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PRIMARY RESEARCH PAPER

Snails have stronger indirect positive effects on submerged macrophyte growth attributes than zooplankton

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Abstract Phytoplankton and epiphyton often compete with submerged macrophytes. Grazing by zooplankton and/or epiphyton grazers should promote an indirect positive effect on submerged macrophyte growth rate. Hence, we mimicked shallow lakes conditions in mesocosms using a factorial design to evaluate the indirect effects of no grazers, zooplankton, snails or both grazers on macrophyte growth attributes. After 16 weeks, both snails and zooplankton had positive effects on macrophyte stem length and biomass. However, only snails had positive effects on macrophyte number of sprouts and root biomass. In addition, the positive effect size of snails on the submerged macrophytes was twice as large as the effect size of the zooplankton. Our study suggests that benthic food chains might be more capable of increasing resilience and affecting the stability of the clear-water state in shallow lakes than pelagic food chains. However, long-term experiments with varying relative proportions of herbivores and different macrophyte species, as well as in situ experiments, will be necessary to test the generality of our findings. Understanding the relative effects of benthic versus pelagic grazers on submerged macrophytes may increase the success of shallow lake restoration and should be taken into account when designing management and restoration efforts for shallow lake systems.

Keywords Snails · Zooplankton · Food chain · Herbivory · Regime shifts

Introduction

Changes in dominance of primary producers in shallow eutrophic lakes provide one of the classic examples of regime shifts (e.g. Scheffer et al., 2001; Hilt et al., 2006; Hilt, 2015). Herbivores of pelagic and benthic food chains, such as zooplankton and snails, respectively, play a key role in determining the dominance or loss of primary producers, such as phytoplankton (e.g. Scheffer, 1998) and epiphyton (e.g. Botts, 1993) in shallow lakes. However, such herbivores also indirectly determine the prevalence of submerged aquatic macrophytes (Brönmark, 1985; Martin et al., 1992; Brönmark, 1994). For example, in the turbid state of shallow lakes, the establishment and growth of submerged macrophytes may be restricted

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due to light attenuation induced by high phytoplankton biomass, which affects the abundance and species richness of macrophytes (e.g. Blindow, 1992, Arthaud et al., 2012). In contrast, in the clear-water state, a high grazing pressure from zooplankton reduces the biomass of phytoplankton, which then increases light availability and promotes macrophyte growth (e.g. Hilt, 2015). Thus, variations in submerged macrophyte dominance is a key feature indicating shifts in shallow lake ecosystem state along a gradient of nutrient loading, where lakes with high nutrient concentrations are in a turbid state, whereas lakes with low nutrient concentrations are in a clear-water state. At intermediate nutrient levels, however, the lake may shift between states.

Macrophyte growth may, however, also be affected by epiphytic algae through competition for light and nutrients (Brönmark, 1985; Li et al., 2008). Epiphytic algae have a high capacity of primary production in lakes (Brothers et al., 2016) and provide a food resource for a diverse guild of invertebrate grazers including snails, crustaceans and insect larvae (e.g. Botts, 1993; Mormul et al., 2010a, b). At high densities, grazers control the growth of epiphyton (Martin et al., 1992; Brönmark, 1994). The grazer–epiphyton interactions may thus be of great importance for submerged vegetation, and a number of studies in both freshwater and marine habitats have shown that grazing on epiphytic algae increases the growth rates of macrophytes, potentially by reducing competition for light and/or nutrients (Brönmark, 1985; Baden et al., 2010; Baden et al., 2012). Brönmark & Weisner (1992) even suggested that cascading interactions in the benthic food chain affecting snail density would result in reduced grazing pressure on epiphyton and reduced macrophyte growth and would eventually cause a transition from the clear-water, macrophyte-dominated state in shallow lakes to the turbid, phytoplankton-dominated state. Thus, the strength of herbivore–macrophyte interactions in both the benthic and the pelagic food chains could affect macrophyte growth (see also Phillips et al., 2016).

Despite the importance of indirect effects from both zooplankton and snails on the growth of submerged macrophytes, aquatic ecologists have for decades emphasized the importance of interactions in the pelagic food chain for the maintenance of shallow lake states, whereas benthic food chain interactions have been considered less important (but see e.g. Brönmark & Vermaat, 1998; Vadeboncoeur et al., 2002; Jones & Sayer, 2003; Hölker et al., 2015). In this study, we used a factorial experimental design crossing the presence/absence of zooplankton and snails, herbivores of phytoplankton and epiphytic algae, respectively, to evaluate the relative importance of interactions in the pelagic and benthic food chains for the growth of a submerged macrophyte, *Myriophyllum spicatum* Linnaeus (Haloragaceae). If competition with epiphyton (benthic food chain) is the strongest determinant of macrophyte growth, then macrophyte growth will be the highest in the treatments with snails. Conversely, if competition with phytoplankton (pelagic food chain) is the most important, macrophyte growth will be the highest in zooplankton treatments. In addition, our experimental design allowed for the identification of potential additive or synergistic effects of the different herbivore groups on macrophyte growth.

Methods

We carried out a 2 × 2 factorial experiment using 24 opaque plastic containers (inner diameter = 0.4 m, depth = 1.0 m, volume = 100 l) placed in the greenhouse facility of Lund University, Sweden. In the greenhouse, the containers received natural light and, in addition, artificial light with a 12:12 light regime. Water temperatures ranged from 13°C at the start of the experiment (January) to 19°C at the end (June). All containers were filled with tap water ($< 5\ \mu g\ l^{-1}$ PO_4, $900\ \mu g\ l^{-1}$ NO_3, $< 10\ \mu g\ l^{-1}$ NH_4; yearly averages, Lund municipality) and kept aerated with air stones. We added $50\ \mu g\ l^{-1}$ of phosphorous (PO_4) and $200\ \mu g\ l^{-1}$ of nitrogen (NO_3) at the beginning of the experiment (December 2011) to set the mesocosms at an intermediate nutrient concentration representative of the shallow lakes in the region (e.g. Blindow et al., 2000). During the experiment, we added nutrients every third week to maintain nutrient concentrations at levels similar to the starting conditions. All containers received a 40 ml inoculate of phytoplankton from a laboratory culture of *Scenedesmus* sp. (class Chlorophyceae). We used *Scenedesmus* sp. due to easy access to a laboratory culture and because it provides a valuable food source for zooplankton (e.g. Makino et al., 2011) and snail (Calow & Calow, 1975).

We also added five plastic strips (length = 100 cm, width = 1 cm; one end with a cork and the other with a screw-nut) extending from the bottom to the surface of each container for later epiphyton chlorophyll-*a* measurements. Earlier studies have shown that epiphyton biomass accumulation on plastic strips closely mimicks that on natural plants (e.g. Brönmark et al., 1992; Tóth 2013).

We randomly assigned four different treatments ($N = 6$) to the containers: controls—no herbivores added; snail—addition of *Radix balthica* (Linnaeus, 1758; Lymnaeidae); zooplankton—addition of *Daphnia magna* (Straus, 1820; Daphniidae); and snail + zooplankton—addition of the two herbivores. The zooplankter *D. magna* was retrieved from a laboratory culture and added to zooplankton treatments at a density of approximately 400 individuals m^{-3}. We collected the freshwater snail *R. balthica* from a small pond close to Lund, southern Sweden, and added 14 adults (13–16 mm total length) to snail treatments. It is worth noting that in snail + zooplankton treatment we have higher herbivores density than in the other treatments. In addition, herbivores density is within the natural range of zooplankton and snail densities found in lakes and ponds within the region (Blindow et al., 2002; Ahlgren J. & Brönmark C. personal observations). We added herbivores to the containers 15 days after inoculation of algae.

We collected apical portions of the submerged macrophyte *Myriophyllum spicatum* in Lake Krankesjön, close to Lund, southern Sweden, and planted 7 cm long fragments in small plastic pots. To avoid recruitment of sediment living algae or invertebrates, we filled the pots with dried sand. Before being transferred to the experimental containers, fragments were kept in tanks with tap water (< 5 µg l^{-1} PO_4, 900 µg l^{-1} NO_3, < 10 µg l^{-1} NH_4; yearly averages, Lund municipality) and nutrients (P:N 50:200 µg/l), until they had grown to 10 cm length. At the start of the experiment (January 14; 10 days after the herbivore addition), we added three macrophyte fragments to each container. We collected macrophytes in nature, i.e. they were colonized by epiphytic algae.

At the end of the experiment, after 16 weeks, we measured phytoplankton and epiphyton biomass as chlorophyll-*a* content. We collected a 50 ml water sample in each container and filtered it through a GF/C membrane to quantify phytoplankton chlorophyll-*a*. For epiphyton, we randomly collected one plastic strip in each container. Using ethanol for chlorophyll extraction and a spectrophotometer according to Jespersen & Christoffersen (1987) and Wintermanns & DeMots (1965), we quantified chlorophyll-*a* from the filters and the strips. We removed all macrophyte fragments from the containers at the end of the experiment (after 16 weeks) and measured four attributes to evaluate the growth of submerged macrophytes: fragment length (cm), fragment dry weight (DW, in g), sprout number per fragment and fragment root dry weight (DW, in g). To obtain the dry weight, we dried fragments and roots in an oven at 60°C until constant weight and weighed them. We did not remove epiphyton biomass from the dried macrophyte fragments as the low biomass of epiphyton compared to macrophytes should not affect macrophyte dry weight comparison among treatments.

Data analyses

The effects of treatments on phytoplankton and epiphyton biomass were analysed with non-parametric two-way analyses of variance based on permutation methods (999 permutations) because the data did not reach the ANOVA assumptions. The effects of treatments on the four macrophyte attributes were analysed with parametric two-way ANOVA. Finally, we applied Fisher's LSD test as a post hoc test performing multiple comparisons among treatments. Macrophyte attributes were log-transformed (*ln*) to meet the requirements of homogeneity of variances. All analyses were performed in R software using the package "vegan" (Oksanen et al., 2015).

To evaluate the relative effect of each herbivore on macrophyte growth, and to verify whether there are additive or synergistic effects of benthic and pelagic food chains on macrophyte growth, we adopted a meta-analytical approach, using the ANOVA results to obtain the effect size of each herbivore on the four macrophyte attributes. In the meta-analytical approach, all F values from ANOVA were converted to Cohen's d statistic (Thalheimer & Cook, 2002), and then transformed into Hedges' g (Borenstein et al., 2009). This procedure resulted in four Hedges' g values for each herbivore treatment. Finally, we calculated the mean effect size (average g) of each herbivore treatment on macrophyte growth with a confidence interval of 95%. The effect of herbivores on macrophyte growth is considered as additive if the effect size of the herbivores in combination is the sum of the individual herbivore's effects, whereas if the effect size of herbivores in combination exceeds the sum of the individual herbivore's effects, the effect is synergistic.

Results

Macrophyte fragment length (min–max = 43–116 cm) significantly increased by 68% in the snail ($F_{1,\ 19} = 8.53$, $P < 0.001$; Fig. 1A) and 71% in the zooplankton treatment ($F_{1,\ 19} = 10.77$, $P < 0.001$). However, the effect of one grazer on the macrophyte fragment length depended on the presence of the other grazer, leading to a significant interaction between snail and zooplankton treatment ($F_{1,\ 19} = 6.59$, $P =$ 0.01). In addition, there was no difference between snail, zooplankton and snail + zooplankton treatments, but fragments in herbivore treatments were all significantly longer than those in the control.

Fragment dry weight (min–max = 0.96–12.9 g) significantly increased almost three times in the presence of snails ($F_{1,\ 19} = 11.42$, $P < 0.001$; Fig. 1B) and almost twice in the presence of zooplankton ($F_{1,\ 19} = 5.75$, $P = 0.02$). Similar trends occurred between snail and zooplankton treatments, resulting in a non-significant interaction ($F_{1,\ 19} =$ 0.44, $P = 0.51$) for fragment dry weight. The post hoc test showed that the snail, zooplankton and snail + zooplankton treatments differed from the control. However, there was an increasing trend in fragment dry weight according to snail + zooplankton > snail > zooplankton > control. In addition, the snail + zooplankton treatment did not differ from the snail treatment (LSD test, $P = 0.24$), while the zooplankton treatment marginally differed (LSD test, $P = 0.06$) from the snail + zooplankton treatment.

The number of sprouts per fragments (min–max = 5–60) was used as a measurement of lateral investment and vegetative reproduction in the macrophyte. We found that the presence of snails increased macrophyte investment in sprouts almost three times ($F_{1,\ 19} = 2.38$, $P < 0.001$; Fig. 1C), but we found no significant effect of zooplankton ($F_{1,\ 19} = 0.06$, $P = 0.80$) or any effect of the interaction between snails and zooplankton ($F_{1,\ 19} = 1.87$, $P = 0.18$) on the number of sprouts per fragments. Again, the post hoc test showed that the snail + zooplankton treatment did not differ from the snail treatment (LSD test, $P = 0.27$), while the zooplankton treatment fell below

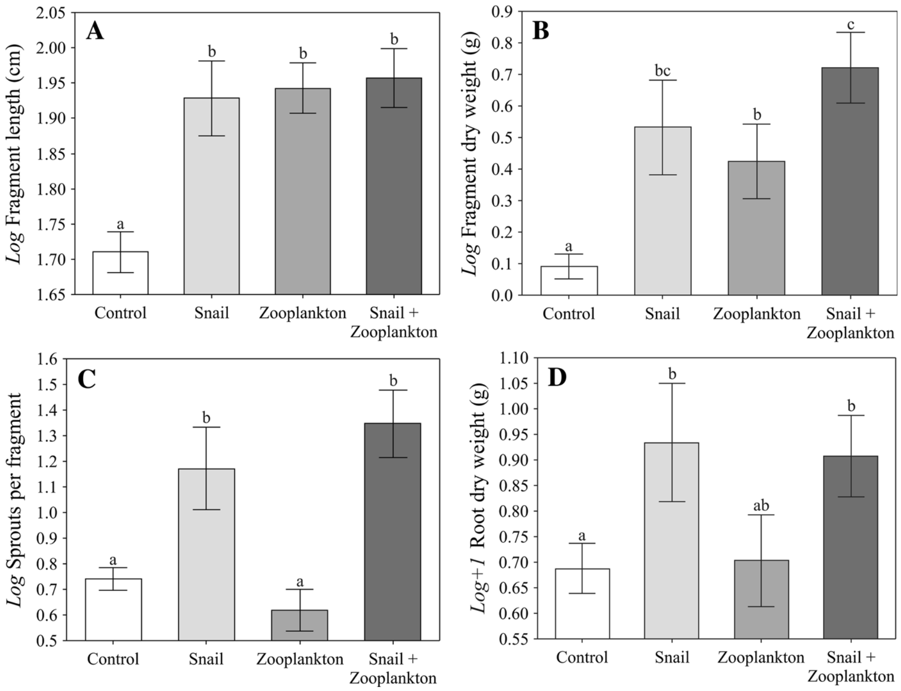

Fig. 1 Means and standard errors of the *log10* macrophyte fragment length (**A**), *log10* macrophyte fragment dry weight (**B**), *log10* of the number of sprouts per macrophyte fragment (**C**), and *log10 + 1* macrophyte root dry weight (**D**). All values were recorded at the end of the experiment in each treatment. Different letters indicate significant difference

the snail + zooplankton treatment (LSD test, $P < 0.001$).

The presence of snails doubled the root biomass, leading to a significant and positive effect on the root dry weight ($F_{1,\ 19} = 7.17$, $P = 0.01$; min–max = 0.31–2.46 g; Fig. 1D). However, there was no significant effect of zooplankton ($F_{1,\ 19} = 0.004$, $P = 0.94$), nor any effect of the interaction between snails and zooplankton ($F_{1,\ 19} = 0.06$, $P = 0.80$) on the root dry weight. The post hoc test showed that neither the snail nor the zooplankton treatment differed from the snail + zooplankton treatment (LSD test, $P = 0.83$ and $P = 0.09$, respectively), although the lower *p* value for the zooplankton versus the snail + zooplankton comparison indicates that snails may affect the root dry weight more, a similar trend found to the number of sprouts per fragment.

Our meta-analytical approach showed that although the mean effect sizes of all treatments were positive, only the snail treatment had a confidence interval with the lower limit higher than zero (Fig. 2). This result suggests that only the overall effect of the snail treatment on macrophyte growth attributes should be considered as significant and, further, that there was no additive or synergistic effect of snails and zooplankton on macrophytes. The snail treatment had a mean effect size (average $g = 1.80$) twice as large as the mean effect size of the zooplankton treatment (average $g = 0.75$), and almost twice as large as the mean effect size of the snail + zooplankton treatment (average $g = 1.02$).

Finally, zooplankton had a negative effect on phytoplankton biomass ($F_{1,\ 19} = 7.13$, $P = 0.01$; Fig. 3A), whereas there was no significant effect of snails ($F_{1,\ 19} = 3.10$, $P = 0.09$) or any interaction between snails and zooplankton ($F_{1,\ 19} = 3.33$, $P = 0.08$) in determining phytoplankton biomass. Epiphyton biomass was reduced in the presence of snails ($F_{1,\ 19} = 5.86$, $P = 0.02$; Fig. 3B), but there was no effect of zooplankton on epiphyton biomass ($F_{1,\ 19} = 2.39$, $P = 0.13$). Further, there was no interaction between snails and zooplankton ($F_{1,\ 19} = 1.52$, $P = 0.23$) determining epiphyton biomass.

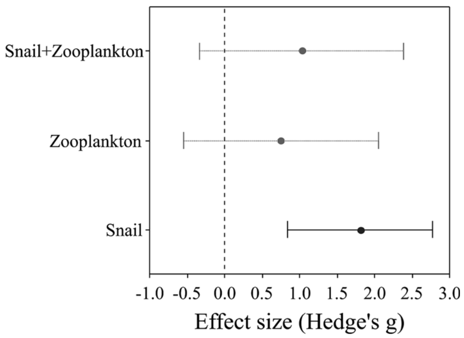

Fig. 2 Mean and confidence interval (95%) of the overall effect size of each herbivore treatment on the macrophyte growth. Gray = non-significant effect; Black = significant effect

Discussion

Snail and zooplankton herbivory efficiently reduced epiphyton and phytoplankton biomass, respectively, and herbivory thereby indirectly determined the growth of the submerged macrophyte. However, our results indicate that snails have a stronger indirect positive effect on submerged macrophyte growth than zooplankton, even at the high phytoplankton chlorophyll-*a* concentrations in the snail treatment. Furthermore, there were no additive or synergistic effects of snail and zooplankton herbivory. On the one hand, both snails and zooplankton positively affected the length and dry weight of the submerged macrophyte. Increasing length and biomass indicate successful macrophyte growth and development in lakes (Sousa et al., 2010), and larger plants tend to be better competitors than smaller plants (Bonser & Aarssen, 2003). On the other hand, only snails increased the number of sprouts per fragment and macrophyte root biomass. The increase in number of sprouts is coupled to successful vegetative reproduction (Grace, 1993), which potentially favours macrophyte population expansion and dominance in lakes (e.g. Hilt et al., 2006). Increasing root dry weight indicates more root biomass, which may enhance nutrient uptake from sediments (e.g. Schulze et al., 2002; Silveira et al., 2009), favouring plant growth and development (Marschner, 1995). Finally, we found that the overall effect size of the snails on macrophytes was stronger than for zooplankton, suggesting that interactions in the benthic food chain might be of greater importance for the maintenance of submerged macrophyte populations, determining lake state.

Earlier studies on indirect effects of algal herbivores on macrophyte growth have shown that submerged macrophytes increase their growth rate in the

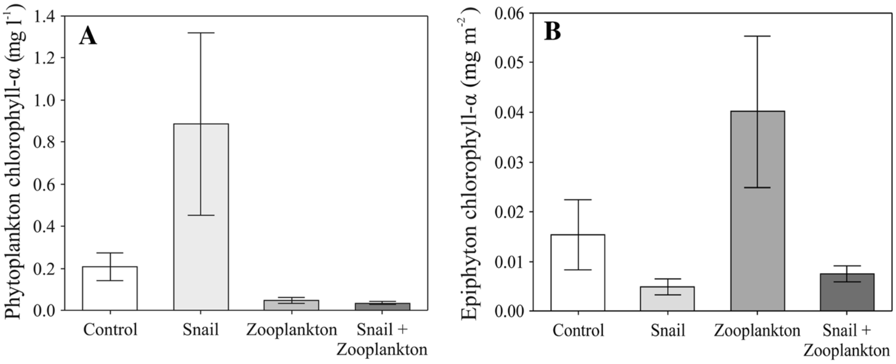

Fig. 3 Means and standard errors of phytoplankton chlorophyll-*a* (**A**) and epiphyton chlorophyll-*a* (**B**) recorded at the end of the experiment in each treatment

presence of epiphyton-grazing gastropods (Brönmark, 1985; Underwood, 1991; Underwood et al., 1992). Increased grazing pressure on epiphyton prolongs macrophyte life as macrophytes become longer and have more leaves (Underwood, 1991). Shading by epiphyton has a negative effect on macrophyte growth (Sand-Jensen & Borum, 1991; Roberts et al., 2003) and, thus, removal of the epiphytic cover by grazers increases light availability and, hence, macrophyte growth.

Similarly, earlier studies showed that shading by phytoplankton may also limit the growth of submerged macrophytes (Blindow, 1992; Arthaud et al., 2012) and, hence, grazing by zooplankton should favour macrophyte growth by decreasing the competition for light between phytoplankton and submerged macrophytes (e.g. Hilt, 2015). In addition, submerged macrophyte may release allelopathic compounds that suppress phytoplankton and might decrease the competition for light (Gross, 2003), which also facilitate macrophyte growth. Our results suggest that there are positive, indirect effects on submerged macrophyte growth due to grazing by both herbivores. Densities of zooplankton versus snails will affect the relative strength of the indirect effects in natural conditions, but in our study, where we mimicked natural densities of both grazers, we found that the effect of snails grazing on epiphyton is stronger than the effect of zooplankton grazing on phytoplankton. Moreover, it is worth noting that our results could be overestimating the impact of pelagic grazers as we used *D. magna*, a large-bodied zooplankton with high grazing rates, which is the most common in lakes with no fish or low fish density (Dawidowicz et al., 2013; Pietrzak et al., 2013). Thus, we suggest that competition with epiphytes is potentially stronger than with phytoplankton, and this makes the interaction between snails and submerged macrophytes crucial to the persistence of submerged macrophyte in lakes.

In a larger perspective, changes in the top trophic level in benthic food chains may affect submerged macrophyte growth through changes in the grazing pressure on epiphytic algae (Brönmark & Weisner, 1992). Field experiments have shown that manipulations of the density of molluscivorous fish affect macrophyte growth through changes in the benthic food chain, involving snails and epiphytic algae (Martin et al., 1992; Brönmark, 1994). Similar trophic cascade effects have been shown in marine waters, in this case from top predators to seagrass through changes in intermediate predators and herbivores (Baden et al., 2012). Thus, top-down trophic interactions might mediate competition for light between epiphyton and macrophytes, due to changes in predation pressure on the epiphyton-grazing invertebrates, eventually affecting the distribution of submerged macrophytes.

Given the indirect effects of both benthic and pelagic food chains on the submerged macrophyte growth, the ultimate implication of our findings is related to the shifts in alternative stable states in shallow lake ecosystem (e.g. Brönmark & Weisner, 1992; Scheffer, 1998). Aquatic ecologists have for decades mainly emphasized the importance of interactions in the pelagic food chain for the maintenance of shallow lake states, whereas interactions in the benthic food chain were a secondary, less important mechanism. However, our findings support the conceptual model of Brönmark & Weisner (1992) that suggests that interactions in the benthic food chain are fundamental for the success of submerged macrophytes. In addition, in an empirical test of this hypothesis, Jones & Sayer (2003) surveyed ponds with different food web configurations and found that biomasses of natural, multispecies macrophyte communities were unaffected by nutrient concentrations but had a strong negative relationship with periphyton biomass, whereas there was no significant relationship between phytoplankton biomass and macrophytes. Moreover, recent findings suggest that the collapse of submerged macrophyte communities is due to synergistic interactions between omnivorous fish, predation of which on epiphyton-grazing invertebrates' results in increased epiphyton shading, and herbivorous waterbirds (Hidding et al., 2016).

In summary, the indirect effects of benthic and pelagic food chains on macrophyte growth attributes may determine changes in macrophyte distribution and persistence (e.g. Brönmark & Weisner, 1992; Carpenter et al., 2001; Hidding et al., 2016). Snails and zooplankton have a crucial role in benthic and pelagic food chains, respectively, by reducing macrophyte competition with epiphyton and phytoplankton (e.g. Phillips et al., 2016). Moreover, snails and zooplankton could have crucial roles in mediating nutrient cycling, as snails and zooplankton excretions could increase nutrient availability in water and affect macrophyte growth attributes, a subject that should be explored in future studies. However, our results suggest that the role of the benthic food chain is of greater importance to determine the performance of submerged macrophytes in shallow lakes, since snail herbivory on epiphyton had larger positive effect size than zooplankton herbivory, enhancing all macrophyte growth attributes. Naturally, one has to keep in mind that this is a mesocosm study performed with a single zooplankton, snail and macrophyte species, respectively, and at one nutrient concentration. Zooplankton and snails show interspecific differences in grazing rates and, further, different species of submerged macrophytes respond differently to nutrient enrichment and light availability (Cao et al., 2011). Large-scale, long-term experiments with varying densities and diversities of herbivores, and with different macrophyte species, as well as in situ experiments, should be performed to further explore the generality of our findings. However, it should be noted that the conclusions from our mechanistic, mesocosm scale study is supported by Jones & Sayer's (2003) survey of natural lakes and ponds where they emphasized the importance of interactions in the benthic food chain for submerged macrophytes. Thus, we suggest that the high grazing pressure of snails on the epiphyton (benthic food chain) is more capable than the grazing pressure of zooplankton on the phytoplankton (pelagic food chain) to increase resilience of submerged macrophytes and might cause the stability of the clear-water state in shallow lakes. The macrophyte-dominated, clear-water state is preferred as it provides ecosystem services that are of great value for humans, including potable water, harvestable resources, water purification and opportunities for recreation. Thus, we should take into account the relative importance of interactions in the pelagic *versus* the benthic food chain when designing management strategies and restoration efforts (e.g. biomanipulation) for shallow lake systems.

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