



Effect of increasing temperature on periphyton accrual under controlled environmental conditions

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Abstract

Global warming can affect biomass accumulation and the dynamics of periphytic communities, potentially altering their role in aquatic ecosystem functioning. We conducted a 38-day mesocosm experiment to investigate the effects of an increase in winter temperature on periphyton biomass accumulation under eutrophic conditions. We evaluated the warming effect on colonization phases, identifying the most affected phase. The experiment had two treatments (control: current winter temperature of 23.5 °C, warming: + 5.7 °C under IPCC scenario). It was carried out in growth chambers under controlled temperature, light, and humidity. Periphyton and water samplings were performed on days 3, 6, 9, 13, 17, 21, 27, and 38. The increase in temperature did not affect the organic matter accrual rate of the periphyton. However, it negatively affected the net and gross accrual rate of the algal biomass. Ash-free dry mass and chlorophyll-*a* ratio in the periphyton increased at higher temperatures, indicating a decrease in autotrophic components in the periphyton in the warming treatment. We detected losses in algal biomass during the intermediate and advanced colonization phases. Our results showed a decrease in periphytic algal biomass with an increase in average temperature in winter. In conclusion, a warming scenario can negatively influence periphyton biomass in eutrophic ecosystems, where algal growth in the community is generally unfavorable.

Keywords Algal species · Biomass · Biofilm · Climate change · Eutrophic lake

Introduction

Human activities are having a growing impact on natural ecosystems, and climate change is a major threat to the structure of biological communities and the functioning of ecosystems (Meerhoff et al. 2012; Hansson et al. 2013; Salk et al. 2021). In the aquatic ecosystems, eutrophication is one of most threatening the environmental problems affecting aquatic ecosystems globally. In eutrophic environments, high nutrient availability increases phytoplankton biomass causing blooms. Phytoplankton blooms reduce the water

transparency and euphotic depth zone, reducing light availability and increasing nutrient competition between autotrophs (Vadeboncoeur et al. 2003; Havens et al. 1996). In temperate lakes, studies indicate global warming can intensify eutrophication (Salk et al. 2021). Warming can cause an increase in phytoplanktonic biomass and disrupt water C:N:P ratio, affecting the ability of phytoplankton and herbivores to use nutrient use efficiently, with possible consequences for the entire aquatic food chain (Domis 2014; Pacheco et al. 2021). There is still little knowledge on the warming effects on eutrophication in subtropical and tropical lentic ecosystems. Recent studies suggest that temperature rise alone is insufficient to increase phytoplanktonic biomass (Gomes et al. 2020; Pacheco et al. 2021). However, the combined effect of warming and enrichment seems to increase cyanobacterial bloom in phytoplankton (Gomes et al. 2020). Understanding of how environmental warming effects on aquatic communities can support monitoring strategies and predictive methods to minimize impacts, especially in tropical and subtropical ecosystems, where knowledge is still limited.

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In aquatic communities, periphyton is a crucial primary producer and participates in nutrient cycling and the food web, contributing significantly to ecosystem functioning (Vadeboncoeur and Steinman 2002; Dodds 2003). The periphyton can adhere to the most diverse types of substrates (e.g., sediment, macrophytes, rocks) and is typically abundant in shallow lakes. In these ecosystems, periphyton can contribute from 99 to less than 1% of primary production (Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2003). In addition to their crucial ecological role, periphyton can remediate eutrophic ecosystems by removing phosphorus (Wu et al. 2014) and can act as an indicator of environmental changes (De Nicola and Kelly 2014; Dunck et al. 2016).

Several environmental factors, such as light and nutrient availability, can affect periphyton structure and functioning (Vadeboncoeur and Steinman 2002; Meerhoff et al. 2012; Hansson et al. 2020). Some abiotic factors can act as modulators, such as temperature, pH, and salinity (Stevenson 1996; Lambert et al. 2016). While high temperature has physiological effects on periphyton, such as denaturation of proteins and nucleic acids, and degradation of photosystem (Wahid et al. 2007), it can affect the periphyton community structure (Hao et al. 2020). In the ecosystem, global warming has a direct effect on the physical properties of water, such as stratification and mixing processes, and indirect on light and nutrients (Jeppesen et al. 2009; Röhland et al. 2015), which may influence periphyton growth. Furthermore, studies have shown that warming favors the water brownification process, which also can also negatively impact benthic and pelagic algal biomass and primary production (Vasconcelos et al. 2016). Thus, the global warming can influence primary production, abundance, and algal composition of the periphyton (Mahdy et al. 2015; Bondar-Kunze et al. 2021; Silva et al. 2019; Hao et al. 2020). The ideal temperature for periphyton growth ranges from 10 to 30 °C and higher temperatures lead to thermal stress, reducing community growth (De Nicola 1996). Increased temperature can cause changes in periphyton, which can negatively affect biomass availability for primary consumers (Bondar-Kunze et al. 2021), leading to changes in the food chains (Pacheco et al. 2021). Despite some advances in knowledge of the effects of warming on the periphyton, gaps in knowledge still exist, such as the effect on the community colonization process.

Periphyton colonization involves a sequence of steps that lead to the formation of a structurally complex and very dynamic microbiota. During colonization, there is an exponential accrual phase of biomass that reaches a maximum and can remain at a plateau for some time, usually days or weeks, after a loss phase begins (Biggs 1996). The accrual phase dominates immigration/colonization and growth, and the loss phase dominates the loss by death, emigration, sloughing, and grazing (Biggs 1996). However,

physical or chemical disturbances can alter colonization phases, increase losses, and/or restart community development (Stevenson 1996). A better understanding of the warming effect on periphyton colonization allows the identifying changes in successional trajectory, biomass accumulation rates, and community structure.

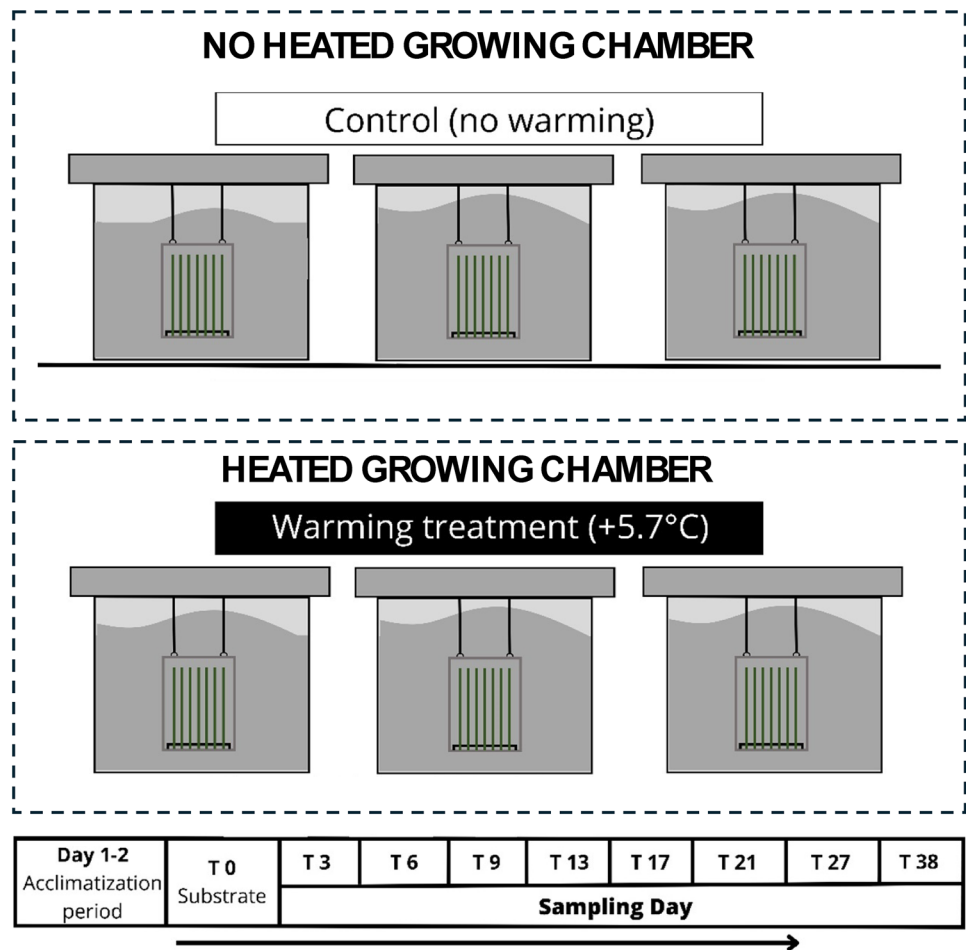
Considering that global warming can intensify eutrophication (Moss et al. 2011; Salk et al. 2021) impairing periphyton biomass accumulation (Vadeboncoeur et al. 2001), we investigated the warming effects on this community under eutrophic conditions. Specifically, we evaluated the changes in periphyton biomass accumulation during colonization under controlled environmental conditions in response to warming in the winter. In eutrophic lakes and reservoirs, intense phytoplankton blooms can promote shading and strong competition for nutrients, impairing primary production, biomass accumulation and algal growth in the periphyton (Vadeboncoeur et al. 2001; Zhang et al. 2015; Borduqui and Ferragut 2012). Thus, the peak of periphyton biomass commonly occurs in phases of low phytoplankton biomass in eutrophic lake ecosystems, as observed in the winter of the studied reservoir (Borduqui and Ferragut 2012). Thus, we hypothesized that a temperature increase in winter would decrease the periphyton biomass peak and accrual rate, affecting the colonization phases under eutrophic conditions.

Materials and methods

Experimental design

We conducted a mesocosm experiment in growth chambers (2) with controlled environmental conditions in two temperature scenarios to determine the effects of global warming on the periphyton (Fig. 1). For the current scenario, we use the average winter temperature (dry season) of the last ten years in the study area as the basis for the current scenario (<http://www.estacao.iag.usp.br/boletim.php>). To simulate the warming scenario, we established the higher air temperature based on the worst-case scenario proposed by the Intergovernmental Panel on Climate Change (IPCC 2021), which predicts a potential increase of 5.7 °C in 100 years. The treatments inserted inside the growth chambers were as follows: control (current scenario) with a maximum air temperature of 23.5 °C in winter; and warming with a maximum air temperature of 28.8 °C simulating the future scenario in winter. Both treatments were performed in triplicates. In the study area, periphyton biomass tends to be higher in autumn–winter than in other seasons, see Borduqui and Ferragut 2012 for details, and the community is dominant in algal biomass (Santos et al. 2020). For this reason, the winter temperature was used as a baseline.

Fig. 1 Scheme of the experimental design, showing the treatments inserted inside the growth chambers and the sequence of steps in the experiment (acclimatization, placement of substrates at time zero, and sampling on 3–38 days after the substrate placement)



The photosynthetically active radiation (PAR) was $488 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a 12-h photoperiod in the two growth chambers. The mesocosms were positioned beneath the light source at a fixed distance of 1.2 m (1200 C3 luminaires full spectrum, Apogee model Spectrum Quantum Sensor). To simulate the daily thermal oscillation, the air temperature in chambers was programmed to gradually increase from 1 am to 9 pm and gradually decrease from 9 pm to 1 am every day, maintaining the difference of 5.7°C between treatments. The temperature settings for each time were based on the average of the last five years in the study area. A full spectrum quantum sensor connected to a digital electronic microprocessor measured the PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$). A digital electronic microprocessor regulated the temperature with a precision of $\pm 0.5^\circ\text{C}$. The air relative humidity was maintained at 80%, controlled by a digital electronic microprocessor with variation between 60 and 90% and a precision of $\pm 8\%$. Air temperature, humidity, and irradiation were recorded every 15 min.

Six mesocosms were used in the experiment, each consisting of white plastic boxes made of high-density polyethylene (HDPE) with an average volume of 62 L. The

mesocosms were previously sterilized before being placed in growth chambers to prevent contamination. They were filled with 55 L of water from the supereutrophic Garças Reservoir ($23^\circ38'40.6'' \text{S}$ and $46^\circ37'28.0'' \text{W}$), located in the Parque Estadual das Fontes do Ipiranga, São Paulo, Brazil, which is situated at 1 km from the growth chambers. The experiment used unfiltered lake water to simulate natural conditions and retain inoculum for periphyton colonization. In cases in which fish and snails were found in the chamber, they were manually removed throughout the experimental period to avoid any interactions with periphyton. The lake water was collected with previously sterilized polyethylene gallons. After one day of acclimation (T0), two acrylic supports containing ten glass slides ($26 \times 76 \text{ mm}$) were submerged in the water of each mesocosm to allow for periphyton colonization (Fig. 1). The glass slides were positioned vertically to minimize particle sedimentation and at a depth of 10 cm to avoid photoinhibition.

Water and periphyton samples were collected on days 3, 6, 9, 13, 17, 21, 27, and 38 (07/12 to 08/19/2022). In both treatments, sampled water was replaced with distilled water to avoid the decrease in the water column, which could affect

the light availability during the experimental period. The water lost to evaporation was not replaced to maintain the warming effect on the periphyton. Water replacement was carried out carefully to avoid physical disturbance to the developing periphytic community.

Periphyton samples were collected by randomly selecting one colonized glass slide from the mesocosms. The colonized substrates were placed in opaque vials and stored at low temperatures for transport. In the laboratory, the periphyton was removed from the substrate by scraping it with steel blades and jets of distilled water.

Environmental variables

Temperature, relative humidity, and PAR in the growth chambers were monitored daily through sensors coupled to a digital electronic microprocessor. The temperature, electrical conductivity, total dissolved solids (TDS), dissolved oxygen (DO), and pH were measured with a water probe (Horiba U52, HORIBA Corporation, Japan) and underwater radiation (PAR) with Li-Cor 250 (Lincoln, NE, USA). We estimated the total nitrogen and phosphorus concentrations (APHA 2012), and chlorophyll-*a* concentration (Sartory and Grobbelaar 1984).

Periphyton samples were filtered through a glass fiber filter (Whatman GF/F) previously calcined (500 °C; 1 h) in a vacuum pump under low pressure (0.3 atm) to measure of the dry mass (DM; g m^{-2}) and ash-free dry mass (AFDM; g m^{-2}), according to APHA (2012). After filtration, the filters were placed in an oven at 105 °C and weighed the dry mass 24 h later when the mass reaches constant. Subsequently, the filters were placed in a muffle furnace at 500 °C for 1 h to obtain the ash mass and calculate the AFDM. To measure periphyton chlorophyll-*a* concentration on the glass slide surface (mg m^{-2}), the samples were filtered and posteriorly frozen at -20 °C until analysis within 30 days. Extraction of chlorophyll-*a* (corrected for pheophytin) from periphyton was performed with 90% ethanol, according to Sartory and Grobbelaar (1984). Chlorophyll-*a* concentration was used as a proxy for algal biomass in periphyton. To evaluate the trophic nature of the periphyton community, we calculated the ratio of AFDM (mg m^{-2}) to chlorophyll-*a* (mg m^{-2}) based on APHA (2012). We consider the possibility that nonviable organic material affects this index. We calculated the gross and net accrual rate of periphyton biomass ($\text{g m}^{-2} \text{d}^{-1}$) according to Stevenson (1996).

Trophic State Index (TSI) was calculated using chlorophyll-*a* (Chloa) and total phosphorus (TP) concentrations, according to Cunha et al. (2013). The TSI categories are: The trophic state classes are ultraoligotrophic (≤ 51.1), oligotrophic (51.2–53.1), mesotrophic (53.2–55.7), eutrophic (55.8–58.1), supereutrophic (58.2–59.0), and hypereutrophic (≥ 59.1).

Data treatment

Two-way repeated measures analysis of variance (two-way RM-ANOVA) was applied to test the significant differences in periphyton biomass and environmental variables between treatments. Tukey' test was applied for multiple comparisons of means to the determination of the minimum significant difference between treatments. Homogeneity of variance and normality were checked, and data were logarithmized. All analyses were performed using the statistical program Sigma Plot 12.0 (Systat Software, Inc, Germany).

Results

Environmental variables

Throughout the daily air temperature profile, we maintained a consistent temperature difference of 5.7 °C between the control and warming treatment. The air temperature ranged from 13.8 to 23.5 °C in control, following the average daily winter air temperature drop for the study area (tropical altitude). Temperature variation ranged from 13.5 to 23.5 °C in the warming treatment, allowing us to evaluate periphyton biomass responses. Despite the warming treatment experiencing three times greater evaporation, both were classified as hypereutrophic. TSI ranged the 59.3–64.5 in the control and 60.0–63.9 in the warming treatment. Furthermore, underwater radiation availability did not differ significantly between treatments during the experimental period.

The growth chambers maintained an air temperature difference of 5.7 °C between treatments throughout the experiment (Fig. 2). Based on average ($n=3514$), light irradiation was $419.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SD=48.6) in the control and $460.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SD=52.4) in the warming treatment. The air humidity ranged from 48.6% to 92% (SD=8.7) in the control and, in the warming treatment ranged from 38.6% to 87.3% (SD=12.3).

Considering the variables of mesocosm water, conductivity, DO, free CO_2 , temperature, and TDS differed between treatments and time (Table 1). The pH, TN, and TP concentrations differed only among days. The interactions between treatment and time factors were significant for TN and TP. The chlorophyll-*a* concentration and light did not differ between treatments. The water temperature was higher in the warming treatment, reflecting the environmental temperature increase (Fig. 3A). In the warming treatment, we observed an increase in conductivity and free CO_2 and chlorophyll-*a* concentrations and a decrease in DO and TP (Fig. 3A–F).

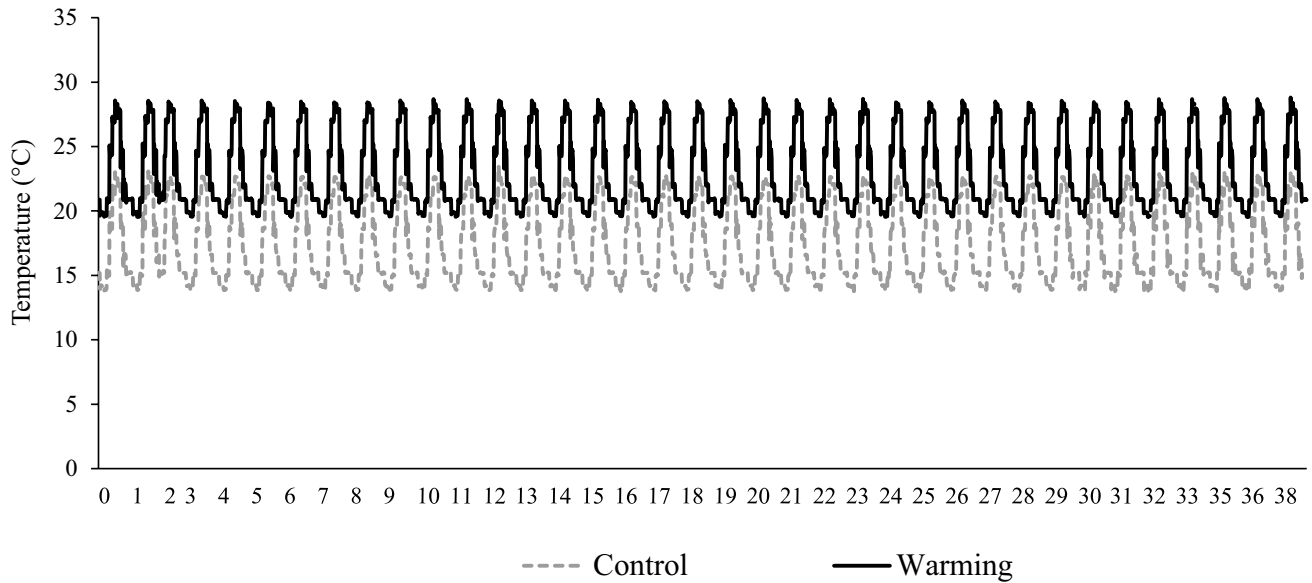


Fig. 2 Daily temperature variation in the control and heated growth chambers during the experimental period

Table 1 Minimum, maximum, mean, and standard error (SE) of environmental variables in the control and warming treatment during the experimental period

Variables	Control				Warming				Two- way RM-ANOVA					
	Min	Max	Mean	SE	Min	Max	Mean	SE	Treatment		Time		Interaction	
									<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Conductivity ($\mu\text{S cm}^{-1}$)	220	250	230	10	210	290	240	0.00	195	<0.001	135.7	<0.001	33.52	<0.001
DO (mg L^{-1})	6.33	12.5	8.76	0.33	4.80	7.78	5.48	0.15	62.45	<0.001	5.55	<0.001	–	<i>ns</i>
Free CO_2 (mg L^{-1})	0.54	3.81	1.65	0.18	0.23	8.85	4.21	0.49	99.88	<0.001	12.35	<0.001	4.82	<0.001
Light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	310	498	438	9.03	396	526	472	9.86	–	<i>ns</i>	–	<i>ns</i>	–	<i>ns</i>
pH	7.4	9.3	8.6	0.5	7.7	9.5	8.7	0.4	–	<i>ns</i>	6.73	<0.001	–	<i>ns</i>
TP ($\mu\text{g L}^{-1}$)	165	593	367	22.6	198	494	296	16.7	–	<i>ns</i>	6.98	<0.001	3.57	<0.001
TN ($\mu\text{g L}^{-1}$)	100.0	2647	1259	174.7	78.9	2557	1236	149.2	–	<i>ns</i>	126.18	<0.001	5.38	<0.001
Water temperature ($^{\circ}\text{C}$)	13.16	16.93	15.18	0.20	19.08	22.47	20.77	0.19	4.52	<0.001	112.39	<0.001	8.99	<0.001
TDS (mg L^{-1})	0.142	0.158	0.147	0.005	0.138	0.196	0.159	0.0021	281.67	<0.001	186.10	<0.001	45.54	<0.001

Results of two-way RM-ANOVA on the effects of treatment ($df=3$), time ($df=7$), and treatment-time interaction on the environmental variables

Periphyton

Periphyton AFDM increased until day 27 in control and warming treatments (Fig. 4A). However, no difference was found between treatments. Based on AFDM, the net and gross accrual rates were similar between the control and warming treatment (Fig. 4B). During colonization, the temperature increase had a negative effect on periphyton chlorophyll-*a* (Fig. 5A). Between 17 and 38 days, the periphyton had consecutive losses of chlorophyll-*a* concentration compared to the control treatment. The temperature increase caused an average decrease of 69.3% in the chlorophyll-*a* concentration compared to the control. In

both treatments, the periphyton chlorophyll-*a* peak was on 38 days of colonization. Chlorophyll-*a* differed between treatments (RM-ANOVA: $df=3$, $F=9.39$, $p=0.039$), and the interaction between the factors was significant ($df=4$, $F=2.97$, $p=0.049$). Based on chlorophyll-*a* concentration, the net and gross accrual rates in the warming treatment were, respectively 9.1 and 5.6 times lower than those of the control (Fig. 5B). The AFDM: chlorophyll-*a* ratio was higher in the warming treatment than in the control, except on day 13 (Fig. 6). This ratio also differed between the control and warming treatments (RM-ANOVA: $df=3$, $F=15.66$, $p=0.017$).

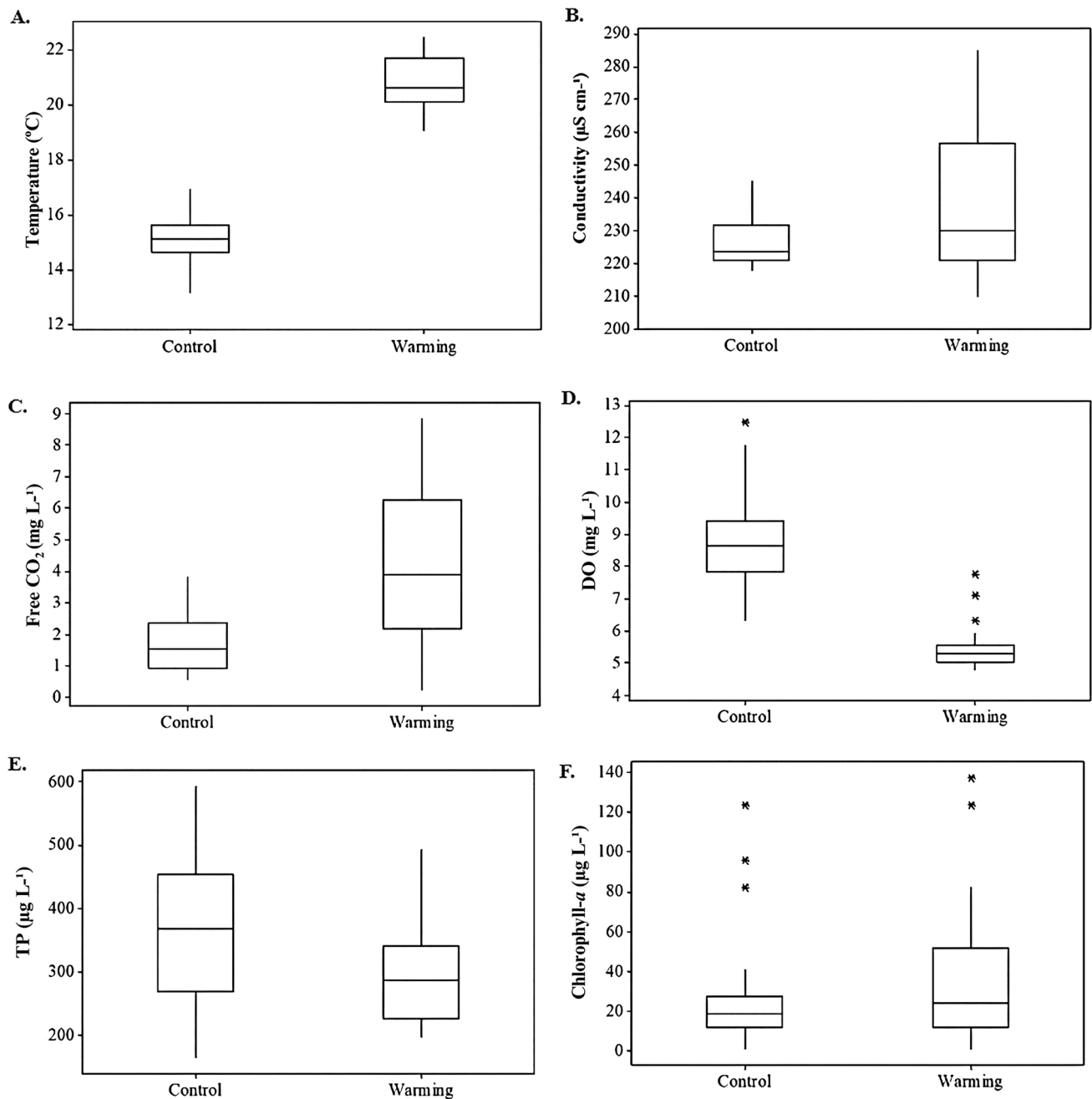


Fig. 3 Boxplot of temperature (A), conductivity (B), free CO₂ (C), dissolved oxygen (D; DO), total phosphorus (E; TP), and chlorophyll-*a* (F) concentrations ($n=24$) in the control and warming treatments during the experimental period. In each box, the upper and lower lim-

its indicate the 25th and 75th percentiles, respectively. The vertical bars represent the median, the horizontal bars indicate the standard error, and asterisks highlight potential outliers

Discussion

In warming treatment, conductivity, free CO₂, and chlorophyll-*a* concentrations increased, and DO concentration decreased, evidencing that warming during winter can worsen eutrophic conditions. As a result, we found a negative impact on the algal biomass accrual rate

in the periphyton. The increase in winter temperature can cause significant losses of periphyton algal biomass. Specifically, our findings suggest that a temperature rise of 5.7 °C in winter can decrease photosynthetic periphyton biomass. In the supereutrophic reservoir studied, the highest periphytic biomass occurs in winter, when the intensity of phytoplankton bloom is reduced (Borduqui and Ferragut

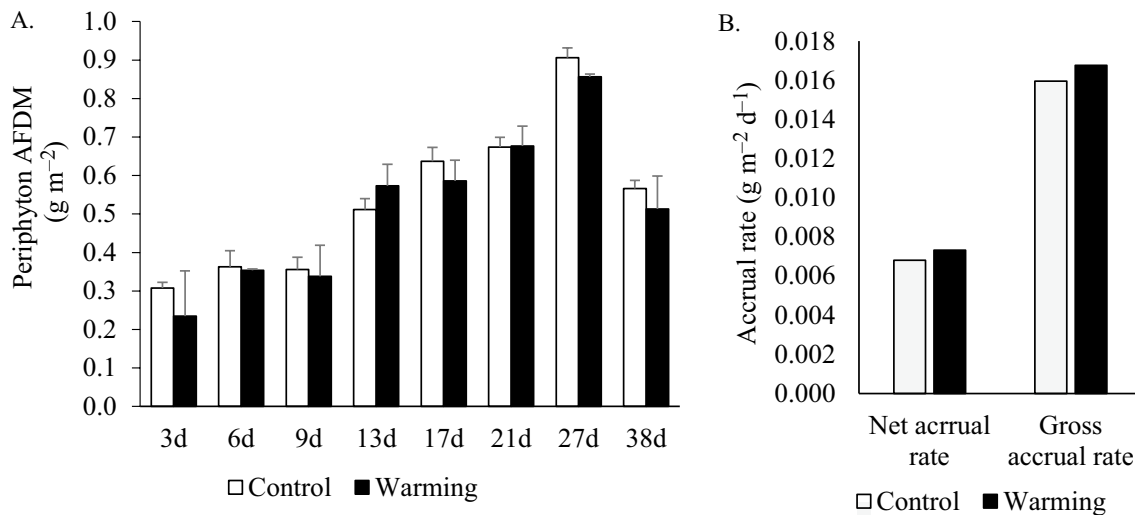


Fig. 4 Periphyton AFDM (A, $n=3$) and accretion rate (B) on the artificial substrate in the control and warming treatment during the experimental period. Vertical bars in the panel A represent standard error

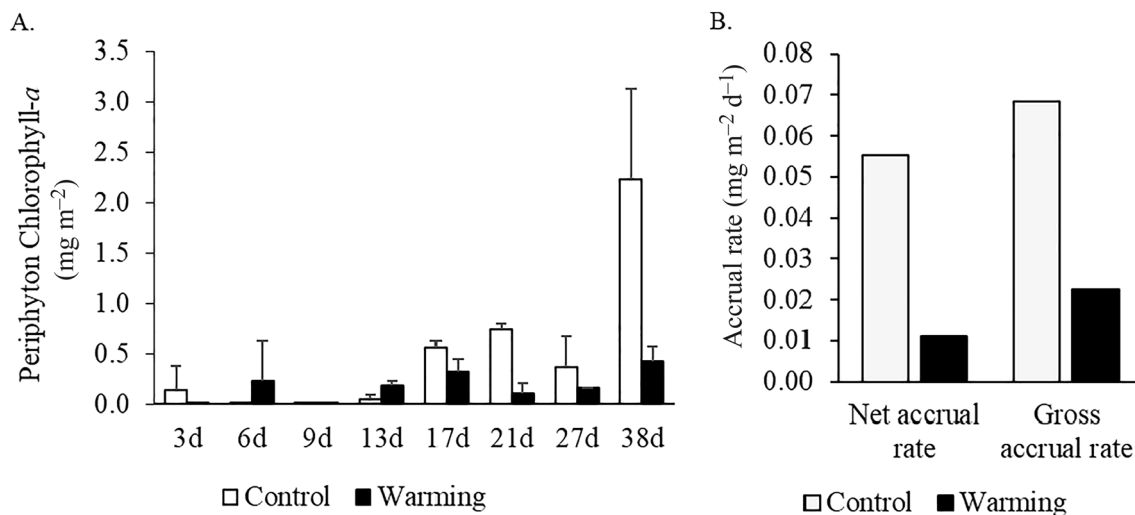


Fig. 5 Periphyton chlorophyll-*a* (A) and accretion rate (B) on the artificial substrate ($n=3$) in control and warming treatments during the experimental period. Vertical bars in the panel A represent standard error

2012). The surface water cooling in winter promotes column mixing, contributing to the reduction of phytoplanktonic biomass (Bicudo et al. 2007; Crossetti et al. 2019), which favor periphyton growth. In eutrophic conditions, studies reported that a decline in periphyton biomass accumulation can be associated with nutrient competition among autotrophs (Zhang et al. 2015) and with shading (Borduqui and Ferragut 2012). A long-term experimental study in a temperate channel also has evidenced that warming during the winter reduced the periphyton biomass (Bondar-Kunze et al. 2021). In addition, warming effect on periphyton abundance and species composition can vary with seasonality, trophic state, and host macrophyte species (Hao

et al. 2020; Kazanjian et al. 2018). In contrast, Kazanjian et al. (2018) found that warming impaired phytoplankton growth due to competition for resources with periphyton and macrophytes. According to Vasconcelos et al. (2016), lake ecosystem responses to climate change can be mediated by cross-habitat feedback between benthic and pelagic producers. As a result, the response of periphyton algal biomass to warming may be linked to the response of phytoplankton in eutrophic environments.

Based on AFDM, our findings showed that the organic matter accretion rate in the periphyton did not reflect the increase in temperature in our experiment. Although warming negatively impacted the algal biomass accretion in the

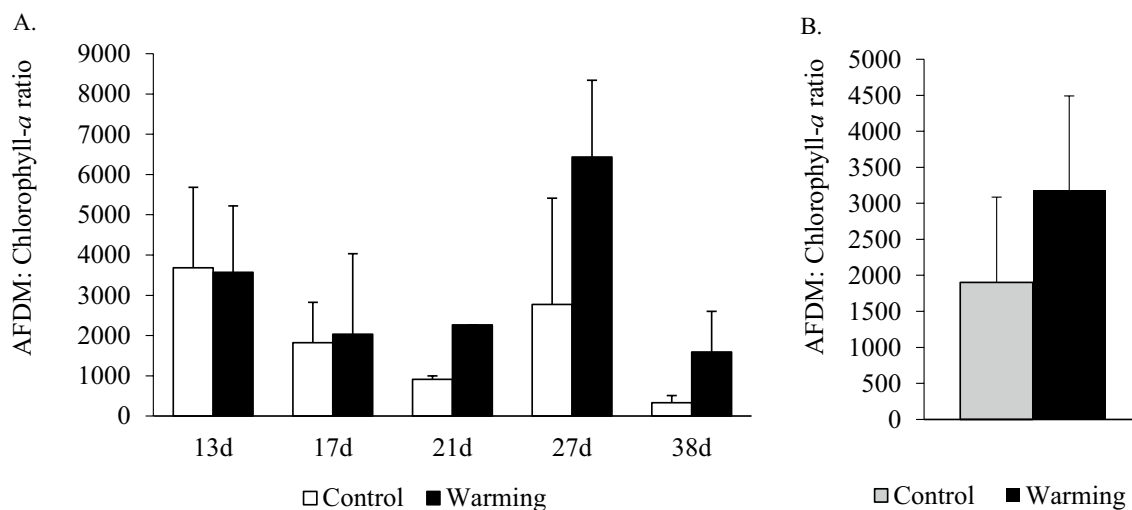


Fig. 6 AFDM: chlorophyll-*a* ratio in the periphyton on artificial substrate ($n=3$) during the colonization time (**A**) and on average (**B**) in control and warming treatments. Vertical bars in the panel A and B represent standard error

periphyton, it did not affect the organic matter accumulation rate. However, AFDM: chlorophyll-*a* ratio in periphyton, on average, increased with the warming, indicating a decrease in the autotrophic components. The increase in the organic matter could be linked to increased heterotrophs or excess organic debris in the periphyton (Stevenson 1996). Algal biomass was expected to increase during periphyton colonization, especially in the advanced stages, due to the increase of filamentous algae (Biggs 1996), as observed in the community of other lakes (Dunck et al. 2015; Casartelli et al. 2016; Lan et al. 2018). Thus, considering that warming decreased algal biomass and increased AFDM: chlorophyll-*a* ratio in advanced colonization stages, it is possible that global warming reduces the contribution of autotrophs in the periphyton in eutrophic lakes. Since periphyton plays a crucial role in shallow lakes, contributing up to 99% of primary productivity (Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2003), losses in algal biomass can impact the lake ecosystem functioning.

Regarding the colonization period (up to 38 days), we found that the warming affected periphyton algal biomass (chlorophyll-*a*) from day 17 when the amount in the control was significantly higher than in the warming treatment. Our findings indicate that warming negatively affected biomass accumulation during the intermediate and advanced colonization stages. The initial colonization phase involves the formation of an organic matrix that accommodates bacteria and ruderal algae, which have adaptations that enable them to maintain populations in highly disturbed sites (McCormick 1996; Flemming and Wingender 2010). Consequently, the colonization initial phase of the periphyton may be less affected by warming than the intermediate and advanced phases, as observed

in our experiment. However, the most mature phases are commonly characterized by high biomass due to the abundance *k*-strategist species, especially filamentous species. The loss of algal biomass in the periphyton during the biomass accumulation phase, as observed here, can affect the ecological functions of the community in the ecosystem. Furthermore, warming impacted the biomass accumulation phase, which may affect its ecological functions in the ecosystem.

Other factors may also have influenced changes in algal biomass in the periphyton, such as grazing pressure, photoadaptation, and brownification. Admittedly, grazing can determine periphyton biomass and structure (e.g., Beck et al. 2019). However, some aspects suggested that the grazing pressure must have had little effect on periphyton in our experiment. Firstly, the animals such as fish and snails were manually excluded, reducing grazing during the experiment. Additionally, the grazing pressure exerted by zooplankton is considered low in the studied reservoir, with top-down control not being detected (Amaral et al. 2020). Generally, the traditional control of phytoplankton by large zooplankton does not occur in warm lakes (Jeppesen et al. 2007). In eutrophic environments, the effect of zooplankton herbivory on phytoplankton is size-specific, which may explain the limited control exercised by this community in tropical ecosystems (Wong et al. 2016). Despite the absence of significant difference in light availability in water between treatments, algal photoadaptation may have influenced biomass results, especially chlorophyll-*a*, due to the difference in ambient light. Microalgae grow in different light intensities and wavelengths and must have specific mechanisms of photoacclimation and photoadaptation, as evidenced in algal species and groups

(Richardson et al. 1983; MacIntyre et al. 2002; Huysman et al. 2013). According to Enberg et al. (2015), increased PAR availability, especially with the exclusion of UVR, can cause changes in algal biomass, photosynthetic activity, and community composition. The other aspect not measured in this experiment that can affect biomass accumulation in periphyton is water brownification, which refers to water darkening, often related to increasing organic matter. The brownification can affect algal community growth (Urrutia-Cordero et al. 2017), including the periphytic algae (Puts et al. 2023). Although it was not measured in this study, the warming treatments showed a noticeable change in the color of the water, becoming more brownish, which must have shaded the periphyton. Considering that global warming can affect grazing on the periphyton (Pacheco et al. 2021) and favor the brownification of the waters (Puts et al. 2023), future studies should examine its effects on community colonization.

Our findings indicate that warming may negatively impact photosynthetic biomass accumulation in eutrophic environments by impairing algal biomass accumulation in periphyton, particularly during the most favorable seasons for growth, such as winter in the studied reservoir. The warming negative effect on algal biomass in the intermediate and advanced phases of periphyton colonization suggests the persistence of the initial phase, damaging the accumulation phase. We conclude that warming can affect the periphyton colonization process by reducing autotrophic biomass accumulation under eutrophic conditions in a global warming scenario. We emphasize that periphytic algal growth is generally impaired in eutrophic lakes and reservoirs, where warming can further reduce primary producers of this community. Our results suggest that the effects of global warming on periphyton deserve further attention, given the importance of the community for primary production and food webs.

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Author contributions L.D. Sapucaia, R.O. Carneiro, and C. Ferragut: conceptualized experimental sampling, wrote, and edited the original draft; L.D. Sapucaia generated the biotic data; all authors generated the abiotic results. All authors revised and approved the final manuscript.

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Availability of data and materials The datasets generated and analyzed during the present study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

Ethical approval Not applicable/not required.

Consent to participate All the authors consent to participate in this manuscript.

Consent for publication All the authors consent the publication of this manuscript.

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