P < 0.05$  for C–T comparison). In addition, the timing of the biomass peak of *L. redekei* occurred about 6 and 8 weeks earlier (in May and June) under constant warming (T) and fluctuating warming (F), respectively, compared to the control (July; Fig. 4a; one-way ANOVA, TP,  $P = 0.001$ ; Tukey post hoc,  $P < 0.05$  for C–T and C–F comparisons).

The species *A. gracile* also showed a tendency for phenology changes with a 2-weeks-earlier established biomass peak (in May) under constant warming (T) and fluctuating warming compared to the control (Fig. 4b; one-way ANOVA, TP, significant treatment effect,  $P = 0.034$ ; Tukey post hoc,  $P < 0.05$  for C–T comparison,  $P < 0.1$  for C–F comparison).

Although our analyses did not capture significant effects of fluctuating warming (F) on the recruitment rates and pelagic biomass level of neither *L. redekei* nor *A. gracile* (Table 1), effect-size analyses revealed a slightly positive response relative to the control in the

TABLE 1. Summary of one-way ANOVA analyses evaluating treatment effects on cyanobacterial recruitment rates and established biomass at both species and community level.

Recruitment	Area under the curve (AUC)			Timing of the peak (TP)		
	$F_{2,21}$	$P$	Treatment difference (Tukey)	$F_{2,20}$	$P$	Treatment difference (Tukey)
Total cyanobacteria	4.75	<b>0.019</b>	C–T	6.30	<b>0.007</b>	C–T, C–F
<i>Limnothrix redekei</i>	6.40	<b>0.041</b>	–	9.60	<b>0.001</b>	C–T, C–F
<i>Aphanizomenon gracile</i>	0.03	0.971	–	3.97	<b>0.034</b>	C–T (C–F)
<i>Microcystis</i> spp.	6.52	<b>0.006</b>	C–T, C–F	0.45	0.641	–
Establishment						
<i>L. redekei</i>	2.99	<b>(0.073)</b>	(C–T)	2.92	<b>(0.077)</b>	(C–F)
<i>A. gracile</i>	0.21	0.813	–	1.433	0.262	–
<i>M. spp.</i>	22.84	<b>&lt;0.001</b>	C–T, C–F	0.003	0.997	–

Notes: The area under the curve (AUC) represents the overall change in the intensity of recruitment rates and established biomass across the entire experimental study. The timing of the peak (TP) represents the change in phenology of recruitment rates and established biomass. Treatments are the control (C; ambient temperature), constant-heated treatment (+4°C above control; T), and fluctuating-heated treatment (+0–8°C above control; F). Denominators of F values denote the degrees of freedom.  $P$  values in bold denote significant differences among treatments based on  $\alpha = 0.05$ , whereas marginally significant results are indicated in both bold and in brackets. Tukey's post hoc test for multiple comparisons displays which treatments differed from one another.

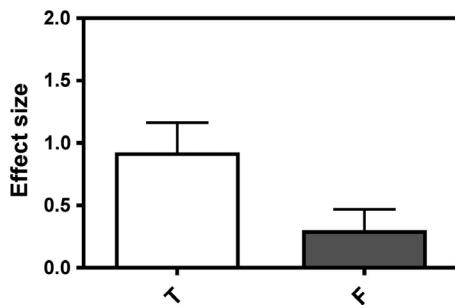


FIG. 3. Temporal effect sizes of the total cyanobacterial biomass. Mean effect sizes ( $\pm$ SE; Cohen 1988) are calculated from all sampling occasions (February–October 2015), in the constant-heated treatment (T; white bars) and fluctuating-heated treatment (F; gray bars). Note that the X axis ( $Y = 0$ ) denotes control conditions.

case of *L. redekei*, although at a lower level than shown under constant warming (Fig. 5). These effect sizes were below 0.5, which are not strong according to Cohen (1988).

Both heated treatments (T and F) had higher recruitment rates (Fig. 4c; Table 1, one-way ANOVA, AUC, significant treatment effect,  $P < 0.001$ ; Tukey post hoc,  $P < 0.05$  for both C–T and C–F comparisons) and established biomass of *Microcystis* spp. (Fig. 4c; Table 1, one-way ANOVA, AUC, significant treatment effect,  $P = 0.006$ ; Tukey's post hoc,  $P < 0.05$  for both C–T and C–F comparisons) than the control. The positive effects of both heated treatments on recruitment rates and established biomass of *Microcystis* spp. were also confirmed by the effect size analyses, which showed that *Microcystis* spp. were the most affected cyanobacterial species (Fig. 5). None of the heated treatments affected the timing of the peak for the recruitment and establishment in the water column of *Microcystis* spp. (Table 1).

## DISCUSSION

Our findings revealed two important aspects with respect to how ongoing climate warming can affect harmful cyanobacterial bloom formation. First, our findings demonstrate, for the first time, that a warmer environment not only increases species-specific cyanobacterial biomass and induces an earlier peak biomass in the pelagic environment, but also increases recruitment rates from the sediments. Many studies have shown the importance of recruitment processes as a source for cyanobacterial pelagic growth in natural environments, as well as how the seasonal natural variation in water temperature correlates with these patterns (Barbiero 1993, Hansson 1996, Rengefors et al. 2004, Verspagen et al. 2005, Carey et al. 2014). However, previous studies evaluating effects of warming on cyanobacteria only provide information on their pelagic dynamics, neglecting the benthic recruitment process (Kosten et al. 2012, Ekvall et al. 2013, Hansson et al. 2013, Urrutia-Cordero et al. 2016). Secondly, our results show that the recruitment rate and pelagic biomass of specific species were affected differently depending on whether climate warming expresses only as an increase in mean water temperatures or, in addition, through increased warming variability (including heat waves). Hence, these results are highly important because they do not only identify a part of the life-cycle of cyanobacteria (benthic recruitment) that is affected by climate warming and that was previously unknown, but it also stresses that species-specific response patterns may be different as a consequence of changes in the variability of warming conditions.

According to hypothesis H1, under a constant elevation in water temperatures (T-treatment), the total cyanobacterial biomass developed earlier and more intensively (30% and 59% more accumulated biomass over time and maximum peak biomass, respectively) relative to control conditions. The observed increase in

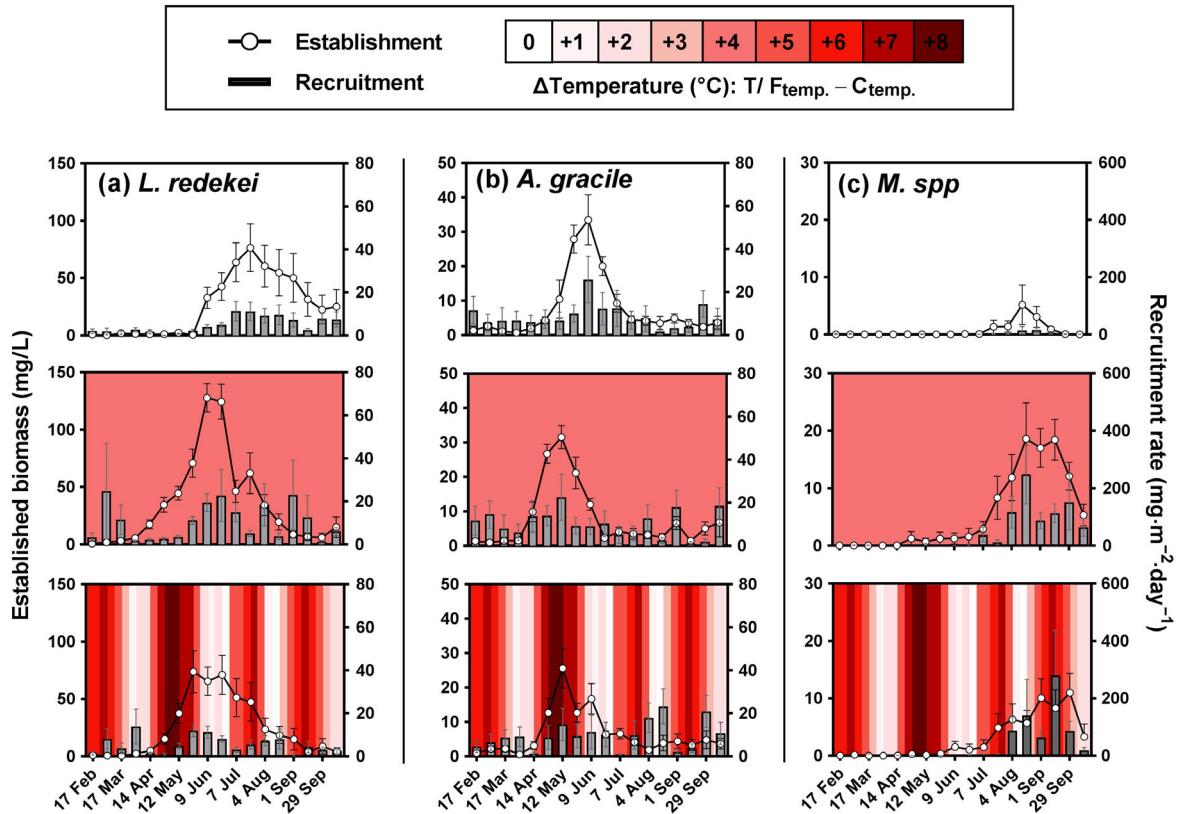


FIG. 4. Temporal dynamics of the biomass in the water column (lines) and recruitment rates of the cyanobacterial species (a) *Limnothrix redekei*, (b) *Aphanizomenon gracile*, and (c) *Microcystis* spp. Time-series development (means ± SE) are shown for the control (upper row; C), constant-heated treatment (+4°C above control; middle row, T) and fluctuating-heated treatment (+0–8°C above control; bottom rows, F) of recruited (mg·m<sup>-2</sup>·day<sup>-1</sup>; gray bars) and established biomass (mg/L; white circles). The temperature experienced in the heated treatments (T and F) with respect to the control (C) is represented by the increase in red intensity of the background (i.e., ΔTemperature ranging from +0 to 8°C).

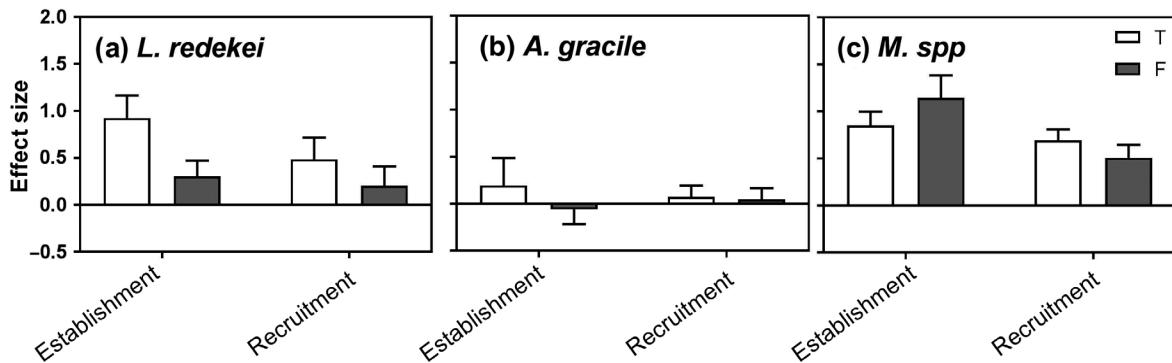


FIG. 5. Temporal effect sizes in establishment and recruitment of the cyanobacterial species (a) *Limnothrix redekei*, (b) *Aphanizomenon gracile*, and (c) *Microcystis* spp. Mean effect sizes (±SE) are calculated from all sampling occasions (February–October 2015) in the constant-heated treatment (T; white bars) and fluctuating-heated treatment (F; gray bars). Note that the X axis (Y = 0) denotes control conditions, and that values above or below that line indicate positive or negative treatment effects, respectively.

overall bloom biomass in the pelagic environment was driven by strong responses of the dominant cyanobacterial species during spring (*L. redekei*; 40% increase in pelagic biomass) and summer (*Microcystis* spp.; 72% increase in pelagic biomass). The observed seasonal

advancement was mainly driven by phenology shifts of the dominant species in spring (with 6 and 2 weeks earlier biomass peaks for *L. redekei* and *A. gracile*, respectively). Importantly, we also observed increases in recruitment rates of dominant cyanobacterial species

during both spring (*L. redekei*; 113% increase in recruitment rate) and summer (*Microcystis* spp.; 1,741% increase in recruitment rate), thus also corroborating H2.

It is notable how positively *Microcystis* spp. responded to a constant elevation in mean water temperatures in our mesocosms (T-treatment). We predicted that *Microcystis* spp. would show much greater sensitivity to warming than other cyanobacterial species in terms of their pelagic biomass development (corroborating H2). Such strong sensitivity of *Microcystis* spp. is expected based on the very high rate of acceleration in growth shown with water temperature increases (Q10) in the laboratory (Reynolds et al. 2006; Lürling et al. 2013), but it has also been observed in complex natural communities during mesocosm experiments (Hansson et al. 2013, Ekvall et al. 2013). Interestingly, our study adds to these findings that the recruitment rate of *Microcystis* spp. can increase to a similar extent as their pelagic biomass in response to warming, which was previously unknown. Other phytoplankton species with similar dormancy strategy as physiologically resting vegetative cells may become active within hours in response to water temperature increases (Sicko-Goad et al. 1986). We may then speculate that the observed positive response in *Microcystis* recruitment in response to constant warming (T-treatment) may be because they become inactive as resting colonies without the need to undergo cellular differentiation as akinetes. Akinete-forming cyanobacteria require more time to develop into mature active life forms, and they might be less sensitive in tracking environmental changes (Barbiero 1993, Karlsson-Elfgren et al. 2004). Although to a lesser extent, the observed positive response to constant warming (T-treatment) in the recruitment rate of the non-akinet-forming cyanobacterium *L. redekei* also supports this notion. Moreover, it is important to stress that cyanobacteria can grow at the sediment surface following activation from resting stages, and that the growth of *Microcystis* spp. is particularly enhanced at elevated water temperatures (Reynolds et al. 2006). Hence, the observed response in *Microcystis* recruitment to constant warming (T-treatment) may also be influenced by increased biomass production in the benthic environment before recruitment to the water column.

Although our experimental setup cannot disentangle how much of the recruited biomass of each species contributed directly to its subsequent pelagic biomass development (because this depends on other factors, such as their rate of growth and mortality within the water column), studies have shown that recruitment-derived subsidies can be responsible for more than 50% of their pelagic biomass. This strong influence of benthic recruitment to pelagic biomass development is because recruited colonies and filaments are crucial as initial inoculum for pelagic growth (Verspagen et al. 2005, Carey et al. 2014). Hence, these results pinpoint, for the first time, that recruitment rates can increase

considerably under a warmer environment and that further studies should focus on assessing the relative importance of changes in this life-history trait in order to predict better how blooms develop as climate warming proceeds.

Our results were also in line with predictions from our second hypothesis (H2) with respect to the effects of fluctuating warming. The positive effects of fluctuating warming were mainly observed on *Microcystis* spp. during summer (1,420% and 347% increase in recruitment rate and pelagic biomass level, respectively), but also this treatment affected the phenology of *L. redekei* and *A. gracile*. However, this treatment did not induce higher recruitment rates or higher pelagic established biomass of the dominant species in spring (*L. redekei*), and so these effects diverged from those of a constant warming (T-treatment), thus corroborating our third hypothesis (H3).

Theoretical as well as empirical studies have shown that environmental variation around mean conditions (e.g., heat waves) can either increase or decrease population growth rates (Lawson et al. 2015), and the nature of such contrasting responses is highly dependent on species-specific growth temperature dependencies (Bozinovic et al. 2011, Estay et al. 2014). A general assumption is that cyanobacterial growth rates increase with water temperature and then start to saturate at around 20–25°C, above which many cyanobacteria can maintain relatively high growth rates (Paerl and Huisman 2009, Paerl et al. 2011, Paerl 2014). Responses of cyanobacterial species to extreme water temperature fluctuations around mean warming conditions are then expected to be stronger when baseline water temperatures are low and the slope of the temperature-performance curve is greater, for example, during spring (Paerl 2014, Lawson et al. 2015). Our results also align with this conception. We did not find notable differences between the effects of fluctuating warming (F-treatment) and constant warming (T-treatment) on cyanobacterial pelagic biomass during summer (*Microcystis* spp.), but we did so during spring (*L. redekei*). These patterns are in accordance with observations in natural systems, where stronger effects of heat waves on cyanobacterial pelagic dominance have been observed during autumn and winter periods, compared to summer when baseline water temperatures are higher (e.g., see Anneville et al. 2015). Recruitment from the benthic environment may also be affected in the same way as cyanobacterial pelagic biomass because of similar temperature influences on growth at the sediment surface prior to recruitment into the water column (Ståhl-Delbanco 2004). Nevertheless, it is important to stress that studies have also found substantial differences in response to elevated water temperatures among different cyanobacterial species, and even among strains (Lürling et al. 2013). These differences suggest that conclusions based on a general assumption of the shape of the cyanobacterial temperature-performance curve should be made with caution

(Carey et al. 2012), also because temperature can indirectly affect other drivers of cyanobacterial bloom formation (e.g., trophic interactions, including parasitism; Frenken et al. 2015, Ger et al. 2016). Therefore, the combination of mesocosm studies with laboratory assays measuring species-specific thermal-growth performance curves would indeed help to confirm the actual mechanism behind the observed patterns in future studies.

It is important to remark that the observed effects of warming were largely facilitated by the environmental preference of many bloom-forming cyanobacterial species for eutrophic conditions (Kosten et al. 2012, Visser et al. 2016, Urrutia-Cordero et al. 2016). In other words, the eutrophic conditions in our mesocosms largely displaced (in the first place) phytoplankton taxa other than cyanobacteria with potential to cope with warm water temperatures and that may increase competition for resources (e.g., green algae; Lürling et al. 2013), as confirmed by the almost exclusive dominance of cyanobacteria within the phytoplankton community regardless of the experimental treatment (Appendix S1: Fig. S5). These environmental conditions mimicked eutrophic systems with both high nutrient supply and a dominance of inefficient, small-bodied grazers with limited grazing control of cyanobacteria (Ger et al. 2016). Hence, the effects of warming could be different under other trophic conditions (e.g., oligotrophic or mesotrophic), as competitive outcomes among phytoplankton taxa are the result of the interplay between multiple factors and not only by water temperature changes.

We conclude that in shallow systems, climate warming can indeed affect cyanobacterial dynamics at different life-history stages, all the way from benthic recruitment up to their pelagic dynamics. In addition, our experimental study enabled us to identify that effects of a climate scenario with increased frequency of heat waves differ from those of a constant increase in mean water temperatures, and that this divergence is linked to species-specific responses, and possibly to the seasonal temperature variation. These results should, however, be put in context, as other factors, such as changes in food web structure, nutrient supply, or other predicted climatic changes (e.g., storms), may interact and amplify the effects of different warming scenarios in the future (Kosten et al. 2012, Hansson et al. 2013, Rigosi et al. 2014, Urrutia-Cordero et al. 2016, Richardson et al. 2018). Harmful cyanobacterial blooms pose a serious public concern for the ecological stability of biological communities and ecosystem services, especially given the ability of many species to produce toxic metabolites. The observed species-specific responses in this study are therefore not trivial. *Microcystis* spp. showed the strongest responses to warming in our mesocosms, and many species from this genus can produce a wide range of toxic compounds to human and animal health, including the potent hepatotoxic microcystins (Codd et al. 2005). Hence, in a broader context, we argue that these findings

are a critical first step to further our mechanistic understanding of the relative importance of increased cyanobacterial recruitment rates for harmful cyanobacterial bloom formation and in response to different climate change scenarios.

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