ORIGINAL ARTICLE

Shallow lakes at risk: Nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails

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Abstract

1. In shallow lakes, submerged macrophytes can stabilise clear-water conditions and prevent phytoplankton blooms. Nutrient enrichment can promote their abundance. Above critical thresholds in water nutrient concentrations, however, submerged macrophytes have collapsed in many lakes worldwide with negative consequences for important ecosystem functions. The mechanisms behind this decline are complex and subject to debate.

2. We conducted mesocosm and laboratory experiments to investigate the top-down effect of invasive herbivorous snails (*Pomacea canaliculata*) on native submerged macrophytes (*Vallisneria natans*) under low and moderate nutrient treatment. We tested whether effects of nutrient addition to the water column on snail herbivory were influenced by shading by phytoplankton and epiphyton, macrophyte elemental tissue content and snail nutrient release.

3. We found that herbivorous snails had strong negative top-down effects on macrophytes, which were amplified by nutrient enrichment in the water column leading to higher macrophyte consumption rates. In moderate nutrient treatment, macrophyte consumption was faster and snails grew better than in low nutrient treatment. Additionally, snail treatments had higher nitrogen concentrations in the water leading to a negative feedback loop.

4. Our results suggest that snail herbivory may increase the chance for macrophyte collapse and shifts of shallow lakes to turbid states, and this effect occurs at lower snail densities when nutrient concentrations increase. Shallow lakes are thus severely at risk from projected increases in nutrient loading and spread of invasive herbivorous molluscs.

KEYWORDS
eutrophication, herbivory, *Pomacea canaliculata*, regime shift, submerged macrophyte

1　|　INTRODUCTION

Submerged macrophytes are of key importance for aquatic carbon and nutrient cycling, the provision of food and habitat for diverse aquatic communities (Hilt et al., 2017) and numerous other ecosystem services with links to the majority of Sustainable Development Goals (Janssen et al., 2020). In shallow lakes and lowland rivers, they can stabilise clear-water conditions and prevent phytoplankton blooms (Hilt et al., 2011; Scheffer et al., 1993). Although nutrient enrichment can increase the abundance of submerged macrophytes in freshwater ecosystems (Feuchtmayr et al., 2009), a complete loss of macrophytes often occurs above critical thresholds (Sand-Jensen et al., 2000, 2017; Zhang et al., 2017). This can be accompanied by a shift from clear to turbid, phytoplankton-dominated

conditions, in particular in shallow lakes (Hilt et al., 2013; Scheffer & Jeppesen, 2007). A recent review revealed that factors contributing to macrophyte collapse were usually studied individually, even though they are likely to interact with, or be reinforced by higher nutrient concentrations (Phillips et al., 2016).

One such factor that is likely to be reinforced at higher nutrient levels is top-down control by herbivory. Herbivory on macrophytes is widespread across freshwater and marine habitats (Bakker et al., 2016) and may trigger macrophyte losses and subsequent regime shifts of shallow lakes (Van Altena et al., 2016). Field studies of top-down control of macrophyte abundance by vertebrate consumers, however, yielded contrasting results (Marklund et al., 2002). Hidding et al. (2016) showed that herbivory alone does not typically cause macrophyte collapse, but that additional stress by epiphyton shading can enhance the effect of herbivores. Nutrient enrichment can facilitate epiphyton shading (Jones et al., 2002) and could thus increase the susceptibility of macrophytes to herbivores. Additionally, nutrient enrichment can increase macrophyte tissue nutrient content and decrease their carbon to nutrient ratio (Cronin & Lodge, 2003; Demars & Edwards, 2007; Zhang et al., 2020), making them more palatable and increasing consumption by herbivores (Dorenbosch & Bakker, 2011). Bakker and Nolet (2014) indeed demonstrated an enhanced top-down control of mallard ducks on submerged macrophytes with nutrient enrichment. A model study by Van Altena et al. (2016) confirmed that the impact of herbivorous birds on macrophyte biomass increases with nutrient loading and that improved food quality enhances the impact of birds on macrophytes. Whether an improved food quality also facilitates the growth of grazers, which in turn may impose higher grazing pressure on submerged macrophytes, remains unclear.

Compared to birds, herbivorous molluscs could have an even larger top-down impact on aquatic plants, since they cannot easily move away from the foraging site (Wood et al., 2017). The greatest effect of herbivory on plant abundance is that of invasive herbivores on native plant assemblages (Wood et al., 2017). The herbivorous apple snail (*Pomacea canaliculata*) ranges in the top 100 of the world's worst invasive species (Lowe et al., 2000). South-American in origin, it has a potential distribution ranging from 40°N to 40°S (Da Silva et al., 2019), and has so far spread to most countries in Southeast and East Asia, as well as to Hawaii, Spain, and multiple southern U.S.A. states (https://www.cabi.org/isc/datasheet/68490). Its invasion has resulted in extreme grazing damage to macrophytes in wetlands (Carlsson & Lacoursiere, 2005; Wong et al., 2010), and indirect effects on wetland water quality and ecosystem processes (Carlsson et al., 2004; Fang et al., 2010). Similar effects have been reported on macrophytes, detritus, and phytoplankton in its native range (Manara et al., 2019).

In this study, we conducted a mesocosm experiment to test the individual and combined effects of nutrient enrichment and herbivory by *P. canaliculata* on the native submerged macrophyte *Vallisneria natans*, a common rosette-type submerged macrophyte species in China, distributed widely in lakes in the middle and lower reaches of the Yangtze River (Zhou et al., 2016). In addition, we conducted a feeding experiment to test whether the plant nutritional quality affects consumption rates of *P. canaliculata*. We hypothesised (Figure 1a, b) that:
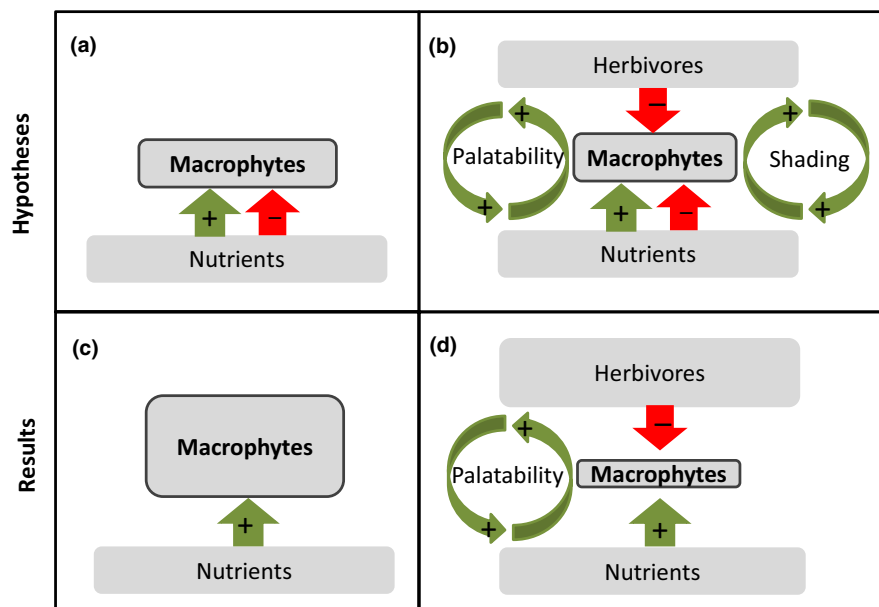
FIGURE 1 Our hypotheses: nutrient enrichment in the water column can have positive or negative (via epiphyton/phytoplankton shading) effects on macrophyte biomass (a) while herbivores have negative effects. Nutrient enrichment enhances the effect of herbivores on macrophytes, either by increasing macrophyte palatability or by an increased susceptibility to herbivory due to additional stress from phytoplankton or epiphyton shading. In both cases, a feedback loop reinforces the effect due to nutrient excretion by herbivores (b). Our experiment revealed that nutrient enrichment in the water column stimulated macrophyte biomass in mesocosms without snails (c) while it enhanced the negative impact of invasive herbivorous snails on macrophyte biomass due to increased plant palatability (d)

1. nutrient enrichment enhances the grazing impacts of invasive *P. canaliculata* on native submerged macrophytes;

2. this effect can be explained by positive effects of nutrient enrichment on shading by phytoplankton and epiphyton, which increases the susceptibility of macrophytes to herbivory, and on macrophyte nutritional quality, the latter leading to higher macrophyte consumption rates of *P. canaliculata*; and

3. higher herbivore grazing activity increases nutrient release into the water, which can reinforce nutrient enrichment effects.

2 | METHODS

2.1 | Mesocosm establishment

A two-by-two factorial design experiment was conducted with or without snails and with two levels of nutrient enrichment in the water column (moderate, low). Each treatment included six replicates. We used 24 polyethylene mesocosms (transparent, height: 1.47 m, diameter: 1.5 m) located outdoors at the Biological Gardens of Nanchang University (28°39′ N, 115°48′ E) and filled with 2000 L of water collected from a natural pond near the experimental area. No further water was added after the beginning of the experiment (except for precipitation). Sediment was collected from Poyang Lake in December 2017, air-dried, and mixed. Total nitrogen (TN), total phosphorus (TP), and organic matter content of mixed sediment were 0.67 ± 0.04 g/kg, 0.27 ± 0.02 g/kg and 6.00 ± 0.25 g/kg dry weight (dw), respectively. Three plastic boxes ($61 \times 36 \times 15$ cm) filled with 10 cm sediment were placed in each mesocosm for culturing the macrophytes. Five grams of *V. natans* seeds (1.67×10^4 seeds) were uniformly placed on the sediment surface of each box. In addition, 6 plastic pots (diameter: 15.5 cm; height: 9 cm) with 9 cm sediment and 0.5 g of seeds were set up in the mesocosms and used for measuring epiphyton on the leaf surface. We added some water into the boxes and pots to moisten the seeds, thus could avoid seed floating when the mesocosms were filled with water. We used ropes to lift the pots, which limited disturbance during sampling. The mesocosm experiment ran from 1 June 2018 until 25 October 2018.

2.2 | Nutrient treatment

Two nutrient treatments were randomly applied to the 24 mesocosms with 12 per treatment on 30 July 2018. The nutrient concentrations in the water column just before the nutrient addition were 0.36 ± 0.13 mg/L TN, 0.015 ± 0.012 mg/L TP, 0.12 ± 0.02 mg/L $NH_4^+ - N$ and 0.02 ± 0.01 mg/L $NO_3^- - N$. NH_4NO_3 and KH_2PO_4 were added to reach the target concentration (moderate nutrient treatment: 1.6 mg/L TN and 0.13 mg/L TP; low nutrient treatment: 0.80 mg/L TN and 0.025 mg/L TP). The target TP concentration of the moderate nutrient treatment was close to the threshold for shifts from clear to turbid states, while low nutrient treatment was mimicking nutrient concentration typical for clear states of

Yangtze River basin shallow lakes (Wang et al., 2014). Nutrient concentrations were monitored biweekly and nutrients were added to maintain the target experimental concentrations until 25th of September 2018 (Figure S1). Since *P. canaliculata* can affect nutrient concentrations, average nutrient additions for each treatment instead of mesocosm-specific additions were applied after snails were added. The mean nutrient concentrations ($\pm SD$) during the experiment (30 July to 25 October 2018) were 1.08 ± 0.041 mg/L TN and 0.082 ± 0.004 mg/L TP in moderate nutrient treatment and 0.570 ± 0.036 mg/L TN and 0.022 ± 0.004 mg/L TP in low nutrient treatment.

2.3 | Herbivorous snails

Apple snails (*P. canaliculata*, species determined following Yang and Yu 2019) were purchased from a local fishery and fed with lettuce for 1 week. Then, 120 apple snails without obvious injuries (shell height: 56 ± 6 mm; fresh weight [fw]: 32 ± 12 g) were randomly divided into 12 groups of 10 snails, which were added to half of the moderate and low nutrient treatment mesocosms on 1st of October 2018. This resulted in six replicates per treatment group (no snails with low and moderate nutrient treatment and snails with low and moderate nutrient treatment). *Pomacea canaliculata* density in the experiment (5.8 individuals/m^2) was in the lower range of their natural density in the field (Carlsson et al., 2004; Kwong et al., 2010), but probably in the higher range regarding biomass/m^2 as adults were used in our experiment.

2.4 | Monitoring and sampling

Phytoplankton chlorophyll a (chl-*a*) concentration and water temperature were measured weekly using a BBE algae analyser (Moldaenke). Water samples were collected biweekly from mesocosms to analyse the concentrations of TN, TP, ammonium ($NH_4^+ - N$), and nitrate ($NO_3^- - N$). Filtered samples (Whatman GF/C glass fibre filters) were used to determine $NH_4^+ - N$ by Nessler's reagent colorimetric method and $NO_3^- - N$ by ultraviolet spectrophotometric methods (State Environmental Protection Administration of China [SEPAC], 2002). Total phosphorus and TN were analysed from unfiltered water, following the ammonium molybdate spectrophotometric method after digestion with $K_2S_2O_8$ solution and the ultraviolet spectrophotometric method after digestion with $K_2S_2O_8$ and addition of hydrochloric acid (SEPAC, 2002), respectively.

Epiphyton biomass on the leaves of *V. natans* was measured every 2 weeks. After adding snails, biomass of plant leaves was too small for epiphyton determination in the snail presence mesocosms and samples were only taken from non-snail mesocosms. Six healthy leaves of *V. natans* were collected randomly from six pots in each mesocosm, placed in beakers containing 300 ml deionised water and sonicated for 5 min. The water was then filtered through pre-weighed (W_i) Whatman GF/C filters, filters were dried at 60°C for 48 hr and

weighed again (W_f) to calculate epiphyton dw. Surface area was calculated for each of the six leaves (A) with ImageJ (Rasband, 2015) after scanning them on A4 paper with scale. The epiphyton biomass per leaf area (B) was calculated as: $B = (W_f - W_i)/A$.

At the end of the experiment, all plants including their roots were harvested, washed with tap water and weighed to determine fw. Part of the plant biomass was dried at 60°C for 48 hr to determine the dw to fw ratio, which was used to determine the final plant dw of all mesocosms.

The number of egg clutches on the wall of mesocosms was counted and all snails were collected to determine their fw and shell height. We found many dead snails, probably due to oxygen deficiency during transport from the fishery to the botanic garden. To calculate the increment in the snails' weight, we calculated the dead snails' weight from their height. Snail fw increased linearly with their shell height (snail fw [in g] = 17.8 × height − 66; $r^2 = 0.84$, $n = 203$). Then, the average weight increment of snails in each mesocosm was calculated as: $W = (W_f - W_i)/10$, where W_i represents the initial total fw of the snails and W_f the final total fw of the snails. The number of living snails was 6.3 ± 2.3 and 7.5 ± 1.3 in moderate and low nutrient treatment, respectively and showed no significant difference between treatments (independent t-test, $t_{10} = -1.05$, $p = 0.32$).

2.5 | Macrophyte elemental tissue content

At the end of the experiment, plant leaves of each non-snail mesocosm were sampled, dried at 60°C for 48 hr and grounded into powder. The total nitrogen (N), phosphorus (P), and organic carbon (C) contents in macrophyte leaves were analysed using standard methods (Shi, 1994), i.e. using the $K_2Cr_2O_7$–H_2SO_4 oxidation method for C, Kjeldahl acid-digestion method for N, and the molybdenum blue colorimetric method for P content.

2.6 | Feeding experiment

No-choice feeding trials were carried out to assess whether nutrient enrichment affected macrophyte consumption rates by snails. *Pomacea canaliculata* from the local fishery were fed with lettuce for 1 week before the experiment. Prior to the feeding trials, all snails were starved for 48 hr. Each experimental box (27 × 19 × 9.7 cm) received macrophyte material (cleaned from epiphyton) from one non-snail mesocosm, yielding six replicates for each nutrient treatment, with in total 12 boxes containing one snail (28 ± 4 g) and approximately 10 g fresh leaves of *V. natans*. Boxes were covered to prevent snails from escaping and aerated using aquarium pumps. The experiment was conducted in the laboratory at 25°C with a natural light regime and lasted for 24 hr. At the end, all remaining macrophyte material in each box was collected and weighed. Macrophyte relative consumption rate (RCR; g/g day^{-1}) was calculated as: RCR = $(W_i - W_f)/Sw/day$, in which, W_i and W_f are the initial and final macrophyte fw of the feeding trial, respectively, and Sw is the snail fw.

2.7 | Data analyses

All statistical analyses were conducted using R statistical computing (R Core Team, 2018).

In our mesocosm experiment, phytoplankton, epiphyton, TN, TP, NO_3^- - N, and NH_4^+ - N samples were collected from each mesocosm more than once and these observations are thus not independent. Therefore, linear mixed effects models (function *lmer*, package *lme4*) with a Gaussian distribution were used to analyse these data (Bates et al., 2015). To test the effects of nutrient treatment and time on phytoplankton chl-*a* concentration (before adding snails) and epiphyton biomass (during the experiment), linear mixed effects models were fitted with nutrient treatment and time as fixed factors and mesocosm as random factor. To test the effects of nutrient treatment, snail presence and time on phytoplankton chl-*a*, TN, TP, NO_3^- - N and NH_4^+ - N concentrations, linear mixed effects models were fitted with nutrient treatment and time as fixed factors and mesocosm as random factor. The analysis of variance parameters for fixed factors of the linear mixed effects models were then calculated using ANOVA function with Wald χ^2 tests from the package *car* (Fox & Weisberg, 2011). Phytoplankton chl-*a* data were log transformed to meet the assumptions of linear mixed effects models. To further examine the impact of snail presence on TN, TP, NO_3^- - N, and NH_4^+ - N concentrations per sampling date for the moderate and low nutrient mesocosms, one-way analysis of variance was used with a Bonferroni correction for multiple testing.

Linear models were used to test density–response relationships between living snail density and final biomass of *V. natans* for each nutrient treatment. To determine whether the density–response relationships for moderate and low nutrient treatment were statistically different, an ANCOVA interaction model was used (*LM* function, package *car*), with living snail numbers as the continuous predictor and nutrient levels as the categorical predictor of final *V. natans* biomass (Fox & Weisberg, 2011). Statistical significance of the interaction term indicated that the slopes of moderate and low nutrient treatment were different from one another (i.e. the effect of snail density was dependent on nutrient level).

One-way analysis of variance (*aov* function, package *stats*) were used to test the nutrient treatment effects on snail weight increment, number of egg clutches, macrophyte RCR in feeding experiment, and macrophyte nutrient tissue content in mesocosm experiment.

3 | RESULTS

3.1 | Effects of nutrient treatment on phytoplankton and epiphyton biomass

Before snail addition (30 July to 1 October), phytoplankton chl-*a* concentration was higher in moderate nutrient treatment (average: 69.6 ± 41.0 µg chl-*a* L^{-1}) than in low nutrient treatment (average: 25.8 ± 14.7 µg chl-*a* L^{-1}; Figure 2, Table 1). Under moderate nutrient treatment, phytoplankton chl-*a* concentration rapidly increased after each nutrient addition and subsequently decreased over time (Figure 2).
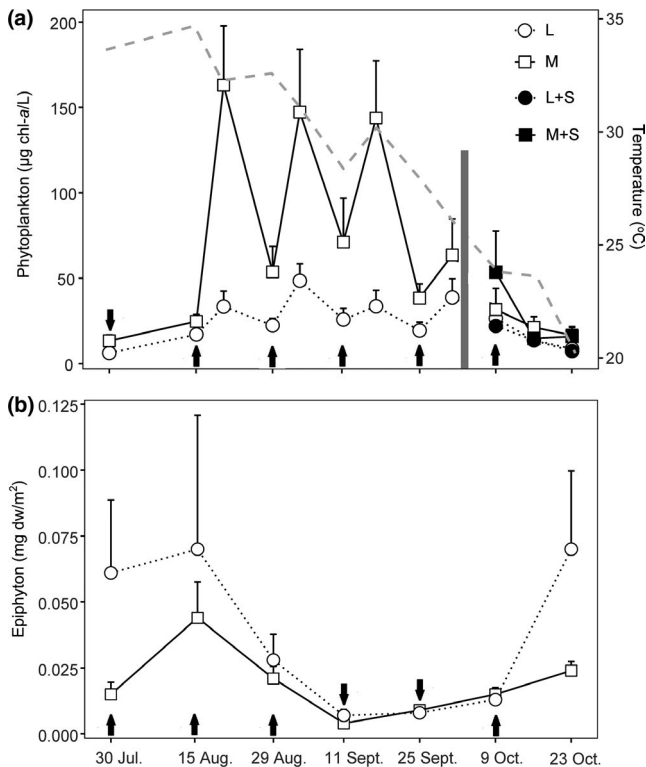
FIGURE 2 (a) Water temperature (grey dashed line), phytoplankton concentration and (b) epiphyton biomass (means + SE) in mesocosms with low (L) and moderate (M) nutrient treatment before and after (indicated by grey bar) adding *Pomacea canaliculata* (S). Epiphyton was not measured in snail treatment due to low plant biomass. Black arrows show nutrient additions. Data were tested with linear mixed effects models; see Tables 1 and 2 for results

The average photosynthetically active radiation (transferred from phytoplankton chl-*a* data) at the sediment surface during the experiment was 15.3 and 10.7% of that just below the water surface in moderate and low nutrient treatment, respectively (Figure S2). Epiphyton biomass did not differ between low and moderate nutrient treatment during the experiment (30 July to 25 October; Figure 2, Table 1).

3.2 | Effects of nutrient treatment and snail presence on macrophyte biomass, phytoplankton abundance and water chemistry

Without snails, the final biomass of *V. natans* was significantly higher in moderate nutrient treatment (mean ± standard deviation:

58.5 ± 28.2 g dw) than that in low nutrient treatment (26.7 ± 12.4 g dw). Addition of *P. canaliculata* decreased final *V. natans* biomass with increasing density of living snails in both nutrient treatments (Figure 3; moderate nutrient treatment: $t = -5.05$, $p < 0.001$; low nutrient treatment: $t = -3.56$, $p = 0.005$). The response of macrophyte biomass to density of living snails depended on nutrient treatment ($F_{1, 20} = 4.68$, $p = 0.043$). Macrophyte biomass decline was more pronounced in moderate than in low nutrient treatment as illustrated by the steeper slope of the regression line (Figure 3). All biomass of *V. natans* was grazed in the mesocosms that showed a density of 4.5–5 individuals/m² of *P. canaliculata* or more at the end of the experiment in both nutrient treatments (Figure 3).

No significant effect of nutrient treatment and *P. canaliculata* presence was detected on phytoplankton chl-*a* concentration after adding snails (Figure 2, Table 2). Snail presence significantly increased TN and NH_4^+ - N concentrations in both nutrient treatments, whereas it had no significant effect on the concentration of TP or NO_3^- - N (Figure 4, Table 2).

3.3 | Effects of nutrient treatment on snail growth, egg clutch number, macrophyte consumption and elemental tissue content

Pomacea canaliculata grew marginally significant faster in mesocosms with moderate nutrient treatment as compared to low nutrient treatment ($F_{1, 10} = 4.76$, $p = 0.058$; Figure 5a). In contrast, the number of egg clutches per living snail showed no significant difference between nutrient treatments ($F_{1, 10} = 0.03$, $p = 0.87$, Figure S3). Macrophyte consumption by snails in the 24 hr feeding trials (expressed as RCR) was significantly higher when macrophytes originated from moderate nutrient treatment as compared to macrophytes from low nutrient treatment ($F_{1, 10} = 8.69$, $p = 0.016$; Figure 5b). The N, P, and organic C content of *V. natans* leaves were significantly higher in moderate nutrient treatment compared to low nutrient treatment (Table 3), whereas C:N ratios were significantly lower in moderate nutrient treatment than in low nutrient treatment (Table 3). There was no effect of nutrient treatment on the N:P ratio of *V. natans* leaves (Table 3).

4 | DISCUSSION

Our experiments support the hypothesis that nutrient enrichment enhances the top-down effect of invasive *P. canaliculata* on native

TABLE 1 Linear mixed effects model results for the effects of nutrient treatment and time on phytoplankton chlorophyll-*a* (from 30 July to 1 October) and epiphyton biomass (from 30 July to 23 October)

	Phytoplankton chlorophyll-*a*			Epiphyton		
	df	χ^2	P	df	χ^2	p
Nutrient treatment	1	7.42	<0.001	1	0.504	0.298
Time	1	0.31	0.808	1	7.612	0.267
Time × nutrient	1	0.25	0.550	1	0.520	0.830
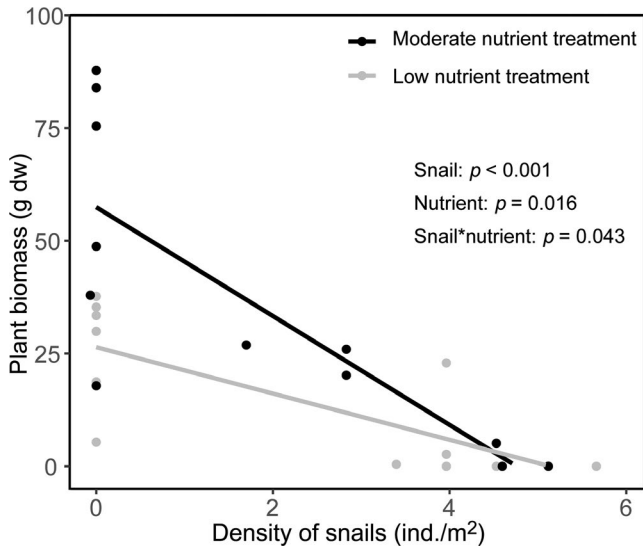
FIGURE 3 Effects of nutrient treatment and living *Pomacea canaliculata* density on final *Vallisneria natans* biomass. Linear regressions for moderate (black) and low (grey) nutrient treatment were used to determine relationships between living snail densities and macrophyte biomass for each nutrient treatment. Results of analysis of covariance (ANCOVA) indicated that the slopes for moderate and low nutrient treatment differed significantly

submerged macrophytes. Nutritional quality of *V. natans* was higher in moderate nutrient treatment than in low nutrient treatment and led to higher macrophyte consumption rates by *P. canaliculata*. We also provide evidence for increased N concentrations in mesocosms with herbivorous snails, which can reinforce effects of nutrient enrichment (Figure 1c). In contrast to our expectation, nutrient-induced negative effects of phytoplankton shading in treatments without herbivorous snails were overcompensated by positive effects of nutrients on macrophyte growth (Figure 1d).

Our results indicate that snail herbivory increases the chance of *V. natans* collapse and subsequent shifts of shallow lakes with a dominance of this species to turbid states. Depending on the initial macrophyte biomass, this effect occurs at lower snail densities when nutrient concentrations increase (Figure 6a, b). Snail presence also leads to increased N concentrations, which reinforces the process. The simultaneous increase in nutrient loading and spread of invasive herbivorous molluscs therefore poses a severe threat to the water quality of shallow lakes. Whether other macrophyte and snail species show similar responses remains to be tested.

4.1 | Effects of nutrient treatment on macrophyte growth, elemental tissue content and consumption

The growth of the native macrophyte species *V. natans* was strongly enhanced by higher nutrient availability in our experiment. In a similar experiment using ponds, Bakker and Nolet (2014) also found enhanced growth of the invasive macrophyte species *Elodea nuttallii*, but at two and six times higher target N- and

TABLE 2 Linear mixed effects model results for nutrient treatment, snail presence and time on phytoplankton chlorophyll-*a*, total nitrogen (TN), total phosphorus (TP), nitrate nitrogen (NO_3^+ - N), and ammonium nitrogen (NH_4^+ - N) concentration after addition of *Pomacea canaliculata*

|	Chlorophyll-*a*			TN			TP			NO_3^+ - N			NH_4^+ - N		
	df	χ^2	p	df	χ^2	p	df	χ^2	p	df	χ^2	p	df	χ^2	p
Nutrient treatment (A)	1	2.40	0.160	1	42.55	<0.001	1	24.23	<0.001	1	11.46	<0.001	1	8.25	0.004
Snail presence (B)	1	0.72	0.651	1	5.48	0.019	1	0.41	0.523	1	3.15	0.076	1	16.18	<0.001
Time (C)	1	20.38	0.001	1	17.89	<0.001	1	3.60	0.058	1	71.80	<0.001	1	10.03	0.002
A × B	1	0.14	0.940	1	0.01	0.926	1	0.00	0.960	1	0.28	0.600	1	0.73	0.394
A × C	1	2.10	0.433	1	0.32	0.574	1	0.04	0.841	1	24.28	<0.001	1	2.15	0.143
B × C	1	2.17	0.187	1	0.63	0.019	1	0.23	0.632	1	15.12	<0.001	1	0.37	0.542
A × B × C	1	1.62	0.553	1	2.17	0.141	1	0.35	0.556	1	11.88	<0.001	1	3.04	0.081
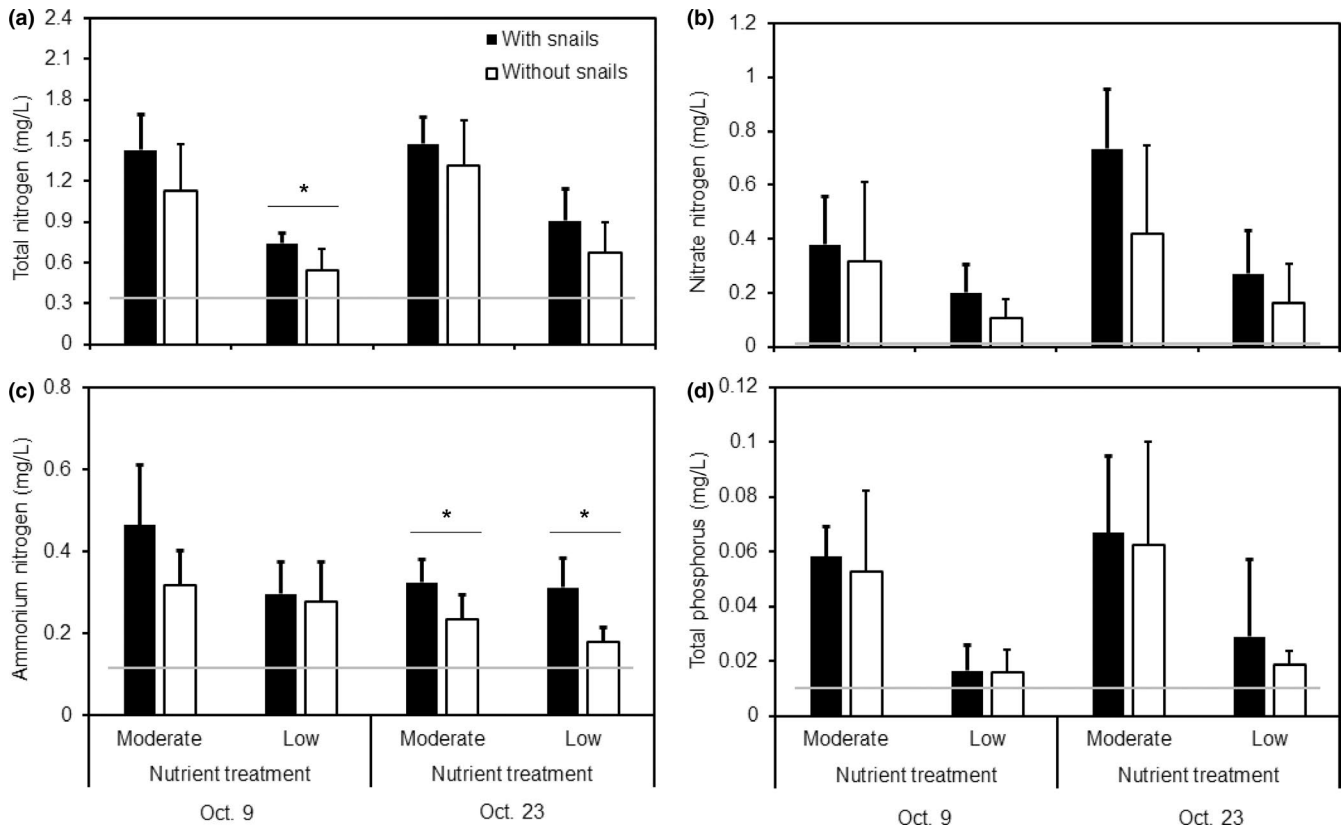
FIGURE 4 Concentrations of total nitrogen (a), nitrate nitrogen (b), ammonium nitrogen (c) and total phosphorus (d) in the water column after adding *Pomacea canaliculata* (means + *SD*). Grey horizontal line shows the initial nutrient concentrations before nutrient addition. Data were tested with linear mixed effects models; see Table 2 for results. Asterisks indicate statistically different between treatments with and without snails (one-way analysis of variance, $p < 0.025$, as a result of Bonferroni correction for two dates tested per parameter)

P-concentrations, respectively. Despite higher phytoplankton biomass in moderate nutrient treatment, growth of *V. natans* was not noticeably limited by light availability, probably due to low water depth in our mesocosms (*c.* 1.2 m depth). The photosynthetically active radiation at the sediment surface during the experiment was sufficient for growth of *V. natans* as this species has been shown to be adapted to low light conditions (Chen et al., 2016; He et al., 2019). Lack of fish predation on zooplankton additionally allowed strong top-down control of phytoplankton. Under such conditions, even higher nutrient enrichment would be required for chl-*a* levels to cause longer-term light limitation for *V. natans* in shallow water. In mesocosms of similar size that were stocked with fish, Olsen et al. (2015) only found a decline of macrophytes due to filamentous algae and phytoplankton shading when TN concentration reached 3 mg/L.

In our experiment, moderate nutrient treatment significantly increased the N and P contents of *V. natans* leaves as compared to treatment with low nutrient concentrations, which is consistent with other laboratory and field investigations on this species (He et al., 2015; Li et al., 2018; Su et al., 2019). A correlation between plant N content, and often also P content, and the respective nutrient availability in the environment has also been observed in many other macrophyte species (Cao et al., 2011; Center et al., 2014; Cronin & Lodge, 2003; Demars & Edwards, 2007; Velthuis

et al., 2017). Tissue C:N ratios were low in *V. natans* as is common in freshwater submerged macrophytes (Bakker et al., 2016), and further decreased in moderate nutrient treatment. Increased N and P contents of *V. natans* resulted in a higher consumption of the plants in our study. An increasing macrophyte palatability as a result of increasing tissue N content or decreasing C:N ratios has also been found by Dorenbosch and Bakker (2011), Bakker and Nolet (2014) and Bakker et al. (2016). There are also several other studies that do not report correlations between macrophyte palatability and tissue nutrient contents or ratios (e.g., Cronin & Lodge, 2003; Cronin et al., 2002; Zhang et al., 2020). Li et al. (2005) found a lower palatability of *V. natans* for snails (*Radix swinhoei*) with decreasing C:N ratio. Low palatability despite suitable tissue nutrient contents and ratios can partially be explained by anti-herbivore defences such as chemical deterrents (Gross & Bakker, 2012). *Vallisneria natans*, however, is supposed to be low in polyphenols (Li et al., 2005) and flavonoids (Sun et al., 2018), common groups of secondary metabolites with anti-herbivore activity in submerged macrophytes (Gross & Bakker, 2012). In general, macrophyte palatability is a multifactorial attribute and potentially depending on both structural and chemical traits (Elger & Lemoine, 2004). The direct and indirect effects of nutrient enrichment on macrophyte palatability to herbivores thus deserve further research to better predict herbivore effects at the ecosystem level.
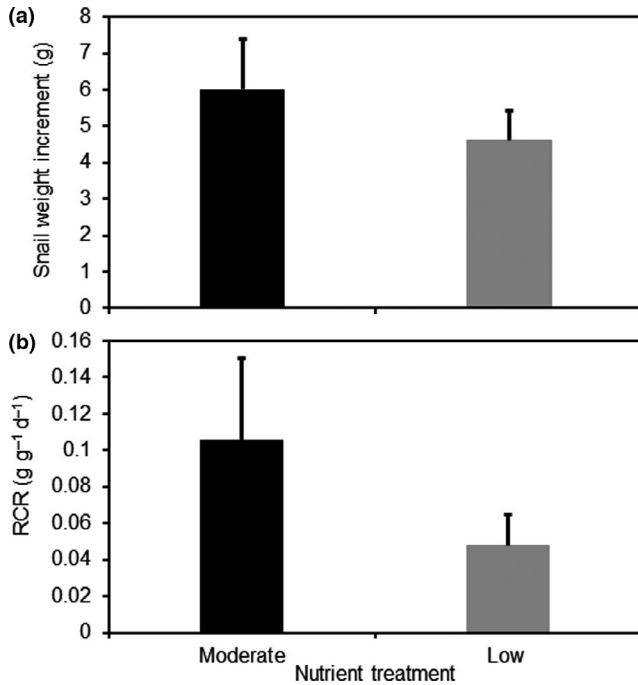
FIGURE 5 Weight increment of snails from 1 to 25 October 2018 in low and moderate nutrient treatment (a) and relative consumption rates (RCR) of *Pomacea canaliculata* on *Vallisneria natans* leaves in 24 hr feeding trials with macrophytes originating from low and moderate nutrient treatment (b). Bars represent mean values + *SD*

TABLE 3 Tissue carbon (C), nitrogen (N), and phosphorus (P) contents (mg/g dry weight) and ratios (g/g) of *Vallisneria natans* leaves in treatments with low and moderate nutrient level and statistical comparison between treatments (one-way analysis of variance [ANOVA])

	Low nutrient treatment	Moderate nutrient treatment	ANOVA	
	Mean ± SD	Mean ± SD	$F_{1,10}$	p
C content	348.5 ± 13.9	367.0 ± 11.2	6.47	0.029
N content	28.19 ± 3.22	33.42 ± 2.66	9.38	0.012
P content	2.26 ± 0.85	3.56 ± 0.92	6.43	0.030
C:N ratio	12.46 ± 1.07	11.05 ± 1.03	5.37	0.043
C:P ratio	173.8 ± 65.5	111.5 ± 39.4	3.99	0.074
N:P ratio	13.96 ± 5.08	9.91 ± 4.3	3.10	0.109

4.2 | Effects of nutrient treatment on snail grazing and nutrient release

Pomacea canaliculata exerted a strong top-down control on macrophytes, as grazing strongly reduced biomass of *V. natans* in both, low and moderate nutrient treatments. In its native range, *P. canaliculata* showed differential top-down effects on macrophytes ranging from total eradication to no effect (Manara et al., 2019).
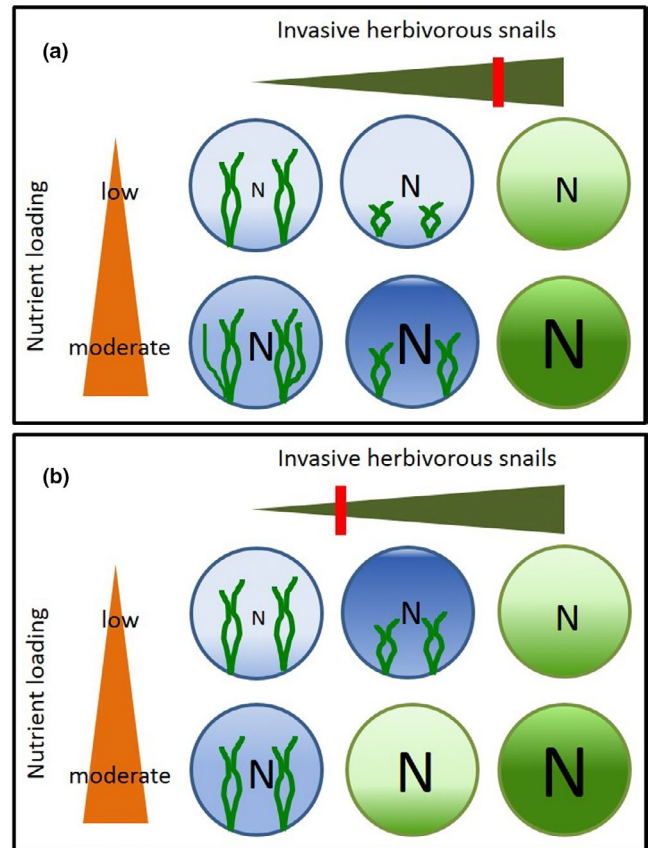
FIGURE 6 Predicted combined effects of invasive herbivorous snails and nutrient loading to the water column of shallow lake ecosystems. Macrophytes stabilise clear-water conditions at low and moderate nutrient loading. Snail herbivory negatively affects macrophyte biomass, thus increasing the chance for shifts to turbid states. When initial macrophyte biomass is lower at low nutrient loading, macrophytes disappear at a similar snail density threshold level (red bar; a). Assuming a similar initial macrophyte biomass at low and moderate nutrient loading, this shift would already happen at lower snail densities at moderate nutrient loading (b). Nitrogen (N) concentrations are higher when snails are present, reinforcing the process

In our experiment, *P. canaliculata* had a higher grazing rate on macrophytes grown under higher nutrient availability. This increased consumption counteracted the positive effects of nutrient enrichment on *V. natans* growth in moderate nutrient treatment when *P. canaliculata* densities passed certain threshold level. Above 2.1 individuals/m² (67.2 g/m²), final *V. natans* biomass in moderate nutrient treatment was lower than in low nutrient treatment with no snails. Above 4.5 individuals/m² (144 g/m²), final macrophyte biomass in moderate nutrient treatment was lower than in low nutrient treatment at similar snail densities. Other studies have reported similar cases of herbivory counteracting positive nutrient enrichment effects on plant growth, including waterfowl feeding on submerged macrophytes in a pond experiment (Bakker & Nolet, 2014) and herbivory on salt marshes in a meta-analysis by He and Silliman (2015). Both studies argue that increased plant palatability with nutrient enrichment is a major factor contributing to plant biomass loss. This

is confirmed by our feeding experiment showing higher consumption rate of the *P. canaliculata* on *V. natans* growth in moderate nutrient treatment compared to low nutrient treatment. Moreover, growth of *P. canaliculata* in moderate nutrient treatment seemed enhanced by the higher quality macrophytes. Qiu and Kwong (2009) and Yam et al. (2016) also found plant N and P contents to be important for enhancing palatability, supporting growth and offspring quantity of apple snails. However, it should be noted that the snail growth might also be influenced by the available plant quantity in our experiment, since plant biomass in moderate nutrient treatment was higher than in low nutrient treatment.

In our experiment, *P. canaliculata* significantly increased the concentrations of TN and NH_4^+ - N in both nutrient treatments. This might have been caused by decreased nitrification and de-nitrification activities due to a lower macrophyte surface available for bacterial attachment. Submerged macrophytes have been shown to support nitrifying and denitrifying microbes in their biofilms (Körner, 1999). In addition, increased snail excretion of nutrients formerly bound in macrophyte tissue can contribute to this effect. In contrast to a previous study (Manara et al., 2019), snail presence did not increase phytoplankton chl-*a* concentrations in our experiment, despite increased N concentrations in the water. This might be explained by a strong decline in water temperature (from 26°C to 20°C) during the period when snails were present, as phytoplankton growth also declined in treatments without snails or by strong zooplankton grazing in both treatments (no data available). Increased N concentrations under snail presence might also increase epiphyton biomass (not measured due to low macrophyte biomass present in these treatments), which might contribute to the observed macrophyte biomass reduction. However, differences in TN concentrations between treatments with and without snails were much smaller than those between low and moderate nutrient treatments, which did not affect epiphyton biomass. More studies are needed to determine whether the findings reported here also hold true for other submerged macrophytes and herbivores.

4.3 | Implications for future lake management

In our rapidly changing world, both nutrient loading in lakes (Jeppesen et al., 2009) and the distribution of *P. canaliculata* (De Silva et al., 2019) are expected to increase. Our results show that this combination will further exacerbate the already severely damaged wetlands invaded by *P. canaliculata*. *Pomacea canaliculata* are generalist herbivores that can exert top-down control on a wide range of aquatic plants, including various submerged macrophytes species (Fang et al., 2010; He & Liu, 2016; Wong et al., 2010). Their effects on N concentrations may trigger other negative interactions, e.g. between macrophytes and benthivorous fish (Gu et al., 2018). Lakes invaded by herbivorous snails will thus increasingly risk the collapse of native macrophyte populations (Figure 6) and subsequent

shifts to turbid states with loss of important ecosystem functions (Hilt et al., 2017). Protection of re-establishing submerged macrophytes against herbivory in invaded lakes will be challenging since herbivorous snails are more difficult to control by enclosures than waterfowl. Control of both external nutrient loading and invasive herbivorous snails will, however, be crucial to avoid extensive degradation of these ecosystems.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.