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Effects of Elevated Temperature on Resources Competition of Nutrient and Light Between Benthic and Planktonic Algae

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Climate warming, a serious environmental problem worldwide, is considered a major threat to aquatic ecosystems. A primary feature of climate warming is elevated temperatures which in shallow aquatic ecosystems might affect competition for light and nutrient between benthic algae on the sediment surface and planktonic algae in the water. The outcomes of such competition would not only affect the distribution of primary production, but also determine the fundamental character of shallow aquatic habitats as clear water or turbid water systems. We conducted a mesocosm study to evaluate the effects of elevated temperature on competition between planktonic algae and benthic algae for light and nutrients. We found that elevated temperature increased the concentrations of total nitrogen (TN), total phosphorus (TP), and total suspended solids (TSS) in overlying water and enhanced the growth of planktonic algae (measured as chlorophyll *a*, Chl *a*), but decreased light intensity and benthic algal biomass (Chl *a*). Our results indicate that elevated temperature can increase the growth of planktonic algae and enhance their competitive advantage over the benthic algae in shallow lakes, thereby contributing to eutrophication and a decline in water quality. These findings shed further light on the effects of global warming on aquatic ecosystems.

Keywords: elevated temperature, planktonic algae, benthic algae, aquatic ecosystem, nutrient

INTRODUCTION

Climate warming has become a serious environmental problem worldwide and is considered a major threat to the natural environment, including aquatic ecosystems (Paerl and Huisman, 2008; Jeppesen et al., 2010). A major feature of climate warming is elevated temperatures (Paerl et al., 2011). According to the Sixth Scientific Assessment Report (IPCC, 2018), global average temperatures increased 1.5°C from 1880 to 2018, and this trend continues. The currents warming rate is projected to be 0.25°C per decade until the middle of the 21st century and 0.36°C per decade in the second half of the century (Andreas-Gobiet et al., 2014). Warming will have profound impacts on ecological processes in aquatic ecosystems (Amundrud and Srivastava, 2019) by affecting primary production, water resource distribution and water quality (Daufresne et al., 2009).

Elevated temperatures can promote the growth of algae in both benthic and planktonic habitats and affect the physiology of primary producers (Butterwick et al., 2010; Liu et al., 2015; Li et al., 2016) because temperature plays a crucial role in metabolic processes, including photosynthesis, nutrient uptake and the enzymatic activity of cells (Claquin et al., 2008; Thorel et al., 2014). However, temperature also influences the chemical and physical processes of aquatic ecosystems (Takano and Hino, 2000; Ozaki et al., 2010; Liu et al., 2015) with implication for the dynamics of the aquatic ecosystems. Increased temperature promotes the release of nitrogen and phosphorus from sediments (Malmaeus et al., 2005), which may enhance planktonic algal growth and thus an increase in TSS. Increases of planktonic algae and total suspended solids (TSS) reduce the light intensity on the sediment surface (Marcus, 1998; Zhang et al., 2015; Razlutskij et al., 2021), limiting the growth of benthic algae (Takano and Hino, 2000; Butterwick et al., 2010). Thus, elevated temperature might affect the growth of both planktonic and benthic algae in aquatic systems.

In shallow lakes, benthic algae growing on sediment surfaces are often limited by light resources as a result of attenuation caused by planktonic algae in the overlying water (Vadeboncoeur et al., 2003). In systems where external nutrient loading has been reduced, internal loading becomes a limiting factor for the planktonic algae (Zhu et al., 2010), while benthic algae benefit from nutrients in the sediment. If abundant, benthic algae may reduce sediment release of nutrients and thereby further hampering growth of planktonic algae (Vadeboncoeur et al., 2003; Zhang et al., 2013; Blottière et al., 2017). Competition between planktonic algae and benthic algae is one of the key factors affecting shallow aquatic ecosystem dynamics (Flöder et al., 2006; Genkai-Kato et al., 2012) and has become an area of great interest in freshwater ecology (Pastcrnak et al., 2009; Zhang et al., 2013; Jäger and Diehl, 2016).

However, the effects of elevated temperature on resource competition between benthic and planktonic algae in shallow aquatic ecosystems are yet to be fully understood. Here, we hypothesized that elevated temperature would benefit planktonic algae and hamper benthic algae, leading to a deterioration in water quality. To test this hypothesis, we designed a mesocosm experiment with elevated temperatures and compared with controls run at ambient temperature. The effects of elevated temperature on the competition between planktonic algae and benthic algae for resources of light and nutrient were investigated using measurements of light intensity on the sediment surface, nutrient content in overlying water, and the development of benthic and planktonic algal biomass over time. The aim of this study is to evaluate the effect of elevated temperature on resource competition between benthic and planktonic algae in shallow aquatic ecosystems. The results may shed light on the effects of global warming on natural aquatic ecosystems.

MATERIALS AND METHODS

Experimental Setup

The mesocosm system consisted of eight white polyethylene plastic tanks (bottom diameter = 46 cm, upper diameter = 57 cm, and height = 72 cm) placed in the agricultural garden of Anhui Agricultural University, Hefei, China. Sediments were collected from a pond at the campus and were air dried and crushed to remove large particles. The treated sediment was then added to the tanks in order to obtain a 10 cm thick layer (Zhang et al., 2016).

Rainwater (TN = 0.96 mg/L^{-1}, TP = 0.02 mg/L^{-1}) was collected and added to each tank to a depth of 70 cm. All eight mesocosms were allowed to equilibrate for 2 weeks before the experiment started. Then four treatments were covered by black plastic paper on the outside wall to create elevated temperature while the controls were covered by heat insulation film. Both the black paper and the heat insulation film are lightproof. So, sunlight did not enter through the sidewall of either the treatment or the control mesocosms. A Petri dish (diameter of 6 cm) containing treated sediments was inserted into the upper sediment layer of each mesocosm, such that the surface the sediments inside and outside the dishes was at the same level for benthic algae growth. Rainwater was added to the mesocosms as required to maintain the water levels during the experiment. The experiment was then run for 60 days from July 23 to 20 September 2020.

Sampling

The tanks were sampled at approximately 12 noon every 10 days during the experimental period. Water samples (500 ml) were taken with a clean glass bottle from 10 cm below the water surface from each mesocosm, and analyzed for total nitrogen (TN), total phosphorus (TP), total suspended solids (TSS) and planktonic algal biomass (Chl *a*). TN was determined by alkaline potassium persulfate UV spectrophotometry and TP was determined by ammonium molybdate UV spectrophotometry (APHA, 1998). 200 ml water was filtered by GF/C grade filter for Chl *a* of planktonic algal biomass and the Chl *a* on the filter was determined by UV spectrophotometry after extraction in 90% acetone (Jespersen and Christoffersen, 1987). TSS was calculated by weighing the residue retained on a GF/C grade filter after filtering 200 ml water and drying at 108°C for 2 h (Qu et al., 2019).

Water temperature was measured using a YSI probe from 30 cm below the water surface. Light intensity was measured using an underwater irradiance meter (ZDS-10W) at 50 cm below the water surface before sampling the water.

The Petri dishes with their benthic algae were removed slowly from each mesocosm and the benthic algae were scraped off and diluted with distilled water to 500 ml, then stored in brown glass bottles prior to analysis of algal biomass (Chl *a*) using the same

TABLE 1 | Water temperature (°C).

Time (d)	Control	Elevated Temperature	Increased	p
0	29.3 ± 0.0	29.3 ± 0.0	—	—
10	33.8 ± 0.2	35.8 ± 0.1	2.0 ± 0.2	$p > 0.05$
20	29.1 ± 0.1	30.6 ± 0.2	1.6 ± 0.2	$p < 0.05$
30	29.7 ± 0.5	30.9 ± 0.4	1.2 ± 0.3	$p < 0.05$
40	30.0 ± 0.1	31.2 ± 0.4	1.2 ± 0.4	$p < 0.05$
50	26.3 ± 0.1	28.3 ± 0.4	2.0 ± 0.4	$p < 0.05$
60	25.3 ± 0.2	27.4 ± 0.3	2.1 ± 0.2	$p > 0.05$

method as for planktonic algae. After sampling, the Petri dishes and the sediments were re-loaded into each mesocosm for further benthic algae growth.

Statistical Analyses

Independent sample *t*-tests were used to analyze differences in water temperature, TSS, light intensity, TN, TP and Chl *a* of both planktonic and benthic algal biomass between the elevated temperature treatment mesocosms and the controls. One-way ANOVA was performed to detect differences between treatments on each sampling occasion. SPSS 19.0 was used for data statistics analysis. All data are presented as mean ± SD and figures were generated by Origin Pro 9.0.

RESULTS

Water Temperature

On average, water temperature was 1.7°C higher in the elevated temperature treatments than in the controls (*t*-test, $p = 0.037$), at 30.7 ± 0.3°C compared to 29.0 ± 0.2°C (**Table 1**). A significant difference in temperature was apparent on every sampling occasion except for day 10 and day 60 (one-way ANOVA, treatment effect, $p < 0.05$).

Total Nitrogen and Total Phosphorus

TN concentrations in the overlying water of the elevated temperature treatments were higher on average than in the controls at 6.43 ± 0.96 mg/L to 5.38 ± 0.42 mg/L respectively

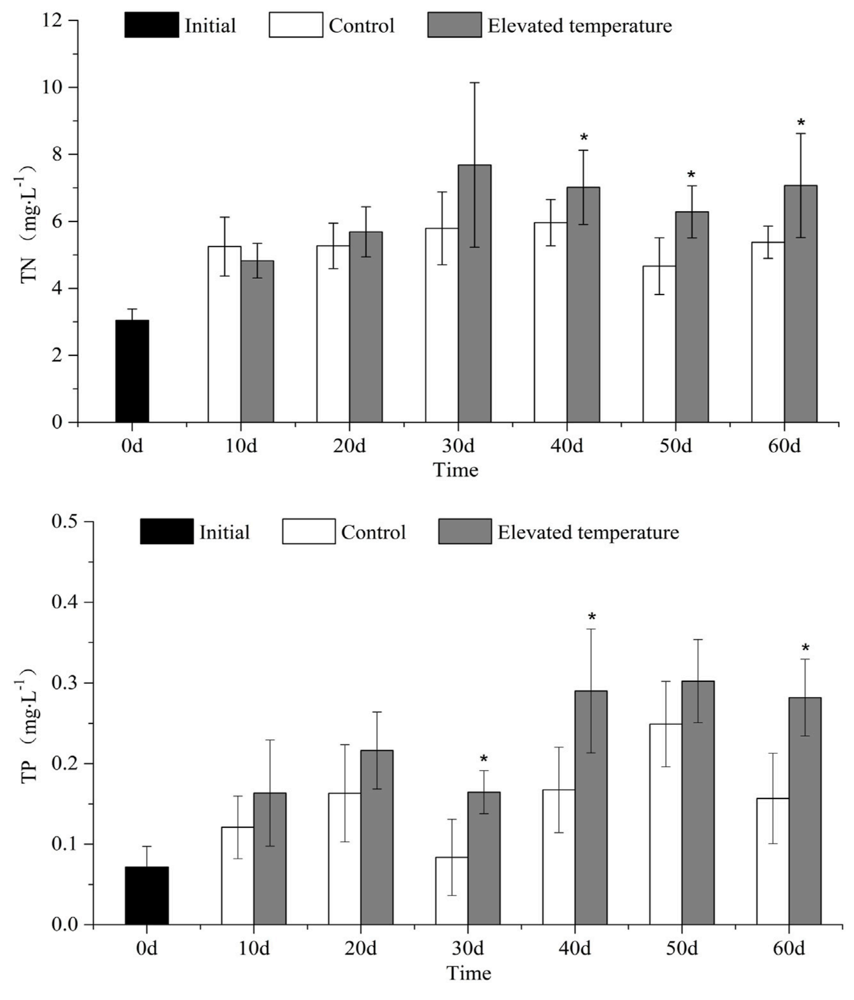

FIGURE 1 | TN (mean ± SD) and TP (mean ± SD) in different treatments over time. Asterisk indicates significant ($p < 0.05$) differences between treatments.

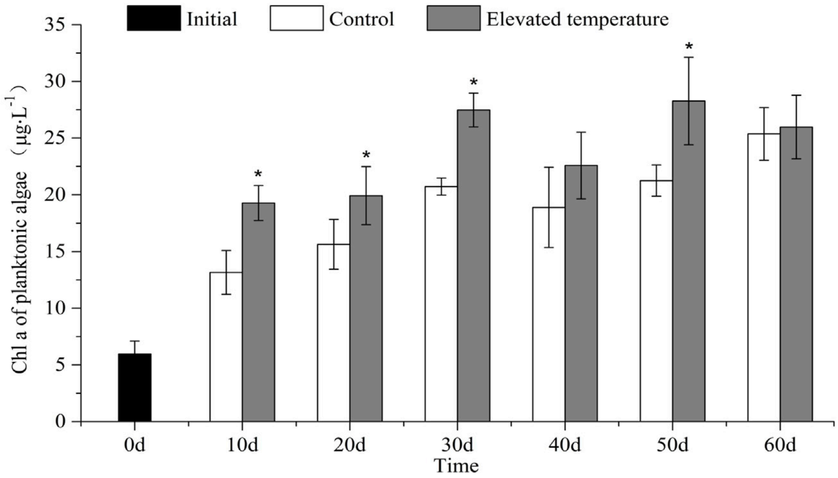

FIGURE 2 | Chl *a* of planktonic algae (mean ± SD) in different treatments over time. Asterisk indicates significant (p < 0.05) differences between treatments.

(t-test, p = 0.049), and also significantly higher in the elevated temperature treatments on day 40, day 50 and day 60 (one-way ANOVA, treatment effect, p < 0.05, **Figure 1**).

TP concentrations in overlying water were also higher in the elevated temperature treatments than in the controls (t-test, p = 0.043) at 0.23 ± 0.06 mg/L and 0.16 ± 0.05 mg/L respectively, being significantly higher in the elevated temperature treatments on three out of six sampling occasions (day 30, 40 and 60, one-way ANOVA, p < 0.05, **Figure 1**).

Planktonic Algal Biomass

The biomass of planktonic algae (Chl *a*) was higher on average in the elevated temperature treatments than in the controls (t-test, p = 0.041) and on each sampling occasion except for day 40 and day 60 (one-way ANOVA, treatment effect, p < 0.05; **Figure 2**).

Total Suspended Solids and Light Intensity

TSS concentrations (**Figure 3**) were higher on average in the elevated temperature treatments than in the controls (t-test, p = 0.012) at 19.50 ± 3.44 mg/L to 13.46 ± 2.78 mg/L respectively. Significantly higher TSS values were recorded in the elevated temperature treatments on each sampling occasion except for day 10 and day 30 (one-way ANOVA, treatment effect, p < 0.05).

Light intensity (**Figure 3**) at the sediment surface was lower on average in the elevated temperature treatments than in the controls (t-test, p = 0.039) at 9565 ± 4403 lx to 15119 ± 3383 lx respectively. Reduced light intensity was recorded in the elevated temperature treatments on all sampling occasions except for day 10 and day 30 (one-way ANOVA, treatment effect, p < 0.05).

Benthic Algal Biomass

The biomass of benthic algae (Chl *a*) was lower on average in the elevated temperature treatments than in the controls (t-test, p = 0.003), and significantly so on every sampling occasion except for day 10 and day 30 (one-way ANOVA, treatment effect, p < 0.05; **Figure 4**).

DISCUSSION

We found that elevated temperature increased the nutrient concentrations of TN and TP in the overlying water, enhanced growth of planktonic algae (Chl *a*), increased TSS concentration, decreased light intensity at the sediment surface and reduced benthic algal biomass (Chl *a*).

The water temperature of the black covered mesocosms was 1.2–2.1°C (1.7°C on average) higher than in the controls. According to the Sixth Scientific Assessment Report (IPCC, 2018), global average temperatures increased 1.5°C from 1880 to 2018. This rate of increase has been observed in lakes worldwide (O'Reilly et al., 2015); and in some lakes, summer temperatures has increased 1.5°C in the last decades alone (Hetherington et al., 2015, Oneida Lake, NY, United States). Globally, the water temperature of rivers is expected to increase 0.8–1.6°C more in between 2071 and 2100 than between 1971 and 2000 (van Vliet et al., 2013). Thus, the treatment applied in our study resulted in heating comparable to real-world examples.

The increased nutrients (both TN and TP) in the overlying water of the elevated temperature treatments probably points to increased release from the sediments (Liu et al., 2017). A water temperature increase of 3–4°C, is sufficient to double the release rate of P (Nicholls, 1999). Further inputs of nutrients may be associated with rain events and atmospheric deposition (Liu et al., 2015). However, in this experiment, both the controls and the treatments mesocosms were maintained in the same garden of Anhui Agricultural University, so the N and P deposition from the atmosphere should be the same in both the different treatments. However, we cannot discount the possibility that some atmospheric N was added to the water N fixation by algae, as we did not monitor these algae separately in this study.

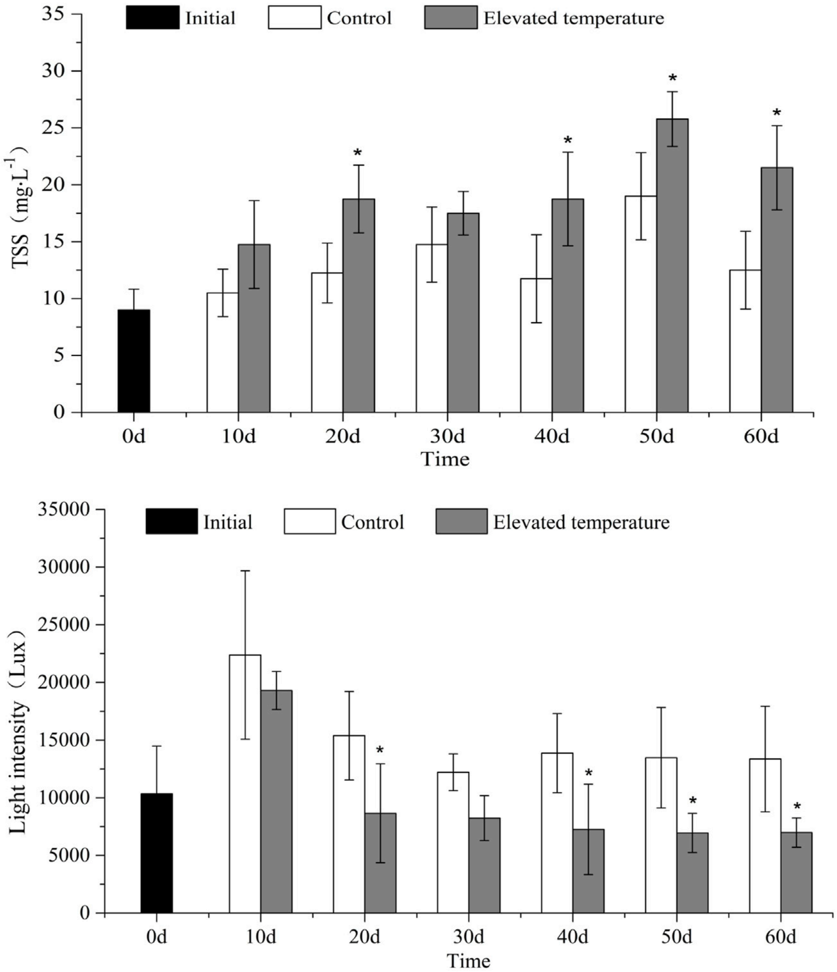

FIGURE 3 | TSS (mean ± SD) and light intensity (mean ± SD) in the different treatments over time. Asterisk indicates significant (p < 0.05) differences between treatments.

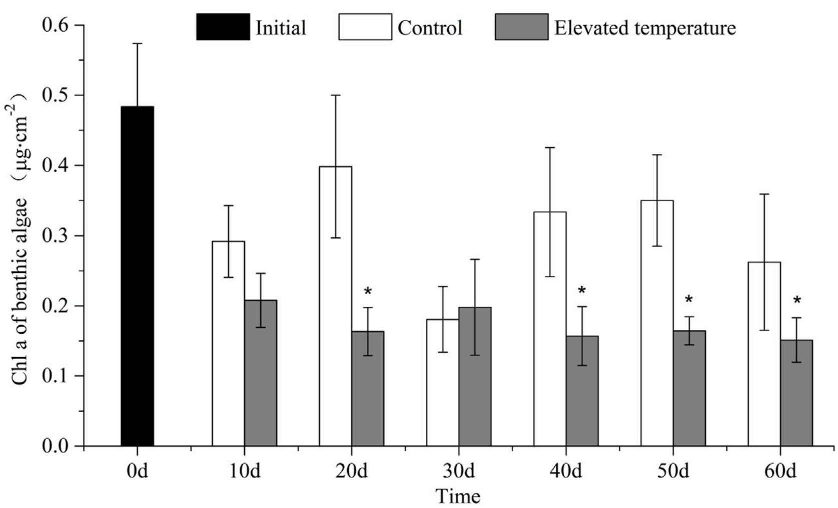

FIGURE 4 | Chl *a* of benthic algae (mean ± SD) in different treatments over time. Asterisk indicates significant (p < 0.05) differences between treatments.

That elevated temperature can enhance the growth of planktonic algae is well-established (e.g., Pedersen and Borum, 1996). Blottière et al. (2017) found a 15% increase in planktonic algae for every 1°C increase in average annual temperature. In addition, elevated temperature can enhance the release of nutrients from the sediment (Jensen and Andersen, 1992), which may lead to an increase in the growth of planktonic algae and thus increase in TSS. Further, increases of planktonic algae and TSS can reduce water clarity and thereby limit benthic algae growth due to increased light limitation. Our results are consistent with this literature. We found a reduction in light intensity at the sediment surfaces of the elevated temperature treatments, and a lower benthic algae biomass compared with the controls, indicating increased competitive advantage of planktonic algae over benthic algae. Such a decline or even disappearance of benthic algae will further enhance the release of nutrients from the sediment into overlying water, creating a positive feedback loop promoting planktonic algae growth (Spears et al., 2008; Zhang et al., 2013). Thus, the elevated temperature leads to the transfer of nutrients from benthic to planktonic habitats (Nicholls, 1999; Genkai-Kato et al., 2012; Zhang et al., 2015).

It is important to acknowledge that the effects of elevated temperature on the dynamics of benthic and planktonic algae in natural aquatic ecosystems will be more complex than in our mesocosm system, which excluded fish, benthic animals and submerged macrophytes, all of which may have important roles in the competitive interplay between benthic and planktonic algae (Zhang et al., 2014; Zhang et al., 2017; Razlutskij et al., 2021; Mei et al., 2021). Furthermore, water flow and wave action typical for natural lake ecosystems were not accounted for in our experiments. However, there are calm, fishless or fish poor aquatic ecosystems, where conditions are similar to those simulated here.

The implications are that in similar natural systems, expected increase in temperature resulting from climate change will be conducive to the growth of planktonic algae and enhance their competitive advantage over benthic algae, leading to increased potential for eutrophication and deteriorating water quality. However, further studies at larger scale conditions and different trophic state and trophic structure are needed before general conclusions can be drawn about the effect of climate change on the benthic-pelagic coupling.

In conclusion, in our experimental system simulating shallow lake ecosystems, elevated temperature increased the growth of planktonic algae and enhanced their competitive advantage over the benthic algae, thereby contributing to eutrophication and a decline in water quality.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

Conceptualization: XM, XZ, and ZL Investigation: XM, SG, YL, and JH Funding acquisition XM Writing original draft: XM and SG. Writing; editing: XM, VR, LR, EJ, ZL, and XZ.

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