Contents lists available at ScienceDirect

Algal Research

journal homepage: www.elsevier.com/locate/algal

The response of phytoplankton communities to experimentally elevated temperatures in the presence and absence of *Potamogeton crispus*

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ARTICLE INFO

Keywords: Climate warming Phytoplankton Functional group Potamogeton crispus Diversity

ABSTRACT

Phytoplankton in shallow lakes will expectedly respond to climate warming and the response may differ between macrophyte and non-macrophyte lakes. To test the responses of phytoplankton to elevated temperature (+4.5 °C) at genus and functional group level, we conducted a 60-day experiment with and without the presence of *Potamogeton crispus* in the winter of Wuhan, China. When *P. crispus* was present, elevated temperature had little or no effect on the biomass and composition of the phytoplankton community. In the absence of *P. crispus*, however, elevated temperature significantly decreased the biomass and changed the composition of the phytoplankton. In contrast to many but not all published results mainly conducted during spring and summer, elevated temperature in winter reduced rather than increased the dominance of Cyanophyta. Instead, Chlorophyta became dominant. Redundancy analyses (RDA) showed that conductivity, light intensity and the ammonium/nitrate ratio (NH₄:NO₃) were the most important environmental variables, accounting for almost similar parts of the variations recorded in both genus and functional group composition. Among treatments, functional models did not show advantages over taxonomic models in depicting the response of the phytoplankton assemblage to the environmental conditions prevailing in our study conducted in winter, characterised by low phytoplankton abundance.

1. Introduction

Phytoplankton plays an essential role in aquatic ecosystems as it supplies oxygen and food to other organisms [1,2], and the community composition of phytoplankton is a useful indicator of environmental changes [3,4].

Temperature is an important environmental factor affecting phytoplankton abundance and community composition. Previous empirical studies have revealed that increasing temperatures may reduce the diversity of phytoplankton [5,6] and boost the dominance of Cyanophyta [7–10]. However, experiments focusing solely on temperature effects on phytoplankton biomass/abundance and composition have shown contradictory results. For example, Velthuis et al. [11] demonstrated that a temperature increase of 4 °C (from spring to late summer) led to a reduction of phytoplankton biomass in ponds but an unaltered composition of the phytoplankton community, while Yvon-Durocher et al. [12] found that a temperature increase of 4 °C during four-month (from winter to spring) pond experiments resulted not only in a reduction of the phytoplankton biomass but also in a shift in the phytoplankton community structure. In a two-year pond experiment in UK, Moss et al. [13] revealed that a temperature increase of 3 °C had only minor influence on phytoplankton biomass and community composition. On the contrary, in a five-year warming experiment (+4 °C) in ponds conducted in UK as well, the biomass and biodiversity of phytoplankton significantly increased with warming [14]. A global-scale study by Kraemer et al. [15] of the association between temperature and phytoplankton biomass (measured as chlorophyll *a*) in 188 of the world's largest lakes showed that the impact of warming on phytoplankton depends on the trophic state of the lake. These contrasting results suggest that the temperature effects on phytoplankton community structure may vary depend on lake size, trophic state, seasonality and heating history (the length of the heating period).

Multiple studies have shown that submerged macrophytes, through competition with phytoplankton for nutrients, excretion of

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https://doi.org/10.1016/j.algal.2018.09.032

Received 16 April 2018; Received in revised form 9 September 2018; Accepted 29 September 2018 2211-9264/ © 2018 Published by Elsevier B.V.





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allelochemicals and provision of refuge for zooplankton, can affect phytoplankton growth negatively [16–18]. *Potamogeton crispus* germinates only in winter and whether it can inhibit the growth of phytoplankton is still subject to debate. Nakai et al. [19] found no allelopathic effects of *P. crispus* on phytoplankton, while Pakdel et al. [20] found a strong inhibitory effect on phytoplankton. Except for allelopathy, Zhou et al. [21] suggested that *P. crispus* may also reduce phytoplankton biomass and alter its community structure by competition for nutrients and light. In contrast, Zhang et al. [22] revealed that only fast-growing *P. crispus* led to reduced abundance of phytoplankton.

Phytoplankton has developed adaptive strategies to maintain its population under various environmental conditions [23]. Based on the physiological, morphological and ecological characteristics of the different algae species, Reynolds et al. [23] proposed a functional classification system, which was later revised by Padisák et al. [24]. Functional group can be regarded as a unit of phytoplankton taxa which are sensitive to the sets of appropriate adaptive specialisms and the clusters of species that have them [24]. An increasing number of studies have suggested that functional groups have advantages in explaining and predicting the relationships between phytoplankton dynamics and environmental conditions [25–28]. Environmental conditions act as a filter to remove all species lacking specific combinations of traits rather than the species themselves [29], whereas species assemble in functional groups would tolerate specified conditions and simplify the complexity of real community structure [30].

In shallow lakes, phytoplankton dynamics are strongly influenced by the seasonal changes in environmental conditions [31,32], the abundance of phytoplankton and the proportion of Cyanophyta in phytoplankton showing minimum values in winter [31,33,34]. Phytoplankton communities are usually dominated by Cryptophyta or/and Bacillariophyta in winter [34]; however, it is an open question whether winter warming also can change the phytoplankton community and boost the dominance of Cyanophyta in shallow lakes. We conducted a 60-day mesocosm experiment in winter to elucidate the responses of phytoplankton to elevated temperatures (+4.5 °C) with and without the presence of *P. crispus*, which is a fast-growing species in winter that can potentially influence the phytoplankton dynamics. We analysed how phytoplankton genera and functional group composition responded to environmental changes among the treatments. We hypothesised that warming would increase phytoplankton biomass and shift the phytoplankton community from Cryptophyta or/and Bacillariophyta dominated to Cyanophyta dominated and P. crispus could suppress this shift. As elevated temperature may eliminate some less heat tolerant species, we further hypothesised that functional classification would provide more explanatory power than classification based on taxa (genera) when relating phytoplankton community to environmental conditions in a warming scenario.

2. Material and methods

2.1. Heating system

The experiment was conducted from 13 December 2015 to 23 February 2016 in Wuhan, China. Two unconnected concrete pools (length × width × depth: $2 \times 2 \times 1$ m) were half-filled with lake water, acting as a temperature buffer, and equipped with two water pumps ($800 \text{ L} \text{ h}^{-1}$) to promote water mixing (Fig. 1). In one of the two pools, two spiral heaters were installed (diameter 9 mm, power 800 W), while the other pool remained unheated. Both pools were equipped with two temperature sensors and the water temperature was measured simultaneously every 15 s to ensure that the temperature in the heated pool was constantly 4.5 °C higher than in the control pool (Fig. 1). Eight glass aquaria (length × width × depth: $40 \times 30 \times 60$ cm) were filled with water from nearby Lake Donghu and placed in the pool. Twelve plastic cups (diameter 6 cm, height 8 cm, volume 220 mL) filled with lake sediment were placed on and covered the bottom of each

aquarium. *Potamogeton crispus* was selected as the target species. Four treatments were randomly allocated in the pool, each in four replicates: low temperature and plant absence (LN), low temperature and plant presence (LP), high temperature and plant absence (HN), high temperature and plant presence (HP).

On 13 December 2015, six cups evenly distributed in each of the LP and HP aquaria were selected and one *P. crispus* shoot was planted in each of the six cups, while no plants were cultured in the LN and HN treatments. All the *P. crispus* shoots were rinsed carefully to remove periphyton. After planting, the sediment in all cups was covered with 1 cm clean sand to diminish nutrient release from sediment to water. On 19 December 2015, after one week of pre-cultivation, phytoplankton was sampled and environmental variables were measured to establish the initial state. Nutrient levels were adjusted to a eutrophic level with a total nitrogen (TN) concentration of 2 mg l⁻¹ and a total phosphorus (TP) concentration of 0.1 mg l⁻¹, similar to the nutrient concentrations in Donghu Lake. Heating was initiated on 20 December 2015. Water nutrient (TN, TP) levels were measured every two weeks and similar eutrophic conditions were maintained among treatments by adding chemicals (KH₂PO₄, NaNO₃) throughout the experiment.

On 23 February 2016, phytoplankton was collected from the surficial water (to a depth of 20 cm) in each aquarium for chlorophyll *a* (Chla) measurements and species identification. Following the counting method of Hao et al. [35], phytoplankton was identified to genus level according to Hu [36] under a light microscope (Motic BA310, China). Then, phytoplankton genera were classified into functional groups according to their physiological, morphological and ecological characteristics proposed by Reynolds et al. [23] and Padisák et al. [24].

Environmental variables were measured in situ concomitantly with phytoplankton sampling. Conductivity, oxidation-reduction potential (ORP), dissolved oxygen (DO), pH, light intensity at air-water interface (E0) and light intensity at 0.2 m depth below the air-water interface (E–0.2 m) were measured for each aquarium. In the laboratory, TN and TP were measured via colorimetry using a UV-visible spectro-photometer (TU-1810PC, Purkinje General, China) [37]. Ammonium (NH₄⁺) and nitrate (NO₃⁻) were analysed with Discrete Chemistry Analyzer (Autochem 1100, Xingrui Technology, China). Total alkalinity was measured by Gran titration with a standard solution of 0.1 M HCl [38].

2.2. Statistical analyses

One-way ANOVA and Kruskal-Wallis Test (when the normality test was violated) followed by post hoc test were used to test the differences in environmental variables, phytoplankton Chla and the relative abundances of main phytoplankton phyla among the four treatments (LN, LP, HN and HP). Pearson correlation analysis was used to test the relation between response variables and environmental variables. All analyses were performed using SPSS (IBM SPSS Statistic 20).

All phytoplankton density data (genera density and functional group density) were square-root transformed to reduce the influence of high density taxa, and a Bray-Curtis matrix of similarity among treatments was constructed. The significance of differences in genus and functional composition was investigated using permutational multivariate analysis of variance (PERMANOVA) in Past (version 3). If significant differences were found, post hoc pairwise tests were conducted (via PERMANOVA).

Redundancy analysis (RDA) was applied to test the effects of environmental variables on phytoplankton composition among treatments. The genera and functional densities of phytoplankton were square-root transformed. All the environmental data (except pH) were log(x + 1) transformed to reduce the variance before selection using forward-selection procedure (P < 0.1). RDA and forward selections were conducted with CANOCO for Windows, version 5.0 [39].

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