



Different climate scenarios alter dominance patterns among aquatic primary producers in temperate systems

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Abstract

In a future climate change perspective, the interactions among different life-forms of primary producers will likely be altered, leading to changes in the relative dominance among macrophytes, filamentous, and planktonic algae. In order to improve the possibilities to forecast future ecosystem services and function, we therefore conducted a long-term mesocosm study where primary producers were exposed to different climate scenarios, including both a mean increase in temperature (4°C) and a similar energy input, but delivered as “heat waves” (fluctuations 0–8°C above ambient). We show that in shallow systems, future climate change scenarios will likely lead to higher total macrophyte biomasses, but also to considerable alterations in the macrophyte community composition. The biomass of filamentous algae (*Cladophora*) showed no significant difference among treatments, although effect size analyses identified a slight increase at heated conditions. We also show that future climate change will not necessarily lead to more phytoplankton blooms, although a considerable alteration in phytoplankton community composition is to be expected, with a dominance of cyanobacteria and Cryptophytes, whereas Chlorophyceae and diatoms will likely play a less pronounced role than at present. In a broader context, we conclude that the total biomass of macrophytes will likely increase in shallow areas, whereas phytoplankton may not show any strong changes in biomass in a future climate change scenario. Instead, the major changes among primary producers will likely be mirrored in a considerably different species composition than at present.

Most lakes and ponds on Earth are small, shallow systems (Downing et al. 2006) and such shallow systems also dominate in most urban areas where they provide important ecosystem services as drinking water reservoirs and hot-spots for recreation

and biodiversity. Moreover, the composition of, and interactions among, primary producers to a large extent determines the quality of the ecosystem services provided by any specific lake or pond, and since submerged macrophytes are important components of shallow lakes they are often a prerequisite for high-quality ecosystem services (Scheffer 1990; Moss 2012). However, submerged macrophytes do not act in isolation, since all primary producers compete for access to nutrients and light. Hence, since those resources are often spatially separated and two-directional with light coming from above and the sediment being a main nutrient source for rooted plants and sediment dwelling algae, the success of different life-forms will vary both spatially and temporally. Those different life-forms have similar resource requirements with respect to nutrients and light, but have solved the access to their resources differently. Hence, many submerged macrophytes are able to utilize nutrients from

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: L.-A.H., P.U.-C., H.Z., and M.K.E. conceived the design of the study. All authors contributed to the setup, sampling, and analyses of samples from the study. L.-A.H. wrote the first version of the manuscript and all authors contributed and commented on the text.

both the water and the sediment, and to harvest light as close to the water surface as possible, whereas phytoplankton have first access to light, but rely on nutrients from the water column (Hansson 1988). If nutrient concentrations in the water increases, phytoplankton, as well as filamentous algae, generally become more abundant (Cao *et al.* 2017), reducing light penetration through the water column and subsequently primary production at the sediment surface becomes light-limited (Hansson 1988, 1989). Hence, there is an ever-ongoing competition among different life-forms of primary producers which to a large extent determines water clarity (Scheffer 1990; Moss 2012). In shallow waters, canopy-forming submerged macrophytes photosynthesize close to the water surface and are thereby less vulnerable to light competition from phytoplankton although it has been questioned if observed declines in macrophyte biomass in eutrophic waters is caused by competition with phytoplankton or a result of overgrowth by filamentous algae (Phillips *et al.* 1978, 2016). Competition for nutrients and light among primary producers may not be the only force determining the actual composition of primary producers in a specific lake. Other forces, such as grazing by invertebrates (Brönmark and Weisner 1992), birds (Chaichana *et al.* 2009), and fish (Hansson *et al.* 1987), may also be of importance. We will here exclusively focus on how changes in climate scenarios may directly or indirectly, for example, through competition, affect different life-forms of primary producers.

As climate on Earth is rapidly changing (IPCC 2013), a major challenge is to understand and predict how interactions among primary producers will change and thereby shape future lakes and ponds. Temperature is a major factor affecting biomass development of primary producers (Mckee *et al.* 2002; Hansson *et al.* 2013; Cao *et al.* 2014, 2017; Urrutia-Cordero *et al.* 2016; Li *et al.* 2017; Velthuis *et al.* 2017), although most studies have focused on a single group of primary producers and fail to provide knowledge on the overall, long-term outcome of the interactions among macrophytes, filamentous, and planktonic algae. Moreover, a major knowledge gap is that despite many studies address increases in the mean temperature, few have focused on how effects of heat waves (Cao *et al.* 2015, 2017; Bertani *et al.* 2016; Li *et al.* 2017), that is, a higher mean temperature delivered as stronger amplitudes in temperature than at present (IPCC 2013), may affect the biomass distribution and competitive interactions among primary producers. Therefore, our main aim has been to provide understanding on how the primary producers develop in climate change scenarios and to disentangle which life-forms or taxa that will likely become more dominant, alternatively decline in importance in future shallow, temperate lake ecosystems.

Albeit long-term monitoring studies in natural systems are very useful for studying macrophyte development, they are not enough if we are to provide predictions and understand on what to expect in the future. A complementary approach to monitoring studies is to use models for climate projections,

such as the ones provided by IPCC (IPCC 2013), and then experimentally create such scenarios and follow how organisms respond. Hence, the rationale for our large-scale and long-term experimental setup was to provide a platform for providing a rough understanding on how biomass development among primary producers may change at different scenarios of climate change, and thereby delivering likely scenarios for decision makers to manage future lake ecosystems. In pursuing this aim, we used mesocosms equipped with an advanced temperature steering system where we addressed two different climate scenarios, one following ambient temperatures at a 4°C higher level, and another providing the same amount of heat energy over time, but delivered with fluctuating temperatures (0–8°C above ambient), that is, as “heat waves,” as predicted by IPCC (IPCC 2013). Those different scenarios are based on predictions that climate change will lead to an increase in mean temperature, whereas recent predictions suggest that we may also experience an increase in temperature fluctuations and that the frequency of “heat waves” will increase. Therefore, we have here focused on how the biomass development of different primary producers, specifically phytoplankton, macrophytes, and filamentous algae, respond to those predicted climate change scenarios. Hence, we specifically analyze the accumulated biomass over two vegetative seasons and one winter season and illustrate the results using effect size as metrics, that is, comparing the different climate scenarios to the present situation. A main hypothesis has been that the way climate warming is delivered, that is, through an increase in mean temperature or as heat waves, will affect the outcome of the competition among primary producers and thereby affect dominance patterns. We then assessed the interactions and biomass developments among primary producers in these scenarios, thereby providing both mechanistic and predictive understanding on how the composition of the primary producer community may be shaped in future lakes and ponds.

Methods

Experimental set-up

An outdoor experiment, consisting of 24 insulated mesocosms with a volume of 400 L each (diameter = 0.7 m, height = 1 m), was run at Lund University (55°42'N, 13°12'E) for 18 months from May 2014 to October 2015, that is, including one winter and two summer seasons. Since our study focused on shallow lake ecosystems, which is the dominant type of lakes worldwide (Downing *et al.* 2006), we do not take water column stratification into account and the mesocosms were therefore gently aerated with aquarium pumps in order to mix the water column and evenly distribute temperature changes. Each mesocosm was filled with 400 L unfiltered lake water from the eutrophic Lake Krankesjön (55°42'N, 13°27'E; mean depth = 1.5 m; mean total phosphorus concentration [\pm SD] during a 10 yr period has been

37 [\pm 15] $\mu\text{g L}^{-1}$), thereby adding inoculum for phytoplankton and filamentous algae. As our aim was that the mesocosms should function as “mini-lakes”, we also introduced one crucian carp (*Carassius carassius*) and two nine-spined sticklebacks (*Pungitius pungitius*) of about 50 mm in length (1.7 g, wet weight). Fish mortality was low, and any dead fish was immediately replaced. The fish also kept invertebrate grazers, including zooplankton at very low levels, suggesting that grazing on primary producers was negligible during the study period.

Three representative macrophyte species for the region, *Chara tomentosa*, *Elodea canadensis*, and *Myriophyllum spicatum*, were, together with sediment, collected from the same lake as the water. Four healthy and clean apices were cut at 15 cm below the top and planted into three small plastic pots in each mesocosm (height = 12 cm, diameter = 15 cm) which were filled with 6 cm of lake sediment with 2 cm of sand on top to stabilize the plants. The plastic pots were placed on a plastic tray (length 50 cm and width 40 cm) at the bottom of each mesocosm, and lines were used to lift and lower the trays. The initial biomass relations among primary producers was similar to what can be expected in a shallow, mesotrophic lake in temperate regions. Before initiating temperature treatments, the mesocosms were given 2 d to equalize. Moreover, the experiment started during spring, that is, in the beginning of the vegetation period when the biological activity was rather low.

Our study consisted of three treatments (each replicated eight times): controls (C, ambient temperatures), mimicking the current climate state in a temperate shallow lake; a treatment where the temperature followed the ambient daily and seasonal variations, but at a 4°C higher level (T); and finally, a treatment with a preprogrammed fluctuating temperature, ranging from 0°C to 8°C above ambient conditions (F; Supporting Information Fig. S1), mimicking the predicted climate scenario of more frequent and intense temperature variations in the future (IPCC 2013). The frequency and amplitudes of the heat waves was based on model predictions from IPCC (2013) and the Swedish Meteorological and Hydrological Institute (SMHI) for a climate scenario about 75 yr into the future. The mesocosms were randomly distributed outdoors on a flat area. It should be noted that the T and F treatments received identical energy input, that is, the mean temperature during the study period was similar; that is, any difference in response among primary producers between those two treatments are due to the way temperature was distributed, not a result of differences in energy input. We acknowledge that experimental studies can never completely mirror natural ecosystems and that experimental data should be interpreted with care. However, by performing identical procedures and samplings in all mesocosms, experiments offer a rare opportunity to identify mechanisms and differences between the ambient control conditions and treatments, in this case “heat waves” and a 4°C mean increase in

temperature, thereby providing a complementary tool to monitoring of natural systems in understanding and predicting direction and strength of the effects from future climate warming.

Maintenance

The increase in temperature in the heated treatments (T and F) was attained by using a computer-controlled temperature system that regulated the elevated temperature in the treatments based on the mean temperatures in the control mesocosms (Hansson et al. 2013; Zhang et al. 2015; Li et al. 2017). Temperatures were automatically measured every 10 s using thermal sensors (National Semiconductor, LM335AZ, precision temperature sensor), and if the temperature in any of the T or F mesocosms differed more than 0.2°C from the desired temperature, an aquarium heater (Jäger 150W, EHEIM GmbH & Co, Stuttgart, Germany) of that specific mesocosm was turned on or off until the desired temperature was re-established. Moreover, heaters were automatically turned off if the temperatures should increase above 30°C, for example, during a hot summer day. Deionized water was added weekly to compensate for evaporation losses and assured that the water levels were similar in all mesocosms throughout the experiment. Although experimental setups can never completely mirror natural conditions, our mesocosms were deployed outdoors ensuring that all mesocosms were exposed to similar weather conditions, including light conditions, as a natural lake. Moreover, to maintain similar nutrient levels among treatments, and to approximately maintain the nutrient status found in many shallow meso- to eutrophic lakes, all mesocosms received the same amount of nutrients during the experiment by biweekly additions of 1 mL of commercially available plant nutrients (Blomstra nutrient solution, Cederroth, Upplands Väsby, Sweden; 50.1 g L⁻¹ dissolved nitrogen and 10.0 g L⁻¹ dissolved phosphorous; Supporting Information Table S1).

Sampling

Samples for phytoplankton were taken from the surface to 0.1 m above the bottom every week. A Plexiglas tube (length = 1 m, diameter = 70 mm) was used to collect an integrated sample of the whole water column. In each mesocosm, three such samples were taken and pooled in a bucket, and then mixed and subsampled for chlorophyll *a* (Chl *a*) quantification and algal pigments. Subsamples for nutrient analyses (total-P and total-N) were also taken from the pooled sample at three occasions (03 March 2015, 23 June 2015, and 13 October 2015) and analyzed by a certified and accredited laboratory (Synlab, Malmö, Sweden) following standard methods by the Swedish Standards Institute. Immediately after sampling, water column concentrations of total chlorophyll *a* (Chl *a*), cyanobacteria, Chlorophyceae, diatoms, and Chryptophyta were analyzed on a fluorometer in the laboratory (AlgaeLabAnalyser, bbe moldaenke, Schwentinal, Germany). Filamentous macroalgae, mainly

Cladophora spp. (hereafter denoted *Cladophora*), growing on the macrophytes or at the water surface were removed by hand every second week (except from November to February when growth was negligible). Between the sampling occasions, the *Cladophora* recovered, albeit at different speed in the different treatments, and our sampling was therefore a measurement of the growth potential at different temperature scenarios. After sampling, the *Cladophora* were left to dry at 55°C for more than 48 h. Thereafter each sample was weighed and at the end of the study, the accumulated biomass, that is, the sum of each sampling occasion, in each mesocosm was calculated. The rationale for using accumulated biomass, that is, the sum of the biomasses recorded at each sampling event, was to include fluctuations in growth and mortality over the whole study period. Removal of *Cladophora* would affect the light attenuation, but since the *Cladophora* recovered within days, the impact of sampling on light attenuation was likely negligible considering the long study period. The macrophyte trays (see above) containing the pots with macrophytes were gently lifted from the bottom of each mesocosm with the attached lines and the plants were hand-washed, dried at 65°C for 72 h and weighed. Macrophytes were sampled 09 December 2014 and 20 October 2015, that is, at the end of the experiment. Plant weights for the two samplings were accumulated to provide an estimate of the long-term response in macrophytes.

Statistics

In this study, we were interested in quantifying the accumulated biomass of each group of primary producer during a long time-period. In order to compare these accumulated biomasses among different primary producers exposed to different climate scenarios, which were sampled at different time scales, we used Kruskal-Wallis one-way ANOVA, complemented with Dunn's multiple comparison test. Differences in nutrient concentrations (Total nitrogen and phosphorus) among mesocosms were tested using a one-way ANOVA with Tukey post hoc test for multiple comparisons.

In order to identify potential changes imposed by the two climate change scenarios in relation to ambient conditions, we tested differences in accumulated biomasses over the investigation period using effect sizes estimated as Cohen's *d* (Cohen 1988).

$$d = \frac{\bar{x}_1 - \bar{x}_2}{s},$$

where x denotes the mean values of control (1) and treatment (2), respectively. s is the pooled standard deviation and is calculated as:

$$s = \frac{\sqrt{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}}{n_1 + n_2},$$

where n denotes the number of replicates and s the standard deviation of control (1) and treatment (2), respectively. Hence, effect size combines mean values and variances and compares treatments with the control (ambient conditions), that is, variances are included in the metrics leading to that graphs of Cohen's *d* are not expressed with error bars. Instead, large differences in mean values between control and treatment, in combination with low variances provide a high effect size, whereas the opposite is the case for small differences in means and large variances. Effect sizes larger than 0.5 are generally considered as strong (Cohen 1988). Hence, this statistical method is suitable for illustrating long-term changes and also provides a graphical presentation of their direction, that is, if a treatment leads to an increase or a decrease in a variable, compared to a control, which in our case was the present climate conditions in temperate lakes. The method has been widely used in biology, for example, in plant ecology (DeMalach et al. 2017). As a complement to the effect size analyses, we performed repeated measures ANOVA's on all response variables except macrophytes since the number of samplings were too low for the analysis.

Results

Biomass developments

None of the macrophyte taxa, including *M. spicatum*, *E. canadensis*, and *C. tomentosa*, showed any response to the different warming scenarios, that is, the response was similar irrespective of if warming was provided through heat waves (F) or an increase in mean temperatures (T). However, the overall production by macrophytes during the investigation period was higher in the two heated treatments than in the controls ($H = 14.060$; $p < 0.001$; Table 1 and Fig. 1). This difference was exclusively a result of a more than doubling in *M. spicatum* biomass in the heated treatments compared to the controls ($H = 14.540$; $p < 0.001$; Table 1 and Fig. 1). On the contrary, *C. tomentosa* showed a more than 20 times higher biomass at ambient than at heated conditions ($H = 8.611$; $p < 0.014$; Table 1 and Fig. 1), whereas *E. canadensis* biomass was similar in all treatments ($H = 3.500$; NS; Table 1 and Fig. 1). The mean total production of the filamentous algae *Cladophora*, mainly attached to macrophytes or floating at the water surface, was between 65 and 90 g m⁻² in all treatments (Fig. 2), but there were no significant differences among treatments ($H = 1.235$; NS; Table 1; Fig. 2). The accumulated phytoplankton biomass showed no differences among treatments ($H = 1.182$; NS; Table 1 and Fig. 2). Similarly, the temporal analysis (rmANOVA) revealed no significant responses to warming for total phytoplankton chlorophyll and *Cladophora*, weak, or nonsignificant responses in Chlorophyceae, cyanobacteria, and Cryptophytes, but a strong negative response of warming for diatoms (Supporting Information Table S2). Despite the lack of a response in total phytoplankton chlorophyll, there were some notable shifts in the temporal patterns

among treatments, for example, an initial temperature response in spring 2014 (Supporting Information Fig. S2).

Effect sizes

Similar to the accumulated biomass calculations, the effect sizes predict that the total production of macrophytes

Table 1. Differences in accumulated biomass under different climate scenarios for phytoplankton, macrophytes (separated into *Chara tomentosa*, *E. canadensis*, *M. spicatum*, and total biomass), and *Cladophora*. Climate scenarios were: ambient temperature (C), an increase in temperature with 4°C above ambient (T) and a similar increase, but delivered as “heat waves,” that is, fluctuating temperatures (F). Differences are tested with Kruskal-Wallis one-way analysis of variance (*H*) and Dunn’s multiple comparison test to disentangle differences between treatments.

	<i>H</i>	<i>p</i>	Multiple comparisons
<i>Cladophora</i>	1.235	NS	NS
Phytoplankton	1.182	NS	NS
Total macrophytes	14.060	<i>p</i> < 0.001	C:T <i>p</i> < 0.002; C:F <i>p</i> < 0.006; T:F NS
<i>C. tomentosa</i>	8.611	<i>p</i> < 0.014	C:T NS; C:F <i>p</i> < 0.016; T:F NS
<i>E. canadensis</i>	3.500	NS	NS
<i>M. spicatum</i>	14.540	<i>p</i> < 0.001	C:T <i>p</i> < 0.002; C:F <i>p</i> < 0.006; T:F NS

NS, nonsignificant differences at the 5% level.

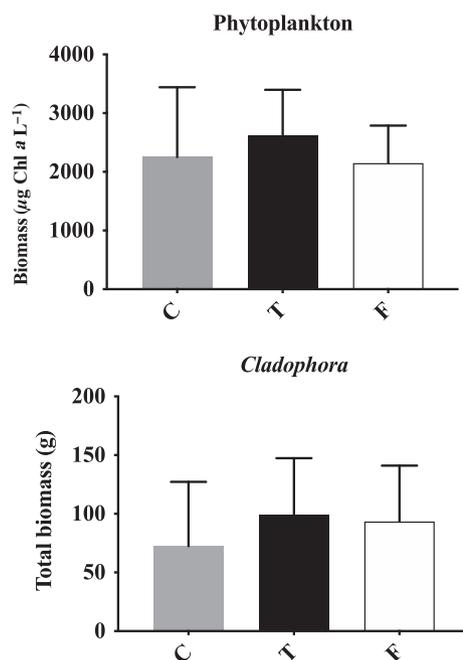


Fig. 2. The accumulated biomass of phytoplankton ($\mu\text{g Chl } a \text{ L}^{-1}$) and *Cladophora* (g m^{-2}) at ambient (C; gray bars), elevated mean temperature of 4°C above ambient (T; black bars), and similar mean temperature elevation, but delivered as fluctuating temperatures with “heat waves” (F; white bars). Bars represent mean values \pm 1SD (*n* = 8). For statistics, see Table 1.

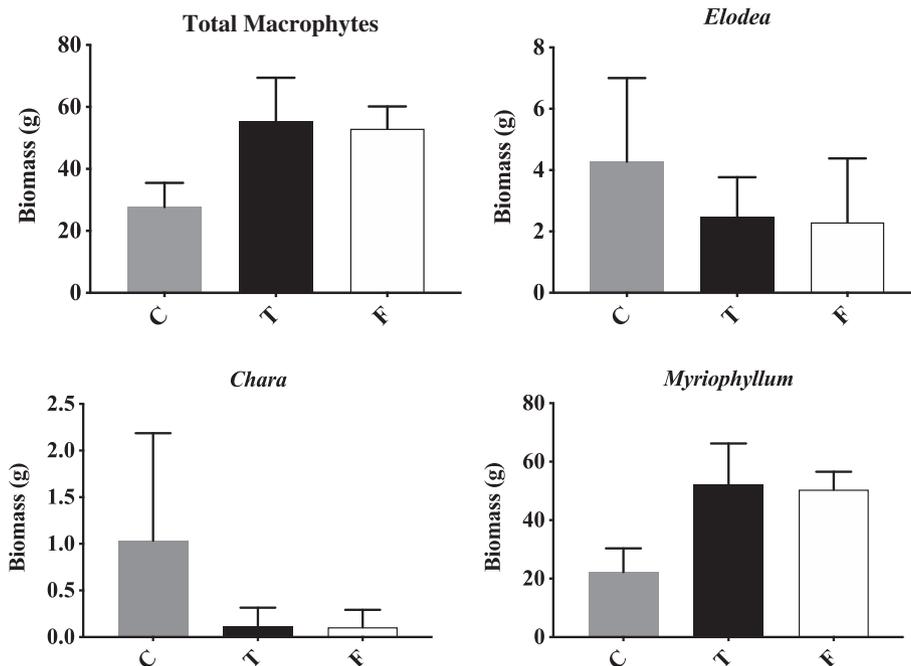


Fig. 1. Final total macrophyte biomasses, and biomasses of each taxa, including *E. canadensis*, *Chara tomentosa* and *M. spicatum* (g m^{-2}) at ambient (C), elevated mean temperature of 4°C above ambient (T), and similar mean temperature elevation, but delivered as fluctuating temperatures with “heat waves.” Bars represent mean values \pm 1SD (*n* = 8). For statistics, see Table 1.

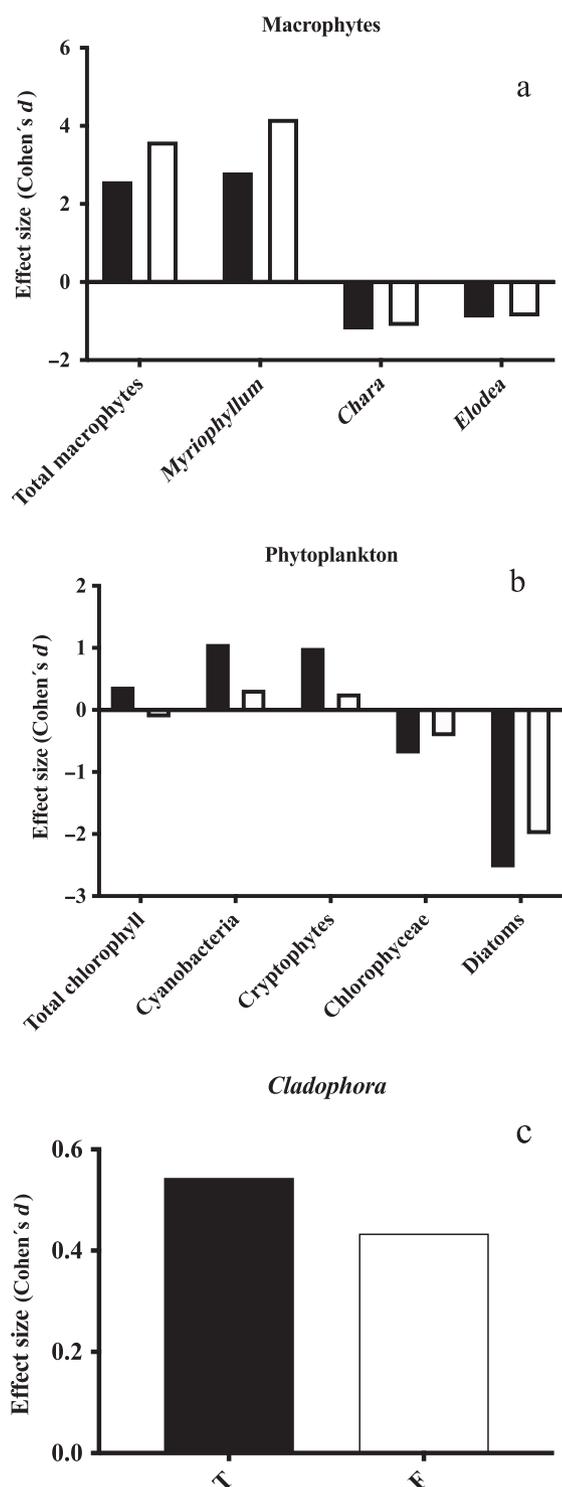


Fig. 3. The effect size (Cohen's d) of a climate change scenario providing a mean increase in temperature (T; black bars) and through heat waves (F; white bars) on macrophytes (a), phytoplankton (b), and *Cladophora* (c). Effects on macrophytes and phytoplankton are also diverted into taxa. Note that the x-axis denotes ambient conditions (C) and positive/negative effect sizes indicate in what direction each taxon has responded in comparison to at ambient conditions.

will increase in a climate change perspective (Fig. 3a) and that the increase was caused by *M. spicatum*. The effect sizes are very strong (above 2), and tend to be more pronounced in the F than in the T treatment (Fig. 3a). Similarly, the other macrophyte species, *E. canadensis* and *C. tomentosa*, responded negatively to elevated temperatures (Fig. 3a). In contrast to the other primary producers, effect sizes of total phytoplankton chlorophyll revealed a positive response to a mean increase (T), but a negative response to heat waves (F) (Fig. 3b). These differences can be directly tracked down to differences in taxa response to the different scenarios. Hence, both cyanobacteria and Cryptophytes showed a positive response to elevated temperatures, but more so to a mean increase (T) than to fluctuating temperatures (F; Fig. 3b). On the other hand, Chlorophyceae and diatoms responded negatively to warming. Hence, due to that different taxa responded differently, the overall effect size on total phytoplankton showed opposite responses to the scenarios, that is, a positive response to a mean increase, but a negative response to fluctuating temperatures (Fig. 3b). In addition to alterations in dominance patterns among phytoplankton taxa, the temporal dynamics differed among treatments, generally showing earlier spring developments in biomass in future scenarios, although not for diatoms and Chlorophyceae (Supporting Information Fig. S2). Although the analyses of total *Cladophora* biomasses showed no significant differences among treatments (Fig. 2), the effect size analysis suggests that *Cladophora* will likely gain from a warmer climate (Fig. 3c).

Temperature and nutrients

Temperatures in the mesocosms followed the natural variability and the maximum temperature difference between the C and the F treatments was 8°C. The highest recorded water temperatures in C, T, and F treatments reached 23.8°C, 27.8°C, and 30.5°C, respectively (Supporting Information Fig. S1). The mean total phosphorus concentrations varied between 29.6 and 83.7 $\mu\text{g L}^{-1}$ among mesocosms, and with the exception of one sampling occasion (03 March 2015; $F_{2,20} = 3.993$; $p < 0.036$; post hoc not significant at the $p < 0.050$ level), there were no differences among treatments (Supporting Information Table S1). Mean total nitrogen ranged between 750 and 2871 $\mu\text{g L}^{-1}$ over the sampling period and showed no differences among treatments at any sampling date (Supporting Information Table S1).

Discussion

Since the climate in many regions of the world is already changing at an unprecedented rate, it is of crucial importance to strive at providing scenarios for how freshwater ecosystems and their ecosystem services may develop in order to provide decision support and allow for planning of management actions (Urrutia-Cordero et al. 2016). Although most studies

addressing effects from climate change focus on alterations in mean temperatures, recent predictions suggest that not only mean temperatures, but also the variation in temperature will increase, suggesting that “heat waves” may become more common. Such variation may affect the establishment of primary producers and our study has therefore focused on if the mode climate warming is delivered will affect the outcome of the interactions among primary producers. However, at the level of total biomass produced, we found no support for this hypothesis since all primary producers showed similar responses irrespective of how warming was provided, that is, we were unable to record any significant differences between the T and F treatments regarding total biomasses of macrophytes and planktonic algae. However, the total macrophyte biomass was about twice as high in the heated treatments than at ambient condition, which was exclusively a result of that *M. spicatum* benefitted from warmer conditions, whereas both *Elodea* and *Chara* tended to show higher biomass development at ambient than at warmer conditions (Fig. 1). Although there is no doubt that *Myriophyllum* became competitively superior to *Elodea* and *Chara* at warmer conditions, all three taxa were grown together, suggesting that direct effects of warming on *Elodea* and *Chara* cannot here be separated from competitive interactions among macrophytes. Irrespective of mechanism, we may predict that in future freshwater systems, *Myriophyllum* will likely become a more dominant actor in the macrophyte community than at present. We found no difference in macrophyte development between the two modes warming was provided, that is, through a mean increase (T) and the similar amount of energy provided as fluctuating temperatures (F). However, it has previously been shown that different macrophyte taxa may respond differently to heat waves (Cao et al. 2015), and also that the timing of heat waves, but not an increase in mean temperature, strongly affect flowering, and thereby the sexual reproduction in *Myriophyllum* (Li et al. 2017). In a broader context, our data suggest that we may expect higher macrophyte biomasses, as well as alterations in the macrophyte community composition in a future climate change scenario. Whether or not this is due to direct effects of temperature or that competition among macrophytes will change with climate, or a combination of both is, however, still an open question for future studies.

In contrast to macrophytes, the accumulated biomass of phytoplankton was, surprisingly, not affected by elevated temperatures during the 18 months the study lasted (Fig. 2), suggesting that a future climate change scenario may not necessarily lead to more phytoplankton blooms (Paerl and Huisman 2008; Kosten et al. 2012), at least not in shallow systems and at time scales covered in this study. Similarly, no significant differences in biomass development of *Cladophora* were detected, although effect sizes indicate that we cannot exclude a positive response to warming (Fig. 3c), suggesting that *Cladophora* may, at a longer time perspective, reduce light availability for macrophytes and thereby pave the road for

phytoplankton blooms, as suggested by Phillips et al. (1978, 2016). Hence, as a lake undergoes eutrophication, phytoplankton may eventually become the dominant primary producer life-form (Moss et al. 2003), and among them, cyanobacteria often become competitively superior as eutrophication proceeds, and also seems to benefit from a warmer climate (Paerl and Huisman 2008, Kosten et al. 2012). At the conditions provided in our long-term experiment, those findings are strengthened and our study also identified Cryptophytes to step up as an algal group likely to benefit from future warming. On the contrary, both Chlorophyceae and diatoms may perform less well under warmer conditions either due to altered species interactions or to direct effects from higher temperatures, suggesting that although the total phytoplankton biomass may remain similar to at present, we may expect considerable alterations in the phytoplankton community composition. There were also some notable differences in the temporal patterns of phytoplankton among treatments, specifically an initial temperature response in spring 2014 (Supporting Information Fig. S2). There was also generally an earlier decline in biomass during fall in heated than in ambient treatments for some of the taxa (Supporting Information Fig. S2), which was likely due to the twice as high macrophyte biomass in heated treatments, leading to nutrient competition.

Submerged macrophytes and phytoplankton generally play specific roles as end points at different alternative stable states of lakes (Scheffer 1990; Moss 2012), where submerged macrophytes are generally associated with clear water, whereas phytoplankton constitute the turbid end point with detrimental effects on ecosystem services for society. Therefore, many management and restoration attempts, for example, nutrient reduction and biomanipulation (Hansson et al. 1998; Hilt et al. 2018) set the target to reach a state dominated by macrophytes, that is, to conserve beds of submerged macrophytes. A major aim of our study was to provide a scenario for how the primary producer assemblage may be shaped by ongoing climate warming, that is, to provide a rough, conceptual estimate on directions in biomass developments among primary producers in a climate change perspective. The heat wave treatment induced oscillations in temperature from 0°C to 8°C above ambient, which are oscillations commonly experienced by aquatic organisms in shallow systems even on a daily basis, for example, between day and night. Our temperature sensors automatically turned off the heaters if temperatures raised above 30°C since heat stress on enzyme systems, and thereby metabolism, may be affected at higher temperatures. However, in a future perspective, natural lakes at lower latitudes may experience temperatures far above 30°C during periods of heat waves, suggesting that physiological injuries cannot be excluded. At higher latitudes, where low temperatures often limit growth rate, we may instead expect heat waves to incur increased growth rate in many taxa, and thereby alterations in the competitive landscape. Our study, performed at a latitude of 55°N, may

be an illustration of this scenario although further studies are needed to disentangle differences in latitudinal effects of a changing climate.

Besides providing predictive guidance regarding possible future developments among primary producers, our study also aimed at stimulating discussion and formulations of hypotheses regarding, for example, mechanisms involved, changes in energy and nutrient flows, as well as short-term, seasonal variations among primary producers. The main, novel results from our study suggest that it is mainly the amount of heat energy, and not the mode the heat is distributed, that affects the biomass development and taxa composition among future primary producers. Moreover, it may be concluded that we may not expect any major changes in phytoplankton total biomass, although there will be considerable alterations in the taxonomic composition. On the other hand, the total biomass of macrophytes will benefit from elevated temperatures, and, just as for phytoplankton, we will likely also see alterations in species composition. Hence, our experimental scenario-approach provides a piece in the jig-saw puzzle of understanding and predicting how the assemblage of primary producers may develop in a future climate perspective, and which conservation efforts that may be needed in order to maintain ecosystem services from freshwaters.

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Acknowledgment

This study was funded by the BiodivERsA project LIMNOTIP through the Swedish Research Council FORMAS, the Swedish Research Council (VR, to L.-A.H.), and the Chinese Scholarship Council.

Conflict of Interest

None declared.

Submitted 27 June 2019

Revised 09 October 2019

Accepted 12 March 2020