

# The golden apple snail *Pomacea canaliculata* shifts primary production from benthic to pelagic habitats in simulated shallow lake systems

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**Abstract** – Biological invasions are among the most serious threats to ecosystems. The golden apple snail *Pomacea canaliculata* (Lamarck, 1822) is considered one of the top 100 worst invasive alien species in the world. These snails consume benthic primary producers, including submerged macrophytes, which may lead to an increase in nutrient concentration in the water, enhance growth of phytoplankton, and decrease growth of macrophytes, thereby shifting the primary production from benthic to pelagic habitats in shallow systems. To test this hypothesis, we conducted a short-term experiment with and without the invasive *P. canaliculata* in mesocosms with high abundance of the native submerged macrophyte *Vallisneria spiralis* (Lour.) Hara. Compared with snail-free control, the snail increased the concentrations of total nitrogen (TN), nitrate nitrogen (NO<sub>3</sub><sup>-</sup>-N), total and organic suspended solids (TSS and OSS), decreased the concentrations of soluble reactive phosphorus (SRP), but had no effect on total phosphorus (TP) and the TN:TP ratio. In addition, the snails decreased the biomass, leaf length and tiller number of *V. spiralis*, and decreased light intensity. Although snail presence did not change the biomasses of nanophytoplankton and picophytoplankton, it did increase the biomass of microphytoplankton leading to an increase in total phytoplankton biomass. Our study shows that *P. canaliculata* shifted primary production from benthic to pelagic habitats, altered the phytoplankton community size structure, and decreased water quality. The results add further evidence of negative ecosystem impacts of this invasive apple snail and call for its control in invaded shallow lake ecosystems.

**Keywords:** Invasive species / benthic primary producer / phytoplankton / nutrients / water quality

## 1 Introduction

Aquatic species have been extensively introduced by humans, intentionally or unintentionally, through trade (Novák *et al.*, 2020), aquaculture (Haubrock *et al.*, 2021), canals (Hulme, 2009) and some area considered invasive to the

region. Biological invasions are among the most serious threats to ecosystems and such invasions can lead to extinction of native species, loss of biodiversity and alteration of ecosystem functions (Vitousek *et al.*, 1997; Ewel *et al.*, 1999; Mack *et al.*, 2000; Sala *et al.*, 2000). Negative impacts of invasive species on aquatic systems have been extensively reported (Carlsson and Lacoursiere, 2005; Matsuzaki *et al.*, 2009; Jackson *et al.*, 2017; Britton, 2023).

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The golden apple snail *Pomacea canaliculata* (Lamarck) is an aquatic species native to South America and it is listed as one of the top 100 worst invasive alien species in the world by the International Union for the Conservation of Nature (Lowe *et al.*, 2000). Because of its high reproductive rate, rapid growth, high adaptability, and few natural enemies, *P. canaliculata* has spread rapidly to many natural aquatic habitats (Naylor, 1996; Lach and Cowie, 1999). Nowadays, it is widely distributed and continues to expand its range (Baker, 1998; Carlsson and Lacoursiere, 2005; Lv *et al.*, 2011; Yin *et al.*, 2022).

Both the juvenile and adult individuals can feed on macrophytes (Lach *et al.*, 2000; Cowie, 2002; Boland *et al.*, 2008; Qiu and Kwong, 2009; Kwong *et al.*, 2010). The species is more selective for submerged plants than emergent plants (Estebenet and Martín, 2002; Carlsson and Brönmark, 2006; Wang and Pei, 2012). Submerged macrophytes, with higher nutritional value and lower defenses, are ideal food for *P. canaliculata* (Qiu and Kwong, 2009) in comparison with other macrophytes, reflecting that nutrient content, physical structure (tough leaves, *etc.*) and dry matter content of macrophytes influence their palatability (Elger and Lemoine, 2005; Boland *et al.*, 2008; Qiu and Kwong, 2009; Wong *et al.*, 2010; Qiu *et al.*, 2011). Snails can therefore affect the macrophyte species assemblage and it is known to greatly reduce the overall biomass of macrophytes in some systems (Carlsson and Lacoursiere, 2005). A survey of natural wetlands in Thailand showed an almost complete disappearance of macrophytes in areas with high densities of this snail (Carlsson *et al.*, 2004).

Submerged macrophytes are essential for maintaining a high-quality ecosystem state in shallow lakes (Jeppesen *et al.*, 1998; Van Donk, 1998). They increase habitat complexity and provide shelter for zooplankton and macroinvertebrates (Timms and Moss, 1984; Brönmark and Vermaat, 1998), absorb nitrogen and phosphorus from the water column (Ozimek *et al.*, 1990; Kufel and Ozimek, 1994), often release allelochemicals that inhibit phytoplankton growth (Jasser, 1995), and enhance sedimentation by reducing resuspension (Petticrew and Kalff, 1992; Barko and James, 1998). In addition, submerged macrophytes are important primary producers in shallow lakes (Jin *et al.*, 2020), providing food for various aquatic animals such as macroinvertebrates and herbivorous fish. Submerged macrophyte restoration has been a key method for remediating eutrophic waters (Liu *et al.*, 2018; Xue *et al.*, 2020).

The existing literature documenting the effects of *P. canaliculata* on aquatic ecosystems have focused mostly on submerged macrophytes (Fang *et al.*, 2010; Wang and Pei, 2012; Liu *et al.*, 2021; Gao *et al.*, 2021; Yang *et al.*, 2021) and phytoplankton (Carlsson *et al.*, 2004). Few studies have simultaneously investigated the effect of invasive species on the location of primary production in shallow lakes (Martín *et al.*, 2019). Benthic and littoral macrophytes and phytoplankton share light and nutrient requirements but grow in different but coupled habitats. A shift of primary production from benthic macrophytes to open water phytoplankton can lead to serious ecological problems.

We hypothesised that the consumption of benthic primary producers by *P. canaliculata* will inhibit the growth of submerged macrophytes, increase nutrient concentrations in

the water column, and thus enhance phytoplankton growth. Therefore, *P. canaliculata* will shift primary production from benthic to pelagic habitat resulting in deteriorating water quality. To test this hypothesis, we conducted a short-term experiment with and without *P. canaliculata* in mesocosms dominated by *Vallisneria natans* (Lour.) Hara. This submerged macrophyte was used because it is perennial, rooted and widely distributed in freshwater lakes, ponds and rivers in China and around the world (Xie *et al.*, 2005; Li *et al.*, 2018). *V. natans* exhibits better survival and growth potential than other submerged plants in eutrophic lakes (Qiu *et al.*, 2001) and is currently the most popular aquatic plant used for ecological restoration in China (Wang *et al.*, 2011).

## 2 Materials and methods

### 2.1 Experimental mesocosm set-up

Eight circular tanks (upper diameter 40 cm, lower bottom diameter 33 cm and height 41 cm) were used as mesocosms holding sediment, water and *Vallisneria natans*. The sediment (TN = 3.40 mg · g<sup>-1</sup>; TP = 1.52 mg · g<sup>-1</sup>) were collected from Ming Lake (23°13'70"–23°13'75" N, 113°35'62"–113°35'74" E), a shallow eutrophic lake in Guangzhou, China, air dried and then sieved through a 0.5 mm mesh sieve to remove coarse particulates and debris as well as large-bodied macroinvertebrates. The water was from Ming Lake and filtered (TN = 1.58 mg · L<sup>-1</sup>; TP = 0.09 mg · L<sup>-1</sup>) on a plankton net (pore size, 64 µm) to remove large zooplankton to avoid unnaturally high grazing pressure on the phytoplankton as fish were absent due to the small scale of the experiment. We added a 5 cm thick layer of sediment to each mesocosm before filling them with water. Thereafter we planted 25 *V. natans* (wet weight 250 ± 2 g and leaf length 35 ± 2 cm) and kept the mesocosms for two weeks under outdoor natural sunlight conditions before the start of the experiment. *P. canaliculata* were purchased from a market in Guangzhou, kept for 24 h in a tank with lake water without food before introducing them to the mesocosms. One individual of *P. canaliculata* (average shell height 4 ± 0.2 cm and fresh weight 12 ± 0.5 g) was added to each of four mesocosms as snail treatment. The other four mesocosms served as control. During the experiment, lake water was added when needed to maintain water level in the mesocosm. The mesocosms were not covered and the experiment was carried out at natural sunlight from May 17 to July 1, 2022 and the air temperature was 17–35 °C during the experiment.

### 2.2 Sampling and analysis

Every nine days, water samples (1 L) were collected from 20 to 30 cm below the water surface of each mesocosm using clean polyethylene bottles. The water samples were used for measurements of total nitrogen (TN), nitrate nitrogen (NO<sub>3</sub><sup>-</sup>-N), ammonium nitrogen (NH<sub>4</sub><sup>+</sup>-N), total phosphorus (TP), soluble reactive phosphorus (SRP), nitrogen to phosphorus ratio (TN:TP), total suspended solids (TSS) and organic suspended solids (OSS).

Phytoplankton biomass was measured as size-fractionated chlorophyll for microphytoplankton (>20 µm), nanophytoplankton (2–20 µm), and picophytoplankton (0.2–2 µm). For

size fractionation, 200 mL of water was filtered on a 20  $\mu\text{m}$  filter (nylon mesh) for microphytoplankton, then a 2  $\mu\text{m}$  filter (nylon mesh) for nanophytoplankton, and finally a 0.2  $\mu\text{m}$  filter (nylon mesh) for picophytoplankton biomass (Rong *et al.*, 2021). Chl *a* of phytoplankton was extracted with 90% acetone for 24 h and Chl *a* was measured spectrophotometrically (MEP of PRC, 2017). The total phytoplankton biomass was calculated as the sum of the biomass of the three components. Nutrients were measured according to the American Public Health Association (APHA, 1998). A 400 mL water sample was filtered on a Whatman GF/C fiber membrane, dried at 108 °C for 2 h, weighed to obtain TSS, and then ashed at 550 °C for 2 h to obtain data for organic suspended solids (OSS) (Huang *et al.*, 1999).

At the end of the experiment, *V. natans* was collected from each mesocosm, washed and then wet weight, leaf length and tiller numbers (branching of plants occurring below or near the ground) were determined. The plants were then dried at 80 °C to constant weight for dry weight determination. The wet weight and shell height of each *P. canaliculata* were also recorded at the end of the experiment.

### 2.3 Statistical analyses

Repeated measures analysis of variance (RM-ANOVAs) was used to analyze the differences in nutrient concentrations, biomasses of phytoplankton in different sizes, TSS and OSS between the snail treatment and the control, with time as the repeated factor. Prior to analysis, Mauchly's test of sphericity and test of homogeneity of variances were performed to meet the assumption. Independent-samples *t*-test was performed to compare differences of wet weight, tiller number, and leaf length of *V. natans* between the control and the snail treatment at the end of the experiment. Prior to analysis, the assumption of equality of variances was tested with Levene's test. Statistical analyses were carried out using IBM SPSS Statistics 25.0 software. All data were presented as mean values  $\pm$  1SD.

## 3 Results

### 3.1 Nitrogen

Concentrations of TN and  $\text{NO}_3^-$ -N were higher in the snail treatment than in the control (RM-ANOVAs, treatment effect,  $p=0.001$  and  $0.016$ , respectively, Fig. 1), while  $\text{NH}_4^+$ -N was not significantly different ( $p=0.114$ ). TN,  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N varied over time (RM-ANOVAs, time effect,  $p=0.002$ ,  $0.004$  and  $0.007$ , respectively). The interaction effects of time and treatment for TN and  $\text{NO}_3^-$ -N were significant (RM-ANOVAs, interaction effect,  $p=0.012$  and  $0.012$ , respectively), but not for  $\text{NH}_4^+$ -N ( $p=0.175$ ).

### 3.2 Phosphorus and TN:TP

The concentrations of SRP were lower in the snail treatment than in the control (RM-ANOVAs, treatment effect,  $p=0.002$ , Fig. 2), while TP and TN:TP ratio were not significantly different (RM-ANOVAs, treatment effect,  $p=0.216$  and  $0.182$ ). TP, SRP and N: P ratio varied with time (RM-ANOVAs, time effect, each  $p < 0.001$ ). The

interaction effects between treatment and time for TP, SRP and TN:TP ratio were significant (RM-ANOVAs, interaction effect,  $p=0.012$ ,  $< 0.001$  and  $0.030$ , respectively).

### 3.3 Total suspended solids (TSS) and organic suspended solids (OSS)

The concentrations of TSS and OSS were higher in the snail treatment than in the control (RM-ANOVAs, treatment effect,  $p=0.012$  and  $0.001$ , respectively, Fig. 3) and varied with time (RM-ANOVAs, time effect,  $p=0.001$  and  $0.001$ , respectively). The interaction effects for TSS and OSS were significant (RM-ANOVAs, interaction effect,  $p=0.001$  and  $0.001$ , respectively).

### 3.4 Biomass of phytoplankton and size-fractionated phytoplankton

The biomass of phytoplankton (Chl *a*) was higher in the snail treatment than in the control (RM-ANOVAs, treatment effect,  $p=0.034$ , Fig. 4). The Chl *a* of phytoplankton varied with time (RM-ANOVAs, time effect,  $p=0.048$ ). The interaction effects for Chl *a* of phytoplankton were significant (RM-ANOVAs, interaction effect,  $p=0.017$ ).

The microphytoplankton biomass (Chl *a*) was higher in the snail treatment than in the control (RM-ANOVAs, treatment effect,  $p=0.002$ , Fig. 5), while the biomasses (Chl *a*) of nanophytoplankton and picophytoplankton did not differ among treatments (RM-ANOVAs, treatment effect,  $p=0.083$  and  $0.278$ , respectively). The microphytoplankton biomass (Chl *a*) varied with time (RM-ANOVAs, time effect,  $p < 0.001$ ), while the biomasses (Chl *a*) of nanophytoplankton and picophytoplankton did not ( $p=0.203$  and  $0.204$ , respectively). The interaction effects for microphytoplankton biomass (Chl *a*) were significant (RM-ANOVAs, interaction effect,  $p < 0.001$ ), but not for the biomasses (Chl *a*) of nanophytoplankton and picophytoplankton ( $p=0.383$  and  $0.095$ , respectively).

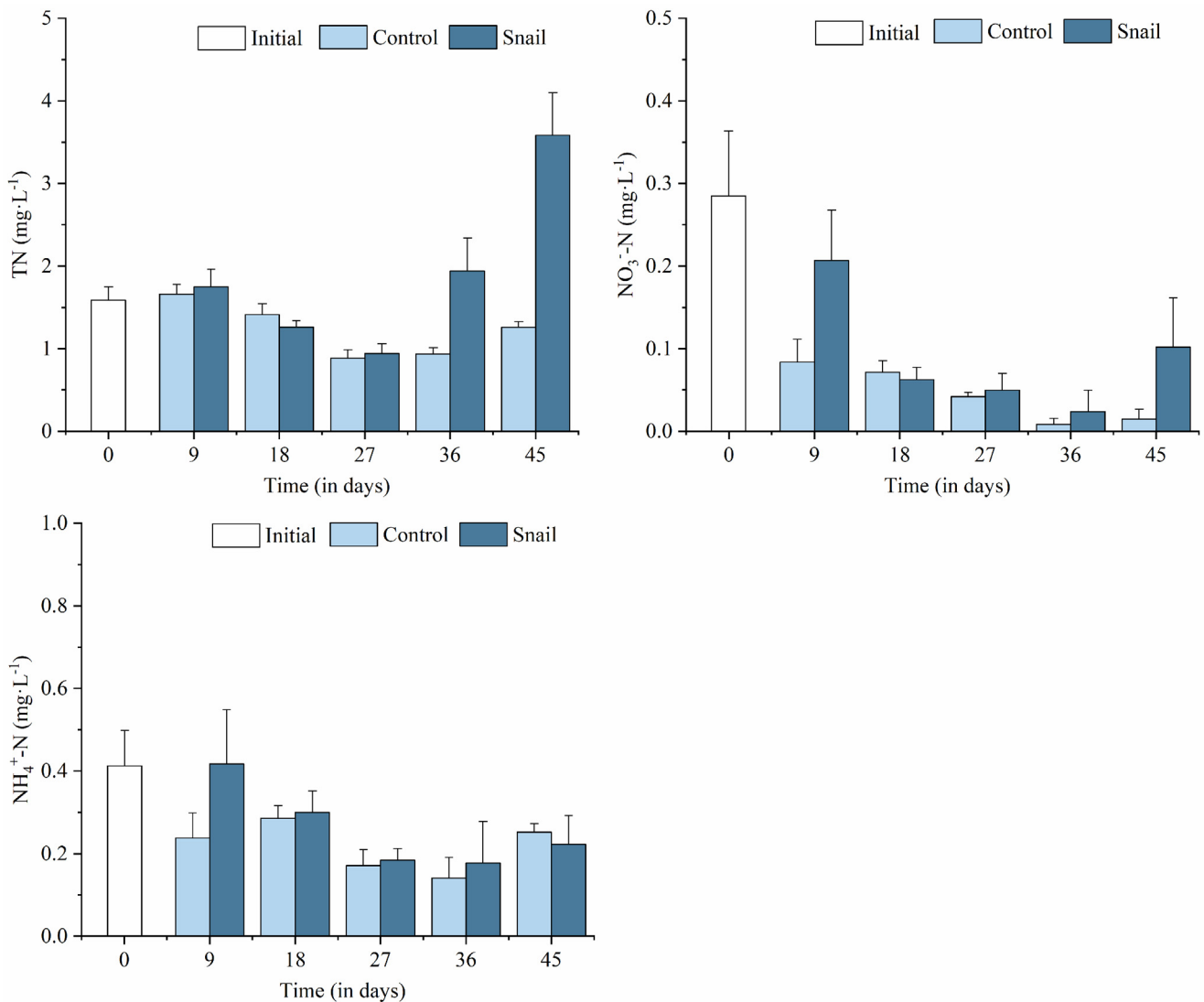
### 3.5 Wet weight, leaf length and tiller number of *Vallisneria natans*

Wet weight, leaf length and tiller number of *V. natans* were lower in the snail treatment than in the control (*t*-test,  $p < 0.001$ ,  $< 0.001$ ,  $= 0.042$ , respectively, Fig. 5).

## 4 Discussion

We found that the presence of *P. canaliculata* increased TN,  $\text{NO}_3^-$ -N, TSS and OSS concentrations, while we did not find any change in TP and TN:TP, but a decrease in SRP. We also found that *P. canaliculata* increased the total phytoplankton biomass and microphytoplankton biomass but did not alter the biomass of nanophytoplankton and picophytoplankton. The biomass, leaf length and tiller number of *V. natans* also decreased markedly in the snail treatment.

The increase in nitrogen concentrations of TN and  $\text{NO}_3^-$ -N in the snail treatment likely derives from the excretion by *P. canaliculata* (Pan *et al.*, 2014). In addition, the consumption



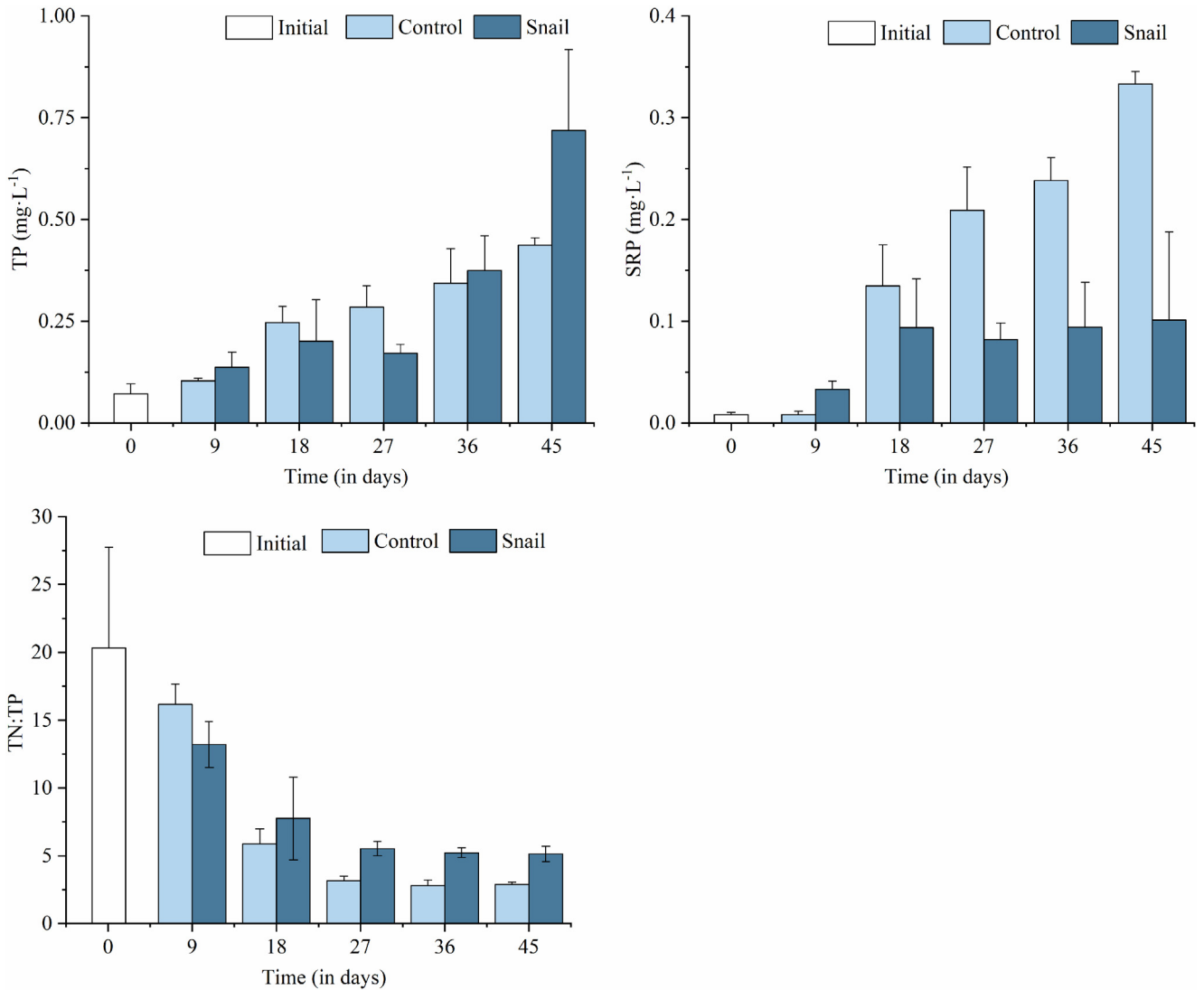
**Fig. 1.** Nitrogen concentration (TN, NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, mean ± 1SD) in the control and the snail treatment over time.

by the animal may also release nitrogen from the submerged macrophyte to the overlying water. Furthermore, the bioturbation of the animal on sediments when moving may enhance the release of nitrogen to overlying water. However, we cannot discount the possibility that some atmospheric nitrogen was added to the water by phytoplankton fixation as the *P. canaliculata* did change the phytoplankton community. Unfortunately, we did not monitor changes in the phytoplankton species composition.

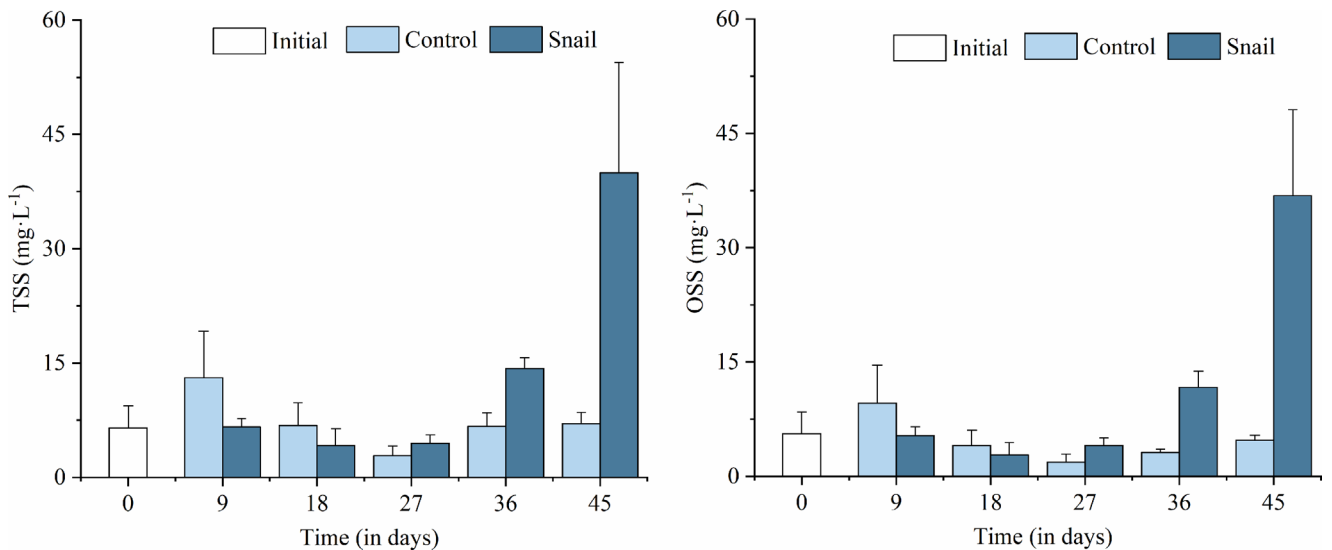
We found a major increase in phosphorus of TP and SRP in both the treatment and the control during the course of the experiment but no difference in TP between them. This pattern can only be explained by a major release of phosphorus from the sediment perhaps associated with the increased temperatures in the mesocosms with the experiment running in summer from May to July, as the release rate increases with increasing temperature (Nicholls, 1999; Søndergaard *et al.*, 2003). However, the concentrations of SRP decreased in the snail tanks compared to the controls, likely reflecting a higher

uptake in phytoplankton due to their higher biomass here than in the control. Nitrogen and phosphorus are often limiting nutrients for phytoplankton growth (Elmgren and Larsson 2001; Bledsoe *et al.*, 2004). *Pomacea canaliculata* can increase both the nitrogen and phosphorus concentrations (Carlsson *et al.*, 2004). We did find that the snail increased total nitrogen in this study, but we did not find any change in total phosphorus and TN: TP.

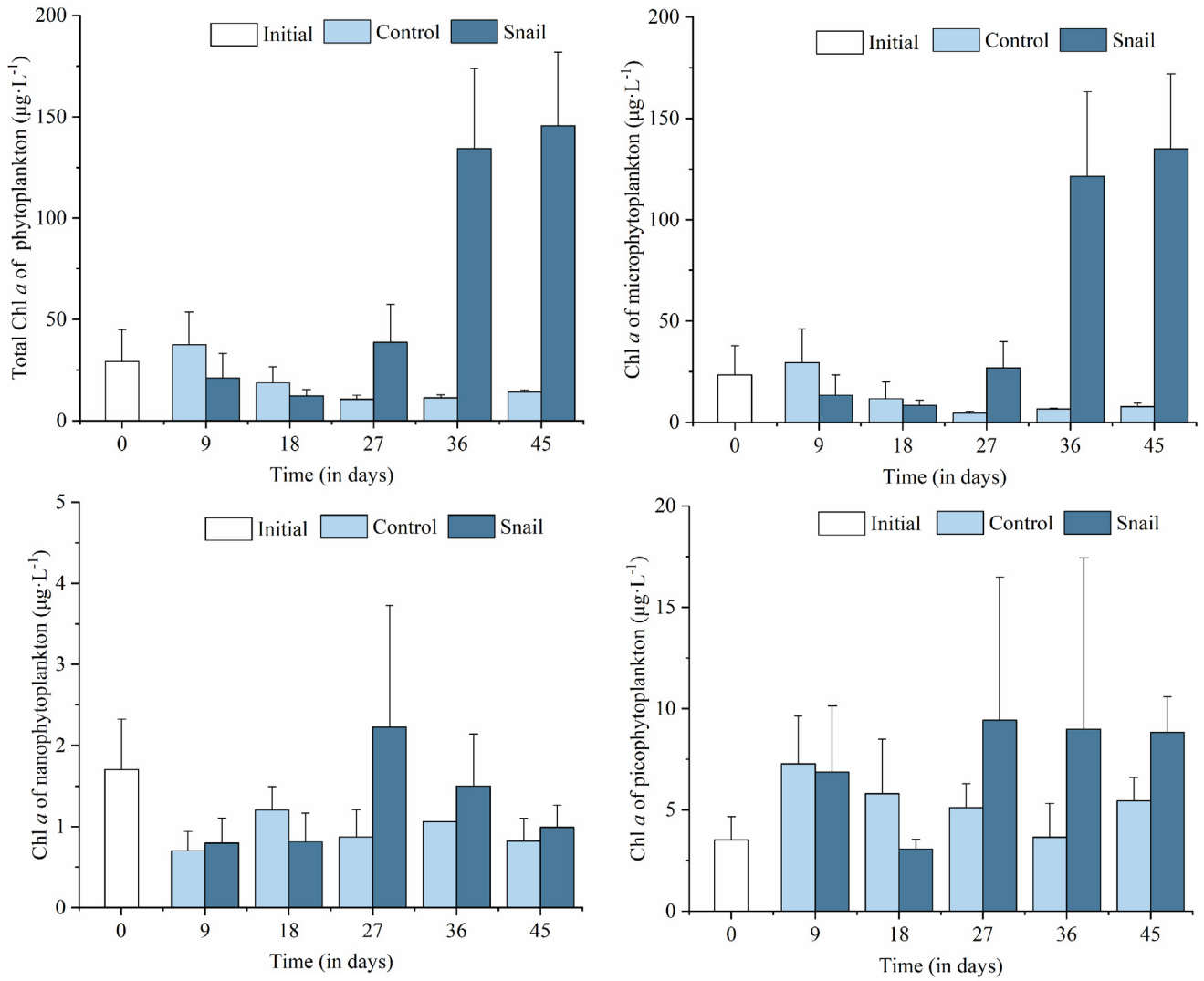
We also found a shift in phytoplankton size structure as only the microphytoplankton increased in the snail treatment while the smaller size fractions were not affected. Although debris particles, phytoplankton, invertebrates and macrophytes can be food sources for *P. canaliculata* (Kwong *et al.*, 2009; Wong *et al.*, 2009; Kwong *et al.*, 2010), its primary food is macrophytes (Carlsson *et al.*, 2004; Carlsson and Lacoursiere, 2005). The changes in phytoplankton size structure is therefore not likely to be directly related to feeding, but instead due to effects of difference in the nutrient concentrations between the snail treatment and the control, or to changes in the



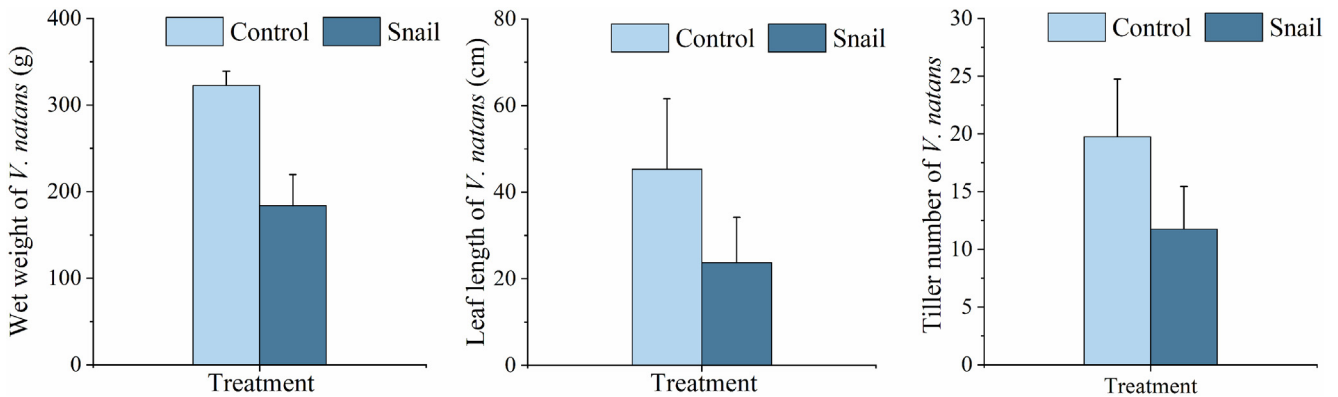
**Fig. 2.** Phosphorus concentrations (TP, SRP and TN:TP, mean ± 1 SD) in the control and the snail treatment over time.



**Fig. 3.** TSS and OSS concentrations in the water (mean ± SD) in the control and the snail treatment over time.



**Fig. 4.** Chl *a* of phytoplankton and size-fractionated phytoplankton (microphytoplankton, nanophytoplankton and picophytoplankton) in the control and the snail treatment over time.



**Fig. 5.** Wet weight, leaf length, tiller number (mean ± 1 SD) of *Vallisneria natans* in the control and the snail treatment.

light condition. However, the changes in phytoplankton size structure can lead to profound change of ecosystem, including food web, efficiency of material transformation, and so on.

With the enhanced growth of phytoplankton in the snail treatment, the TSS and OSS increased thereby increasing the light attenuation and decreasing the light intensity at the sediment surface which may limit the growth of *V. natans*. Thus, *P. canaliculata* can negatively affect the growth of *V. natans* directly by consuming the plant, and indirectly by increasing the light attenuation. We did find that the biomass, leaf length and tiller number of *V. natans* were lower in the *P. canaliculata* treatment than in the control, indicating that the snail hampered the growth of the submerged macrophytes. Similarly, Calvo *et al.* (2019) showed that consumption by *P. canaliculata* can slow the growth of submerged macrophyte (*Hydrilla verticillata* (L. f.) Royle). However, whether the reduction of submerged macrophyte growth is caused by direct consumption of the plant, by shading, or both cannot be determined from our study.

Our results need to be interpreted with caution. The results may be used to assess specific mechanisms of primary production shifting from benthic to pelagic habitats by the snail *P. canaliculata* but may not accurately represent the variations occurring in natural lakes due to scale differences. However, the results coincide with other studies showing that the snail can reduce the growth of submerged plants, increase the turbidity and deteriorate the water quality not only in mesocosms (Liu *et al.*, 2021; Gao *et al.*, 2021; Yang *et al.*, 2021), but also in natural lakes (Martín *et al.*, 2019).

In summary, the *P. canaliculata* increased TN, NO<sub>3</sub><sup>-</sup>-N, TSS and OSS concentrations, did not change TP and TN: TP, but decreased SRP, enhanced the growth of phytoplankton and microphytoplankton, altered the phytoplankton communities, and decreased the light intensity and the growth of submerged macrophyte. Thus, *P. canaliculata* shifted primary production from benthic macrophytes to pelagic phytoplankton, altered the phytoplankton community composition and deteriorated water quality. Removal or control of *P. canaliculata* would be useful to protect submerged macrophyte and maintain clear water in lakes and ponds.

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## References

- American Public Health Association (APHA). 1998. Standard methods for the examination of water and wastewater. *Washington: American Public Health Association*.
- Baker GH. 1998. The golden apple snail, *Pomacea canaliculata* (Lamarck) (Mollusca: Ampullariidae), a potential invader of fresh water habitats in Australia. In Zalucki MP, Drew RAI, White GG, eds. Pest Management-Future Challenges. Proceedings VI Australasian Appl. Brisbane: University of Queensland Printery, pp. 21–26.
- Barko JW, James WF. 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. In Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K eds. The Structuring Role of Submerged Macrophytes in Lakes. New York: Springer Verlag, pp. 197–214.
- Bledsoe EL, Philips EJ, Jett CE, Donnelly KA. 2004. The relationships among phytoplankton biomass, nutrient loading and hydrodynamics in an inner-shelf estuary. *Ophelia* 58: 29–47.
- Boland BB, Meerhoff M, Fosalba C, Mazzeo N, Barnes MA, Burks RL. 2008. Juvenile snails, adult appetites: contrasting resource consumption between two species of apple snails (*Pomacea*). *J Mollus Stud* 74: 47–54.
- Britton JR. 2023. Contemporary perspectives on the ecological impacts of invasive freshwater fishes. *J Fish Biol* 103: 752–764.
- Brönmark C, Vermaat JE. 1998. Complex fish-snail-epiphyton interactions and their effects on submerged freshwater macrophytes. In Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K, eds. The Structuring Role of Submerged Macrophytes in Lakes. New York: Springer Verlag, vol. 131, pp. 47–68.
- Calvo C, Mormul RP, Figueiredo BRS, Cunha ER, Thomaz SM, Meerhoff M. 2019. Herbivory can mitigate, but not counteract, the positive effects of warming on the establishment of the invasive macrophyte *Hydrilla verticillata*. *Biol Invasions* 21: 59–66.
- Carlsson NOL, Brönmark C. 2006. Size-dependent effects of an invasive herbivorous snail (*Pomacea canaliculata*) on macrophytes and periphyton in Asian wetlands. *Freshw Biol* 51: 695–704.
- Carlsson NOL, Brönmark C, Hansson LA. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85: 1575–1580.
- Carlsson NOL, Lacoursiere JO. 2005. Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. *Biol Invasions* 7: 233–241.
- Cowie RH. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. In: Barker GM, ed. Molluscs as Crop Pests. CABI: Wallingford, pp. 145–192.
- Elger A, Lemoine D. 2005. Determinants of macrophyte palatability to the pond snail *Lymnaea stagnalis*. *Freshw Biol* 50: 86–95.
- Elmgren R, Larsson U. 2001. Nitrogen and the Baltic Sea: managing nitrogen in relation to phosphorus. *Sci World J* 1: 371–377.
- Estebenet AL, Martín PR. 2002. Minireview: *Pomacea canaliculata* (Gastropoda: Ampullariidae): life-history traits and their plasticity. *Biocel* 26: 83.
- Ewel JJ, O'Dowd DJ, Bergelson J, Daehler CC, D'Antonio CM, Gómez LD, Gordon DR, Hobbs RJ, Holt A, Hopper KR, Hughes CE, LaHart M, Leakey RRB, Lee WG, Loope LL, Lorence DH, Louda SM, Lugo AE, McEvoy PB, Richardson DM, Vitousek PM. 1999. Deliberate introductions of species: research ne eds benefits can be reaped, but risks are high. *Bio Science* 49: 619–630.
- Fang L, Wong PK, Lin L, Lan C, Qiu JW. 2010. Impact of invasive apple snails in Hong Kong on wetland macrophytes, nutrients, phytoplankton and filamentous algae. *Freshw Biol* 55: 1191–1204.
- Gao J, Yang C, Zhang ZH, Liu ZW, Jeppesen E. 2021. Effects of co-occurrence of invading *Procambarus clarkii* and *Pomacea canaliculata* on *Vallisneria denseserrulata*-dominated clear-water ecosystems: a mesocosm approach. *Knowl Manag Aquat Ecosyst* 422: 29.
- Haubrock PJ, Oficialdegui FJ, Zeng Y, Patoka J, Yeo DC, Kouba A. 2021. The redclaw crayfish: a prominent aquaculture species with

- invasive potential in tropical and subtropical biodiversity hotspots. *Rev Aquac* 13: 1488–1530.
- Huang X, Chen W, Cai Q. 1999. Survey, Observation and Analysis of Lake Ecology. Beijing: Standards Press of China p. 247.
- Hulme PE. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J Appl Ecol* 46: 10–18.
- Jackson MC, Wasserman RJ, Grey J, Ricciardi A, Dick JT, Alexander ME. 2017. Novel and disrupted trophic links following invasion in freshwater ecosystems. *Adv Ecol Res* 57: 55–97.
- Jasser I. 1995. The influence of macrophytes on a phytoplankton community in experimental conditions. *Hydrobiologia* 306: 21–32.
- Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K. 1998. The structuring role of submerged macrophytes in lakes. Berlin: Springer.
- Jin S, Ibrahim M, Muhammad S, Khan S, Li, G. 2020. Light intensity effects on the growth and biomass production of submerged macrophytes in different water strata. *Arab J Geosci* 13: 1–7.
- Kufel L, Ozimek T. 1994. Can *Chara* control phosphorus cycling in Lake Łuknajno (Poland)? *Hydrobiologia* 276: 277–283.
- Kwong KL, Chan RKY, Qiu JW. 2009. The potential of the invasive snail *Pomacea canaliculata* as a predator of various life-stages of five species of freshwater snails. *Malacologia* 51: 343–356.
- Kwong KL, Dudgeon D, Wong PK, Qiu JW. 2010. Secondary production and diet of an invasive snail in freshwater wetlands: implications for resource utilization and competition. *Biol Invasions* 12: 1153–1164.
- Lach L, Britton DK, Rundell RJ, Cowie RH. 2000. Food preference and reproductive plasticity in an invasive freshwater snail. *Biol Invasions* 2: 279–288.
- Lach L, Cowie RH. 1999. The spread of the introduced freshwater apple snail *Pomacea canaliculata* (Lamarck) (Gastropoda: Ampullariidae) on Oahu, Hawaii. *Bishop Mus Occas Pap* 58: 66–71.
- Li B, Gu B, Yang Z, Zhang T. 2018. The role of submerged macrophytes in phytoremediation of arsenic from contaminated water: a case study on *Vallisneria spiralis* (Lour.) Hara. *Ecotox Environ Safe* 165: 224–231.
- Liu C, Zhang L, Fan C, Xu F, Chen K, Gu X. 2017. Temporal occurrence and sources of persistent organic pollutants in suspended particulate matter from the most heavily polluted river mouth of Lake Chaohu, China. *Chemosphere* 174: 39–45.
- Liu Y, He L, Hilt S, Wang R, Zhang H, Ge G. 2021. Shallow lakes at risk: nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails. *Freshw Biol* 66: 436–446.
- Liu ZW, Hu JR, Zhong P, Zhang XF, Ning JJ, Larsen SE, Chen DY, Gao YM, He H, Jeppesen E. 2018. Successful restoration of a tropical shallow eutrophic lake: strong bottom-up but weak top-down effects recorded. *Water R* 2018, 146: 88–97
- Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. 100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN)*.
- Lv S, Zhang Y, Steinmann P, Yang GJ, Yang K, Zhou XN, Utzinger J. 2011. The emergence of angiostrongyliasis in the People's Republic of China: the interplay between invasive snails, climate change and transmission dynamics. *Freshw Biol* 56: 717–734.
- Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10: 689–710.
- Martín PR, Burela S, Seuffert ME, Tamburi NE, Saveanu L. 2019. Invasive Pomacea snails: actual and potential environmental impacts and their underlying mechanisms. *CABI Rev* 14: 1–11.
- Matsuzaki SS, Usio N, Takamura N, Washitani I. 2009. Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* 158: 673–686.
- MEP of PRC (Ministry of Environmental Protection of the People's Republic of China). 2017. Water quality-determination of Chlorophyll a – spectrophotometric method. Beijing: China Environmental Science Press, 3–4.
- Naylor R. 1996. Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* 25: 443–448.
- Nicholls KH. 1999. Effects of temperature and other factors on summer phosphorus in the inner Bay of Quinte, Lake Ontario: Implications for climate warming. *J Great Lakes Res* 25: 250–262.
- Novák J, Kalous L, Patoka J. 2020. Modern ornamental aquaculture in Europe: early history of freshwater fish imports. *Rev Aquac* 12: 2042–2060.
- Ozimek T, Gulati RD, Van Donk E. 1990. Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. *Hydrobiologia* 200: 399–407.
- Pan D, Zhang J, Long J, Zhang J, Zhao B, Luo M. 2014. Impacts of golden apple snail (*Pomacea canaliculata*) on water quality and microbes. *Chinese J Eco-Agr* 22: 58–62.
- Petticrew EL, Kalff J. 1992. Water flow and clay retention in submerged macrophyte beds. *Can J Fish Aquat Sci* 49: 2483–2489.
- Qiu D, Wu Z, Liu B, Beng J, Fu G, He F. 2001. The restoration of aquatic macrophytes for improving water quality in a hypertrophic shallow lake in Hubei Province, China. *Ecol Eng* 18: 147–156.
- Qiu JW, Chan MT, Kwong KL, Sun J. 2011. Consumption, survival and growth in the invasive freshwater snail *Pomacea canaliculata*: does food freshness matter? *J Mollus Stud* 77: 189–195.
- Qiu JW, Kwong KL. 2009. Effects of macrophytes on feeding and life-history traits of the invasive apple snail *Pomacea canaliculata*. *Freshwater Biol* 54: 1720–1730.
- Rong Y, Tang Y, Ren L, Taylor WD, Razlutskiy V, Naselli-Flores L, Liu Z, Zhang X. 2021. Effects of the filter-feeding benthic bivalve *Corbicula fluminea* on plankton community and water quality in aquatic ecosystems: a mesocosm study. *Water* 13: 1827.
- Sala OE, Stuart Chapin F, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- Søndergaard M, Jensen JP, Jeppesen E. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506: 135–145.
- Timms RM, Moss B. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol Oceanogr* 29: 472–486.
- Van Donk E. 1998. Switches between clear and turbid water states in a biomanipulated lake (1986–1996): the role of herbivory on macrophytes. In Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K, eds. *The Structuring Role of Submerged Macrophytes in Lakes*, Springer Verlag, New York, 290–297.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.



- Wang C, Zhang S, Wang PF, Hou J, Qian J, Ao Y, Lu J, Li L. 2011. Salicylic acid involved in the regulation of nutrient elements uptake and oxidative stress in *Vallisneria natans* (Lour.) Hara under Pb stress. *Chemosphere* 84: 136–142.
- Wang Z, Pei Y. 2012. Ecological risk resulting from invasive species: a lesson from riparian wetland rehabilitation. *Procedia Environ Sci* 13: 1798–1808.
- Wong PK, Kwong KL, Qiu JW. 2009. Complex interactions among fish, snails and macrophytes: implications for biological control of an invasive snail. *Biol Invasions* 11: 2223–2232.
- Wong PK, Liang Y, Liu NY, Qiu JW. 2010. Palatability of macrophytes to the invasive freshwater snail *Pomacea canaliculata*: differential effects of multiple plant traits. *Freshw Biol* 55: 2023–2031.
- Xie Y, An S, Wu B. 2005. Resource allocation in the submerged plant *Vallisneria natans* related to sediment type, rather than water-column nutrients. *Freshw Biol* 50: 391–402.
- Xue L, Hou P, Zhang Z, Shen M, Liu F, Yang L. 2020. Application of systematic strategy for agricultural non-point source pollution control in Yangtze River basin, China. *Agr Ecosyst Environ* 304: 107148.
- Yang C, Kang YH, Zhang ZH, Miao T, Liao MJ, Jiao YY, Zhao YJ. 2021. Effect of *Pomacea canaliculata* grazing on three submerged macrophytes and the related physicochemical factors. *J Lake Sci* 33: 1241–1253.
- Yin Y, He Q, Pan X, Liu Q, Wu Y, Li X. 2022. Predicting current potential distribution and the range dynamics of *Pomacea canaliculata* in China under global climate change. *Biology* 11: 110.

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