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PRIMARY RESEARCH PAPER

The response of two submerged macrophytes and periphyton to elevated temperatures in the presence and absence of snails: a microcosm approach

Yu Cao · Wei Li · Erik Jeppesen

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Abstract Global warming may affect snail–periphyton–macrophyte relationships in lakes with implications also for water clarity. We conducted a 40-day aquaria experiment to elucidate the response of submerged macrophytes and periphyton on real and artificial plants to elevated temperatures (3°C) under eutrophic conditions, with and without snails present. With snails, the biomass and length of *Vallisneria spinulosa* leaves increased more at the high temperature, and at both temperatures growth was higher than in absence of snails. The biomass of periphyton on *V. spinulosa* as well as on artificial plants was higher at the highest temperature in the absence but not in the presence of snails. The biomass of *Potamogeton crispus* (in a decaying state) declined in all treatments and was not affected by temperature or snails. While total snail biomass did not differ between temperatures, lower abundance of adults (size >1 cm) was observed at the high temperatures. We conclude that the effect of elevated temperature on the snail–periphyton–macrophyte relationship in summer differs among macrophyte species in active growth or senescent species in subtropical lakes and that snails, when abundant, improve the chances of maintaining actively growing macrophytes under eutrophic conditions, and more so in a warmer future with potentially denser growth of periphyton.

Keywords Snail–periphyton–macrophyte relationship · Elevated temperature · Freshwater ecosystem · Submerged macrophyte

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Y. Cao · W. Li
Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China

Y. Cao · E. Jeppesen
Department of Bioscience, Aarhus University, Vejlsøvej 25, PO Box 314, 8600 Silkeborg, Denmark

Y. Cao
University of Chinese Academy of Sciences, Beijing 100049, China

W. Li · E. Jeppesen
Sino-Danish Centre for Education and Research (SDC), Beijing, China

W. Li (✉)
Hubei Key Laboratory of Wetland Evolution & Ecological Restoration, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China
e-mail: liwei@wbgcas.cn

Introduction

By the end of the twenty-first century, the global average surface air temperature is projected to increase between 1.1 and 6.4°C relative to 1980–1990 temperatures (Solomon et al., 2007), with implications also for lake ecosystems. The effect of warming on the relationship between zooplankton, phytoplankton, and

submerged macrophytes has been intensively studied (McKee et al., 2002; Meerhoff et al., 2007; Kosten et al., 2011; Nicolle et al., 2012), and warming has been shown to enhance the biomass and distribution of submerged macrophytes in clear water lakes (Rooney & Kalff, 2000) but to intensify eutrophication and the disappearance of submerged macrophytes in eutrophic lakes (Moss et al., 2011). Macrophytes are important structuring components in freshwater ecosystems as they contribute to establish and maintain clear water conditions, for example by providing refuge for zooplankton, thereby enhancing the grazing pressure on phytoplankton, and by reducing resuspension of the sediment (Moss, 1990; Scheffer et al., 1993; Schriver et al., 1995; Jeppesen et al., 1998).

Macrophyte growth may be hampered by periphyton growth on their surfaces as this affects light conditions and nutrient availability for the host plants, not least in eutrophic lakes (Phillips et al., 1978); however, high grazing by invertebrates, not least snails, potentially has a modulating effect on this (Jones & Sayer, 2003). The relationship between snails and the periphyton–macrophyte complex is particularly well studied in temperate lakes (Brönmark, 1989; Underwood et al., 1992; Brönmark & Vermaat, 1998). While there is evidence of direct herbivory by snails on aquatic plants (Lodge, 1991; Li et al., 2009), the relationship between snails and macrophytes is most often mutualistic (Thomas, 1990; Underwood et al., 1992)—by reducing periphyton biomass, snails promote macrophyte growth by decreasing shading (Brönmark, 1985; Cattaneo & Kalff, 1986; Brönmark, 1994; Strand & Weisner, 2001; Roberts et al., 2003). Little is, however, known about the effect of warming on snail–periphyton–macrophyte interactions and the results that are available are ambiguous. An experimental pond study conducted in Canada showed that warming reduced the effects of eutrophication on the periphyton of artificial plants due to higher invertebrate grazing (Shurin et al., 2012). Likewise, a mesocosm study conducted by McKee et al. (2003) in the U.K. indicated that invertebrate biomass (mainly snails) will increase with higher temperatures and thus augment the chances of macrophyte presence at high nutrient levels. However, a recent mesocosm experiment run at low nutrient levels in Denmark revealed no change in periphyton on plants (*Potamogeton crispus* and *Elodea canadensis*) in response to heating (Y, Cao, unpublished data), while other mesocosm experiments have shown enhanced periphyton growth with increasing temperature (Patrick et al., 2012) as well as higher periphyton productivity (Kishi et al., 2005).

We conducted a microcosm study of the response of two submerged macrophytes and periphyton to elevated temperatures in early summer under eutrophic conditions, with and without snails. One plant species (*Vallisneria spinulosa*, Hydrocharitaceae) was in the active growth phase, while the other (*Potamogeton crispus*, Potamogetonaceae), being a spring species at our locality, was in a senescent state. We hypothesized that warming would stimulate periphyton growth under eutrophic conditions, with potentially adverse effects on the host plant unless snail grazing is high. We also expected stronger effects of warming on snail–periphyton–macrophyte interactions of plants in the active growth phase than for plants that have passed this phase or for artificial plants as the host plants through their growth may in part compensate for a potentially enhanced shading effect by the periphyton.

Materials and methods

The experiment was conducted from May to June 2012. *V. spinulosa* was collected from Wuhan Botanical Garden, China, where it grew in a concrete pond (length × width × depth: 30 × 15 × 1.5 m) exclusively dominated by this species, and *P. crispus* was collected from Houhu Lake, China, where it dominates the macrophyte community from fall to early summer. For the experiment, we selected approx. 10-cm-long *V. spinulosa* with three leaves and approx. 10-cm-long *P. crispus* with no branches. We also used an artificial plant consisting of a 20 cm metal stick with five long oval-shaped leaves to measure periphyton development without plant interaction and growth. The natural plants were washed carefully to remove snail eggs and periphyton and then cultivated in plastic pots (top diameter 10.6 cm, bottom diameter 9 cm, height 8.5 cm) filled with washed river sand. Five individuals of each plant were chosen to mimic a high coverage (80–100%) plant dominated state in a natural lake and placed in a glass aquarium (length × width × height: 40 × 30 × 60 cm). Two unconnected concrete pools (length × width ×

depth: 4 × 4 × 1 m) were both half filled with lake water and acted as temperature buffer. The heating system consisted of a control unit, two temperature sensors, one in each of the two concrete pools, and a spiral heater (diameter 9 cm, power 800 w) in one of the pools, and four water pumps (800 L h^{-1}), two in each pool. The sensors measured the temperature simultaneously in the two pools, and the heater was switched on/off at 3°C temperature elevation. The recording frequency was 10 ± 0.1 min.

We had four treatments, each in 4 replicates: high temperature and snail presence (HS), high temperature and snail absence (HN), low (ambient) temperature and snail presence (LS), low temperature and snail absence (LN). Five individuals of *Radix swinhoei* (size: around 1 cm), a dominant epiphytic gastropod in the Yangtze lakes (Wang et al., 2006), were used as periphyton grazers. The plants were placed in the aquaria a week before initiating the experiment. After this, the pesticide decamethrin (effective concentration: 2.5%) was added to remove the snails in half of the aquaria prior to initiation of the experiment. For each aquarium, 10 ml of the pesticide solution was diluted with water in a small bucket and subsequently transferred into the aquarium. Dead snails were removed from the pesticide-treated tanks. At the end of the experiment, the water in the aquaria was poured through a 500 μm net to collect the snails after which snails remaining in the aquaria were collected to determine snail biomass.

Every 10 days, one individual of each macrophyte (or artificial plant) was randomly chosen and harvested to determine macrophyte biomass. Macrophytes were separated into leaf and root (or stem) and were subsequently dried at 80°C for 48 h to determine dry weight. The third leaf counting from the shoot apex was extracted by ethanol to measure the chlorophyll *a* (chl*a*) and chlorophyll *b* (chl*b*) content after cleaning the surface (Wang et al., 2008). The periphyton on real plants was carefully sampled before cleaning the plant by adding water to a sealed plastic bag followed by thorough shaking after which the washed-off water was filtered on GF/C filters. After extraction by acetone, the solution was analyzed spectrophotometrically. If the periphyton was too dense to allow determination, a subsample from the washed-off water was used. The periphyton on artificial plants was sampled in a similar manner. Periphyton biomass was calculated according to sampled leaf surface area with the unit of μg chl*a* cm^{-2}.

A 500 ml water sample was gathered to determine water chemistry. For determination of total phosphorus (TP) and total nitrogen (TN), water samples were first digested with $K_2S_2O_8$. TN was then determined using a spectrophotometric method after the addition of hydrochloric acid, and TP and soluble reactive phosphorus (SRP) were spectrophotometrically determined as molybdate-reactive phosphorus (Huang et al., 1999). NH_4–N was determined with the Nessler's reagent colorimetric method and NO_3–N by using the spectrophotometric method with phenol disulphonic acid (Huang et al., 1999). For determination of chl*a*, 200–500 ml of water was filtered through Whatman GF/C filters and extracted using the acetone method (Huang et al., 1999).

The day before the heating was switched on (Day0), water and plants were sampled, and soluble phosphorus KH_2PO_4, nitrogen NH_4Cl, and KNO_3 with a 1:2 nitrogen ratio were added to obtain an initial nutrient level of 0.15 mg l^{-1} TP and 3 mg l^{-1} TN, typical nutrient levels of eutrophic lakes in the middle–low reaches of the Yangtze River and within the range of regime shifts between macrophyte-dominated clear water lakes and phytoplankton-dominated turbid lakes in this area (Wu et al., 2006; Wang et al., 2014). After Day0, water was sampled every 10 days for nutrient and phytoplankton analysis. Efforts were made to maintain similar nutrient levels as at the start of the experiment by adding nutrients after each sampling event. TN and TP loadings needed to maintain nutrient concentrations were calculated from the data obtained in the previous sampling. Total nutrient loadings were calculated by summing up the additions during the experiment. The ratio of periphyton biomass to nutrient loading was obtained by dividing periphyton biomass at the end of the experiment by total nutrient loadings, the ratio being used as an indicator to show the direct effects of nutrient loading on periphyton biomass.

One-way ANOVA was used to analyze nutrient conditions on Day0 and to determine the ratio of periphyton biomass and total nutrient loading. A *t* test was performed to analyze for differences in snail biomass. The data gathered after initiation of the experiment were analyzed by RM-ANOVA (shown in Table 1), and the Student–Newman–Keuls (SNK) method was chosen for the post hoc test. Data were

Table 1 The statistical results of the RM-ANOVA analysis

Measurements	Treatment	Time	Treatment * time	SNK test for Treatment
Macrophytes				
V. spinulosa				
Maximum length	***	***	*	HS > LS, HN, LN
Leaf biomass	**	***	***	HS > LS, HN, LN
Root biomass	NS	*	NS	
Leaf chl*a*	**	***	**	HS, LS > HN, LN
Leaf chl*b*	***	***	***	HS, LS > HN, LN
Periphyton biomass	***	NS	*	HN > LN, LS, HS
P. crispus				
Maximum length	NS	***	NS	
Leaf biomass	NS	NS	NS	
Stem biomass	NS	NS	NS	
Leaf chl*a*	NS	**	NS	
Leaf chl*b*	NS	*	NS	
Periphyton biomass	***	NS	NS	HN, LN > HS, LS
Chemicals				
TN	NS	***	**	
TP	*	**	**	LN > HN
PO_4	**	***	***	LS, LN, HS > HN
NH_4	***	***	***	LN, HN > HS, LS
NO_3	***	***	***	LN, HS > LS > HN
Other				
Periphyton biomass[a]	***	**	**	HN > LN > HS, LS
Phytoplankton biomass	NS	*	NS	

NS not significant

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

[a] Periphyton biomass here indicates the periphyton biomass on the artificial plants

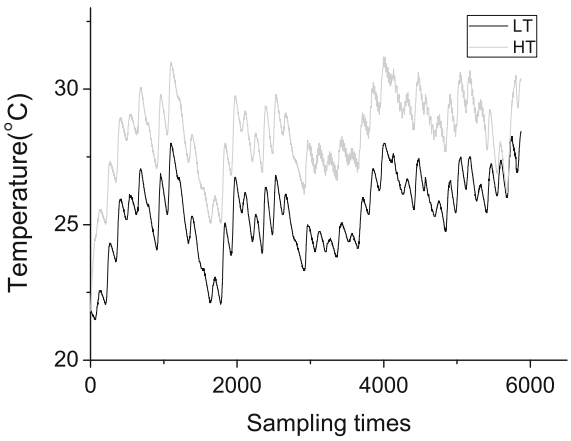

Fig. 1 Different water temperatures in the buffer pools (*LT* lower temperature, *HT* higher temperature)

SQRT-transformed, when needed, to satisfy the assumptions in the Mauchly's test of sphericity; otherwise, the Greenhouse-Geisser value was used for the modification. The related statistical results are included in Table 1 if not explicitly shown in the text. For the statistical analyses, we used SPSS16.0. The data presented are mean ± SD.

Results

Temperature

The average ambient temperature was 25.4 ± 1.4°C (Fig. 1) and was elevated by 2.8 ± 0.5°C during the experiment.

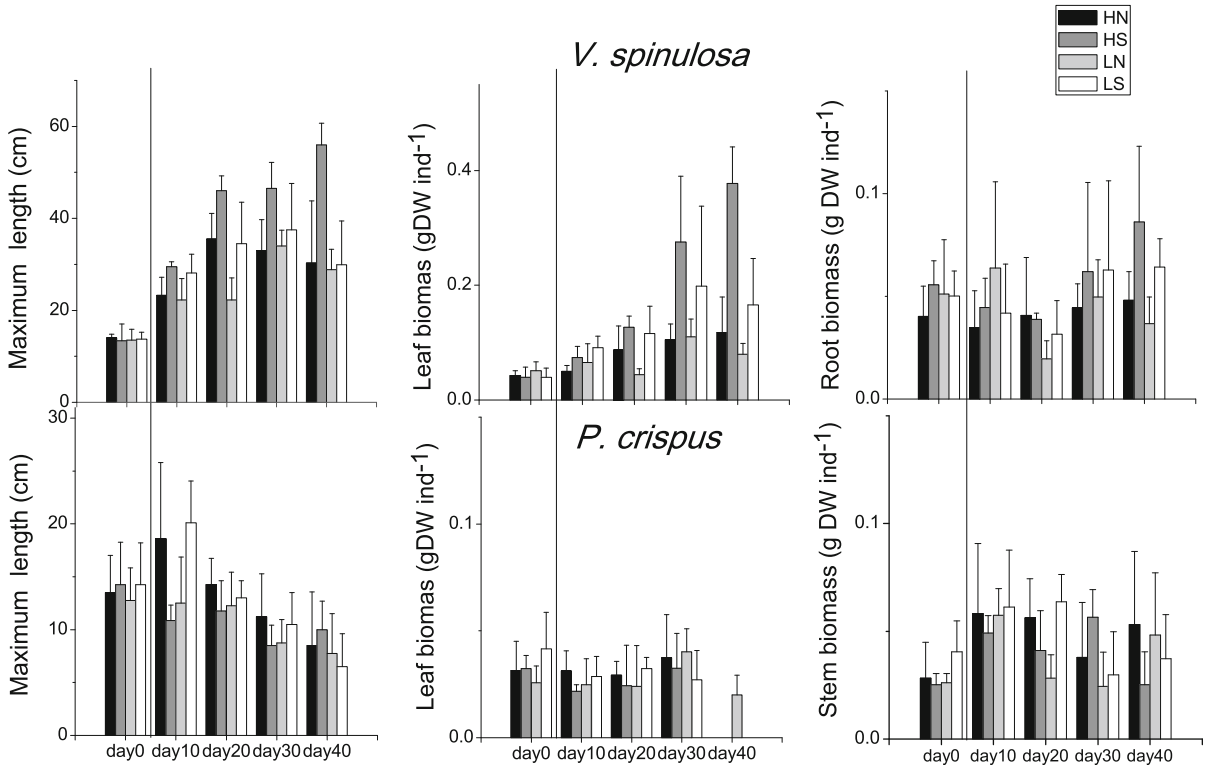

Fig. 2 Maximum leaf length, biomass of the leaf and stem (or root) of macrophytes during the experiment (Day0 is separated by the *black line*). Biomass unit is g dry weight per individual plant (g DW ind^{-1})

Macrophytes

The maximum length of *V. spinulosa* did not differ significantly between treatments on Day0 (ANOVA, $F_{3,12} = 0.056$, $P > 0.05$), indicating similar initial conditions (Fig. 2). During the experiment, the maximum length of *V. spinulosa* in the HS treatment was higher than in the remaining treatments, and it changed with time (Table 1). The root biomass of *V. spinulosa* was not significantly affected by the treatments but changed with time. The leaf biomass of *V. spinulosa* was significantly higher in the HS treatment than in the remaining treatments. The leaf chlorophyll content was higher in the snail treatments than in those without (Fig. 3). Both changed with time and showed significant chlorophyll–time interactions.

The maximum length of *P. crispus* decreased with time but did not differ significantly between the treatments (Fig. 2; Table 1). Leaf and stem biomass of *P. crispus* as well as the leaf chlorophyll content (chl*a* and chl*b*) did not differ between treatments, but leaf chl*a* and chl*b* decreased with time (Fig. 3; Table 1).

Periphyton

The periphyton biomass on *V. spinulosa* was significantly higher in the HN treatment than in the remaining treatments (Fig. 4; Table 1), being up to 1.35 ± 0.33 μg cm^{-2} by the end of the experiment. For *P. crispus*, the periphyton biomass was higher in the two treatments without snails than in those with snails (but the time or interaction effects were not significant). The periphyton biomass on the artificial plants was highest in the HN treatment, while the biomass was higher in the LN treatment than in the HS and LS treatments. The periphyton biomass on *V. spinulosa* and artificial plants increased differently during the experiment as indicated by significant time and treatment interaction, while no such difference was found for *P. crispus*. During the experiment, the periphyton biomass in the HN treatment did not differ among the three plant types (two

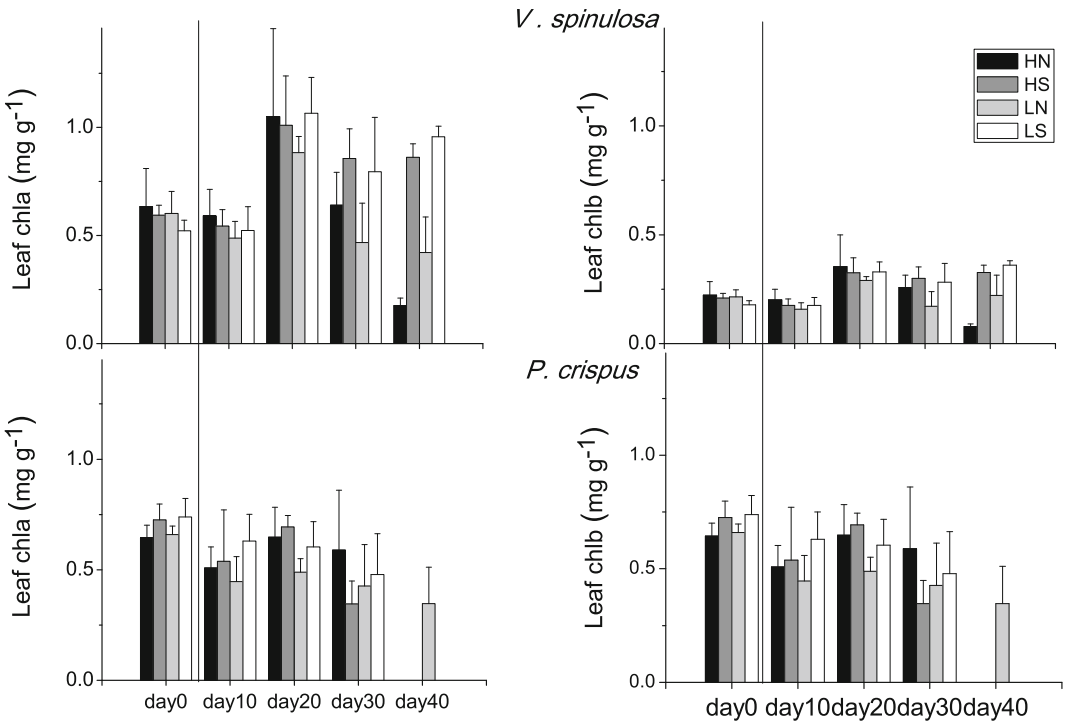

Fig. 3 Leaf chlorophyll *a* and *b* of macrophytes during the experiment (Day0 is separated by the *black line*)

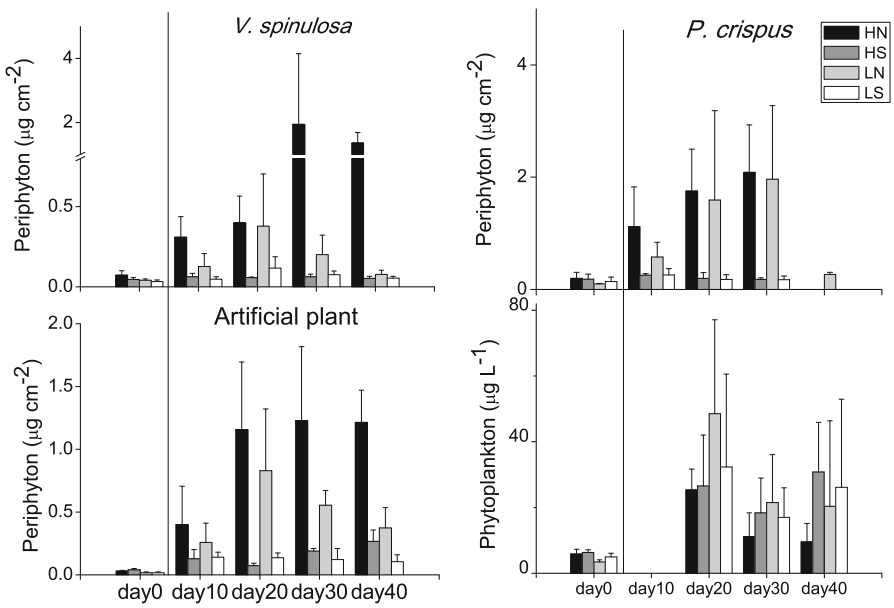

Fig. 4 Periphyton and phytoplankton biomass during the experiment (Day0 is separated by the *black line*)

natural and one artificial) ($F_{2,9} = 2.947$, $P > 0.05$, RM-ANOVA), but it increased with time ($F_{2,9} = 4.598$, $P < 0.05$, RM-ANOVA). In the remaining three treatments, the periphyton biomass on *P. crispus* was higher than on *V. spinulosa* and artificial plants, whereas no significant difference was traced for the periphyton biomass on *V. spinulosa* and on the artificial plants ($F_{2,9} = 7.979$, $P < 0.05$ for LN, $F_{2,9} = 27.436$, $P < 0.001$ for HS, $F_{2,9} = 9.599$, $P < 0.01$ for LS, RM-ANOVA), but it did not increase with time

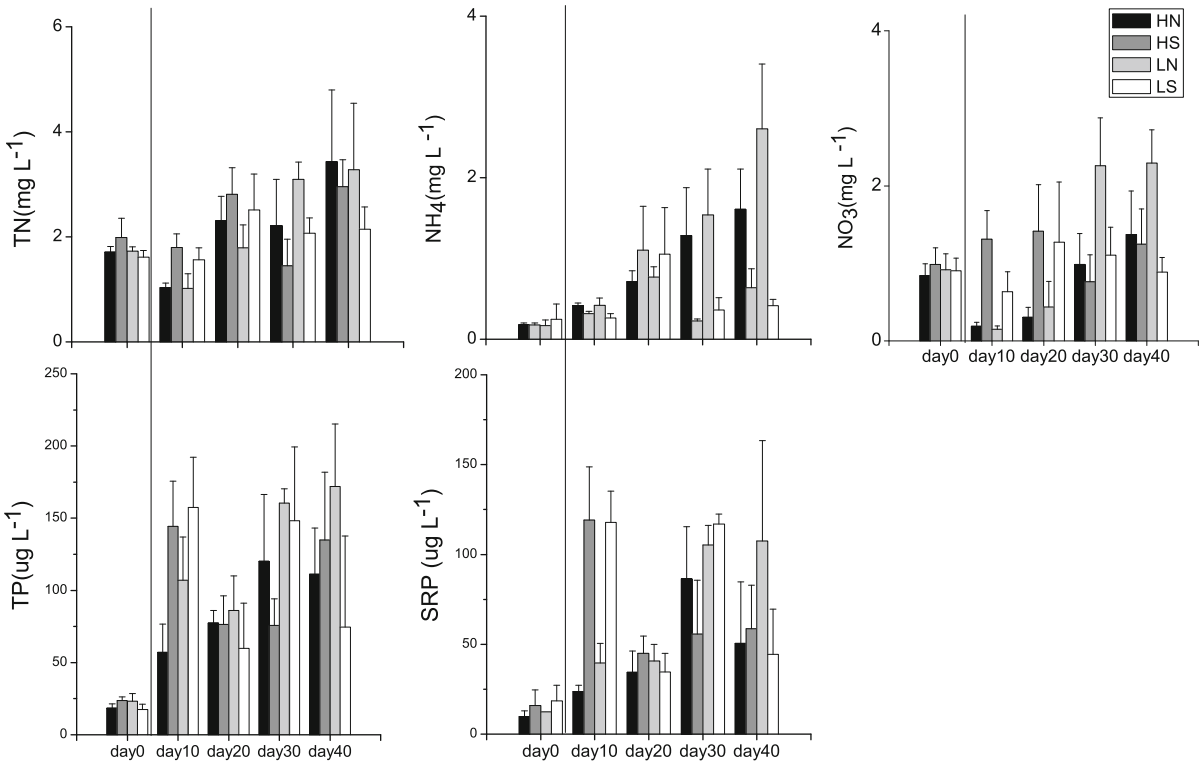

Fig. 5 Nutrient concentrations during the experiment (Day0 is separated by the *black line*.)

($F_{2,9} = 2.724$ for LN, $F_{2,9} = 2.881$ for HS, $F_{2,9} = 0.589$ for LS, $P > 0.05$, RM-ANOVA).

Phytoplankton and water chemistry

Phytoplankton biomass did not differ between treatments (Fig. 4; Table 1). In all treatments, TN fluctuated near the initial concentration of 3 mg l^{-1}, and no significant difference appeared among the treatments (Fig. 5; Table 1). The ammonia concentrations were lower in the two snail treatments than in those without snails. In contrast, the concentration of nitrate was lowest in the HN treatment, while nitrate in the LS treatment was lower than in the HS and LN treatments. Even though efforts were made to maintain similar TP concentrations, TP was still marginally higher in the LN treatment than in the HN treatment. SRP in the HN treatment was lower than in the other three treatments.

Nutrient loading

By the end of the experiment, the total TN loading did not differ between treatments ($F_{3,12} = 1.16$, $P > 0.05$, ANOVA), while total TP loading was marginally higher in the HN than in the LS and LN treatments ($F_{3,12} = 3.977$, $P < 0.05$, ANOVA). The ratio of periphyton biomass to nutrient loading was calculated in order to show the nutrient dependency of the periphyton increase (Fig. 6). The periphyton biomass on *V. spinulosa* and the total TN loading ratio were higher in the HN treatment than in the other three treatments ($F_{3,12} = 61.026$, $P < 0.001$, ANOVA), while the periphyton biomass on artificial plants and the total TN loading ratio were highest in the HN treatment and lowest in the LS treatment ($F_{3,12} = 26.623$, $P < 0.001$, ANOVA). The periphyton biomass and total TP loading ratio were highest in the HN treatment for *V. spinulosa* and higher in the HN treatment than in the with-snail treatments for artificial plants ($F_{3,12} = 61.026$, $P < 0.001$ for *V. spinulosa* and $F_{3,12} = 9.706$, $P < 0.01$ for artificial plants, ANOVA).

Snails

After the experiment, total snail biomass did not differ between the two snail treatments ($P > 0.05$, t test).

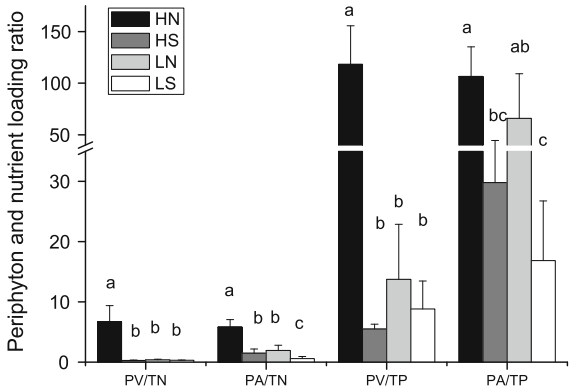

Fig. 6 Periphyton biomass on *V. spinulosa* (PV) and artificial plants (PA) and the total nutrient loading ratio at the end of the experiment, unit: ug chl*a* cm^{-2} per mg nitrogen or phosphorus)

However, the biomass of the larger snails (size >1 cm) was significantly lower in the HS treatment than in the LS treatment ($P < 0.05$, *t* test), while no difference was found for the biomass of small snails (size <1 cm) ($P > 0.05$, *t* test).

Discussion

For the actively growing *V. spinulosa,* leaf biomass and leaf length were higher at the higher temperature when snails were present and higher than in the absence of snails at both temperatures. The optimum temperature for carbon uptake by *V. americana* is around 32.6°C (Titus & Adams, 1979), but is as yet undetermined for *V. spinulosa*. The significant interaction between time and treatment for the leaf biomass and chlorophyll content of *V. spinulosa* suggests, in agreement with our expectations, more pronounced differences by the end of the experiment as has been demonstrated in a warming experiment in the UK (McKee et al., 2002). The abundance of *P. crispus* declined in all treatments, which is in line with summer observations made in other subtropical freshwaters (Rogers & Breen, 1980), and this apparently also affected the chlorophyll content of leaves, which declined during the course of the experiment independent of treatment. *P. crispus* has a lower optimum for photosynthesis (30°C) (Saitoh et al., 1970). In a mesocosm experiment, McKee et al. (2002) observed that warming enhanced the growth of exotic *Lagarosiphon major* but not of two other submerged macrophyte species present (*Elodea nuttallii* and *P. natans*).

Shading by phytoplankton is often a key factor for a decline of macrophytes in eutrophic lakes (Phillips et al., 1978; Hough et al., 1989). In our experiment, however, the phytoplankton biomass was overall low and did not differ among the treatments. The aquaria were transparent to the bottom, indicating low shading effects of phytoplankton. By contrast, the periphyton formed an intact layer on the leaves of the macrophytes and on the artificial plants in the treatments without snails (personal observation), and the biomass ranged from 0.07 to 2.08 μg cm^{-2}. Earlier studies have revealed that a periphyton biomass of 1 μg cm^{-2} induces severe light limitation of the growth of the submerged macrophyte *P. pectinatus* (Roberts et al., 2003). Köhler et al. (2010) found that two-week-old periphyton on *Sagittaria sagittifolia* reduced the light supply by 28%; in older mats the reduction may be as much as 85% (van Dijk, 1993), demonstrating the potential strong shading effect of periphyton. We found that the periphyton biomass on *V. spinulosa* and artificial plants was higher at higher temperatures than at ambient temperatures in the absence of snails, obviously suggesting a temperature effect. Also other mesocosm studies have revealed enhanced periphyton growth with increasing temperature (Patrick et al., 2012) and higher periphyton productivity (Kishi et al., 2005). By contrast, the periphyton biomass on *P. crispus* was not affected by temperature in the treatments without snails (Fig. 4), perhaps reflecting decay of the host plants, causing nutrient release (Guariento et al., 2009; Tarkowska-Kukuryk & Mieczan, 2012) that overrules the positive effects of higher temperatures. Indeed, we found a higher periphyton biomass on *P. crispus* in the without-snail treatment than on *V. spinulosa* and the artificial plants.

We regulated the nutrient loading during the course of the experiment to obtain approximately similar nutrient concentrations in all treatments. In this way, the microcosm with the higher temperatures and absence of snails received a significantly higher phosphorus loading than the other treatments, which potentially may have influenced the response of the periphyton. However, even when correcting for higher loading by using the ratio between the periphyton biomass on *V. spinulosa* and total TP loading, the difference remained significant.

The periphyton concentrations on the two submerged plants and the artificial plants were low in the snail-presence treatments compared to the without-snail treatments, indicating high snail grazing as seen in other studies with natural plants (Brönmark et al., 1992; Underwood et al., 1992; Dillon, 2000; Wojdak, 2005). A temperature effect on periphyton could not be discerned in the with-snail treatments, possibly due to a high grazing capacity of the snails. It has earlier been reported that periphyton declines with elevated temperatures (3°C above ambient) in the presence of invertebrates or fish (Shurin et al., 2012). Moreover, temperature affects the size structure, metabolism, growth, and reproduction of snails (Dillon, 2000). By the end of the experiment, we found that the biomass of large (size >1 cm) snails was higher at the lower temperature. The temperature-size rule predicts that snails mature at a smaller size in warmer environments (Atkinson, 1994) and that small-sized specimens are more efficient at meeting the metabolic demands (Sheridan & Bickford, 2011), leading to higher grazing on periphyton. Laboratory studies have shown, however, that *R. swinhoei* via grazing can negatively affect the growth of submerged macrophytes, such as *P. crispus* and *V. spiralis* (Xiong et al., 2008; Li et al., 2009) when periphyton is removed. However, in our outdoor study we did not find any evidence of a negative effect of *R. swinhoei* on macrophyte growth or decay. Periphyton can, however, also be controlled by fish, and the effect of fish is likely disproportionally higher in warm lakes due to a higher degree of herbivory and dominance of small-sized fish (Meerhoff et al., 2007; González-Bergonzoni et al., 2012). Fish grazing on periphyton may therefore potentially benefit the plant growth in warm lakes if not fully outweighed by an indirect effect of fish predation on snails that may lead to higher growth of periphyton. Dominance of small fish in warm lakes may benefit large-bodied snails such as golden apple snails that may cause high loss of aquatic plants (Carlsson et al., 2004). Our experiment was run at relatively high nutrient concentrations allowing extensive growth of periphyton in the absence of snail grazing. The outcome of warming on periphyton growth might be different at low nutrient concentrations. Trochine et al. (2014) found longer duration of nitrogen limitation of periphyton growth at higher temperatures in mesocosm experiments in Denmark during a 1-year study run at contrasting temperatures as well as a shift from overall single-nutrient limitation to co-limitation of nitrogen and phosphorus.

In conclusion, our results indicate that the response of snail–periphyton–macrophyte interactions to elevated temperatures differs among plants in active growth stages and under decay and that the chances of macrophyte dominance under eutrophic conditions in a warmer future climate rise at high snail abundance. Our results confirm that snails have a vital effect on periphyton under eutrophic conditions via their grazing on the periphyton, and they also suggest that temperature affects the size of snails in a warming world, leading to more efficient grazing provided that the snail abundance is not kept low by fish predation. More studies are, however, needed on fish–snail–periphyton–nutrient interactions in warm lakes to allow general conclusions about the response of periphyton to warming.

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