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Omnivorous shrimp *Neocaridina denticulata sinensis* enhances the growth of submerged macrophyte *Vallisneria denseserrulata*

Jialiang Ye[1], Yali Tang[1], Xiufeng Zhang[1], Ping Zhong[1] and Zhengwen Liu[1,2,3,*]

[1] Department of Ecology and Institute of Hydrobiology, Jinan University, Guangzhou 510632, PR China
[2] State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography & Limnology, Chinese Academy of Sciences, Nanjing 210008, PR China
[3] Sino-Danish Center, University of the Chinese Academy of Sciences, Beijing 101408, PR China

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Abstract – Lake eutrophication often causes declines and even losses of submerged macrophytes through the shading effects of increased periphyton and phytoplankton. The Chinese swamp shrimp *Neocaridina denticulata sinensis* Kemp (Decapoda, Atyidae) is a common omnivore in Chinese lakes, where its presence may impact both periphyton and phytoplankton, with previously unstudied consequences for submerged macrophytes. Here, using a mesocosm experiment, we studied the effect of *N. d. sinensis* on periphyton, phytoplankton and the submerged macrophyte *Vallisneria denseserrulata.* Results showed that in the presence of *N. d. sinensis*, the biomass of periphyton on the leaves of *V. denseserrulata* was significantly reduced, and that growth rate of *V. denseserrulata* increased. The presence of *N. d. sinensis* also significantly increased the total phosphorus concentrations in the water column and phytoplankton biomass (chlorophyll-*a*). The enhanced growth of *V. denseserrulata* is likely to be linked to improved light harvesting due to the reduced periphyton attached to their leaf surface. The results suggest that stocking with Chinese swamp shrimps may enhance the development of macrophytes in eutrophic shallow lakes.

Keywords: omnivorous shrimp / submerged macrophytes / periphyton / eutrophication

Résumé – La crevette omnivore *Neocaridina denticulata sinensis* favorise la croissance du macrophyte submergé *Vallisneria denseserrulata*. L'eutrophisation des lacs entraîne souvent des déclins, voire des pertes de macrophytes submergés en raison des effets d'ombrage dus à l'augmentation du périphyton et du phytoplancton. La crevette des marais chinois *Neocaridina denticulata sinensis* Kemp (Decapoda, Atyidae) est un omnivore commun dans les lacs chinois, où sa présence peut avoir un impact sur le périphyton et le phytoplancton, avec des conséquences non étudiées auparavant pour les macrophytes immergés. Ici, à l'aide d'une expérience en mésocosme, nous avons étudié l'effet de *N. d. sinensis* sur le périphyton, le phytoplancton et le macrophyte immergé *Vallisneria denseserrulata*. Les résultats ont montré qu'en présence de *N. d. sinensis*, la biomasse de périphyton sur les feuilles de *V. denseserrulata* était considérablement réduite et que le taux de croissance de *V. denseserrulata* augmentait. La présence de *N. d. sinensis* a également augmenté de façon significative les concentrations de phosphore total dans la colonne d'eau et la biomasse phytoplanctonique (chlorophylle-*a*). La croissance accrue *de V. denseserrulata* est probablement liée à une meilleure captation de la lumière en raison de la réduction du périphyton attaché à la surface de leurs feuilles. Les résultats suggèrent que l'ensemencement de crevettes des marais chinois pourrait favoriser le développement de macrophytes dans les lacs eutrophes peu profonds.

Mots clés : crevette omnivore / macrophyte submergé / périphyton / eutrophisation

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*Corresponding author: `zliu@niglas.ac.cn`

1 Introduction

Submerged macrophytes are important primary producers in shallow lake ecosystems, playing a key role in maintaining clear water states through the assimilation of nutrients, accelerating the deposition of suspended solids and preventing the resuspension of sediments (Jaynes and Carpenter, 1986; Jeppesen *et al.*, 1990; van Donk and van de Bund, 2002). Replanting with submerged macrophytes has been an important tool in the restoration of shallow eutrophic lakes (Yu *et al.*, 2016; Liu *et al.*, 2018).

Eutrophication often enhances the growth of periphyton on the surfaces of submerged macrophytes, reducing the availability of light and inorganic nutrients to the affected plant. Overgrowth of periphyton is thus a major cause of loss and decline of submerged lake macrophytes under eutrophic conditions (Hough *et al.*, 1989; Jones *et al.*, 2002; Phillips *et al.*, 2016). Many previous studies have also shown that reducing the biomass of periphyton can promote growth of submerged macrophytes (Daldorph and Thomas, 1995; Asaeda *et al.*, 2004; Li *et al.*, 2008). Li *et al.* (2008) showed that periphyton-feeding by snails can boost submerged macrophytes growth in exactly this way, and a variety of aquatic grazing invertebrates have been suggested as potential aids in the management of submerged macrophytes in shallow lake systems (Daldorph and Thomas, 1995; Rao *et al.*, 2015).

Omnivorous shrimps that consume leaf litter, particulate matter, and periphyton are common in many freshwater ecosystems (Pringle *et al.*, 1993; Asaeda *et al.*, 2004; Sultana *et al.*, 2010), and have been shown to exert a variety of ecological effects (Pringle *et al.*, 1993; Crowl *et al.*, 2001; Geddes and Trexler, 2003; Souza and Moulton, 2005; Moulton *et al.*, 2012). While some previous studies have demonstrated a significant reduction of periphyton biomass as a result of direct grazing by omnivorous shrimps (Geddes and Trexler, 2003; Moulton *et al.*, 2012), others have recorded significant increases in depositional material and periphyton on substrata when shrimps are present (Pringle *et al.*, 1993; Geddes and Trexler, 2003). These increases are probably stimulated by nutrients excreted by the shrimps and by the mechanical resuspension of sediment (Geddes and Trexler, 2003).

The Chinese swamp shrimp *Neocaridina denticulata sinensis* Kemp (Decapoda, Atyidae) is common in East Asia. It is also found as an invasive species in Europe (Weiperth *et al.*, 2019) and the Hawaiian Islands (Englund and Cai, 1999). The species is commercially important in lake fisheries in China despite its small size (Li *et al.*, 1990), but its ecological role on lake systems has not been evaluated. We hypothesized that grazing by *N. d. sinensis* can reduce the periphyton biomass and thus enhance the growth of submerged macrophytes, while nutrient concentrations in the water may increase due to shrimp activities. The results provide insights that might be important for the management of submerged macrophytes and the restoration of eutrophic shallow lakes in the region.

2 Materials and methods

2.1 Materials

Specimens of the Chinese swamp shrimp *N. d. sinensis* were purchased from Guangzhou Huadiwan Aquarium, Guangzhou, China. They were 1.5–2.0 cm long and weighed between 0.3 and 0.5 g. Samples of sediment and of the submerged macrophyte *Vallisneria denseserrulata* were collected from the South Lake of Jinan University. The plants were rinsed thoroughly to remove the periphyton.

2.2 Experiment design and sampling

The experiment was conducted outdoors in eight polyethylene plastic tanks set up in the grounds of Jinan University, Guangzhou, China. The tanks were 60 cm high, with a volume of 75 liters. A five-centimeter depth of sediment ($TN = 1.84\ mg\ g^{-1}$, $TP = 1.46\ mg\ g^{-1}$) was added to each tank, and 45 centimeters of tap water ($TN = 1.91\ mg\ L^{-1}$, $TP = 0.04\ mg\ L^{-1}$). The experiment involved four replicates of two different treatments: macrophytes with shrimps (SM) and macrophytes without shrimps (NS). At the beginning of the experiment, we planted about 29 grams (fresh weight) *V. denseserrulata* into each tank, and eight shrimps were added to each SM treatment tanks which resulted in a shrimp density within the natural arrange (Oh *et al.*, 2003). The tank water temperature ranged from 17 to 30 °C during the experiment.

Samples of periphyton and water were collected one week after the experiment began, and then every two weeks thereafter, and the experiment lasted for 17 weeks (119 days). At each sampling, three leaves were randomly taken from each tank, and the periphyton attached to each leaf was brushed and rinsed into a beaker using pure water, which was later filtered by GF/C filter. As a proxy for periphyton biomass, the chlorophyll-*a* (Chl-*a*) content of the matter retained on the filter was measured spectrophotometrically, after extraction in a 90% (v/v) acetone/water solution for 24 h. No correction was carried out for pheophytin interference (SEPA, 2002). The lengths and widths of the sampled leaves were measured and used to calculate leaf surface area and the biomass of periphyton was expressed as chlorophyll-*a* (μg) per unit leaf surface area (cm^2). Water samples were taken and analyzed for total nitrogen (TN), total phosphorus (TP), total dissolved nitrogen (TDN), total dissolved phosphorus (TDP) and Chl-*a* content in the laboratory according to Chinese standard methods (Jin and Tu, 1990), and Chl-*a* was analyzed using the method described for periphyton above. At the end of the experiment, all *V. denseserrulata* were harvested and their total fresh weight recorded. The relative growth rate (RGR) of *V. denseserrulata* was calculated using the formula $RGR\ (mg\ g^{-1}\ d^{-1}) = 1000 \times \ln\ (Wf/Wi)/days$, where Wf (g) and Wi (g) were final and initial total fresh weight of plant per tank, respectively.

2.3 Statistical analysis

Time series data (nutrients and chlorophyll *a*) were statistically tested for effects of treatment, time and their interactions by repeated measurements ANOVA (rmANOVA) after checking for normality and homogeneity of variance in the samples and residuals. If the assumption of sphericity of the variance–covariance matrices of the rmANOVA analyses was violated, the degrees of freedom were Huyn-Feldt corrected, resulting in an adjustment of the significance of the F ratio. RGR was statistically tested by student *t*-test after checking for normality and homogeneity. All comparisons were performed

Table 1. Summary of rmANOVA results on the effects of different treatment on the concentrations of total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), chlorophyll *a* of water (W-Chl-*a*) and chlorophyll *a* of periphyton (P-Chl-*a*).

Effects	TN	TDN	TP	TDP	W-Chl-*a*	P-Chl-*a*
Shrimp	**0.028**	0.063	**0.001**	0.112	< **0.001**	**0.047**
Time	**0.001**	< **0.001**	< **0.001**	**0.025**	0.093	**0.001**
Shrimp × Time	0.859	0.118	**0.016**	**0.013**	0.126	0.088

Notes: Values indicate probability levels; values in bold are below significance level (0.05).

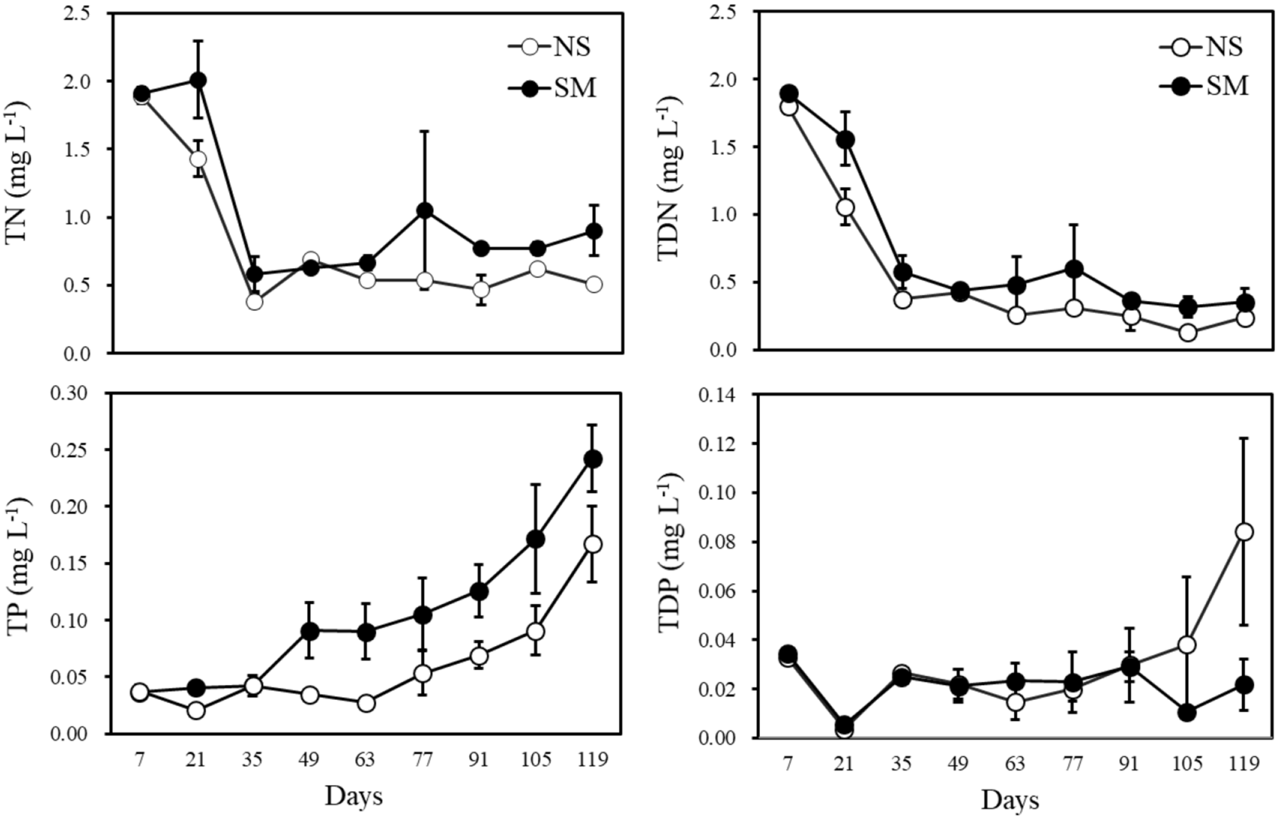

Fig. 1. Variations in nutrients during the experiment (NS = macrophytes without shrimp; SM = macrophytes with shrimp). Values represent mean ± SE.

with the statistical package SPSS version 19.0 (IBM Corporation, Somers, NY, USA).

3 Results

3.1 Changes in water nutrients and Chl-a

The concentrations of total nitrogen (TN), total phosphorus (TP) and chlorophyll *a* (W-Chl-*a*) in water were significantly higher in tanks with shrimps (SM treatment) than tanks without shrimps (NS treatment), while total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) concentrations were not significantly different between NS and SM treatments (Tab. 1; Fig. 1).

Mean concentrations of Chl-*a* in tank water in the NS treatment were 5.09 ± 4.04 mg L^{-1}, significantly lower than the 11.78 ± 7.73 mg L^{-1} observed in the SM treatment water (Tab. 1; Fig. 2).

3.2 Changes in the biomass of periphyton (Chl-a)

Variations in periphyton biomass (Chl-*a*) over the course of the experiment are shown in Figure 3. The mean Chl-*a* content of periphyton on the leaves of *V. denseserrulata* in the NS treatment was 6.79 ± 9.23 $\mu\text{g cm}^{-2}$, while that of leaves in the SM treatment was significantly lower, at 3.69 ± 4.65 $\mu\text{g cm}^{-2}$ (Tab. 1; Fig. 3).

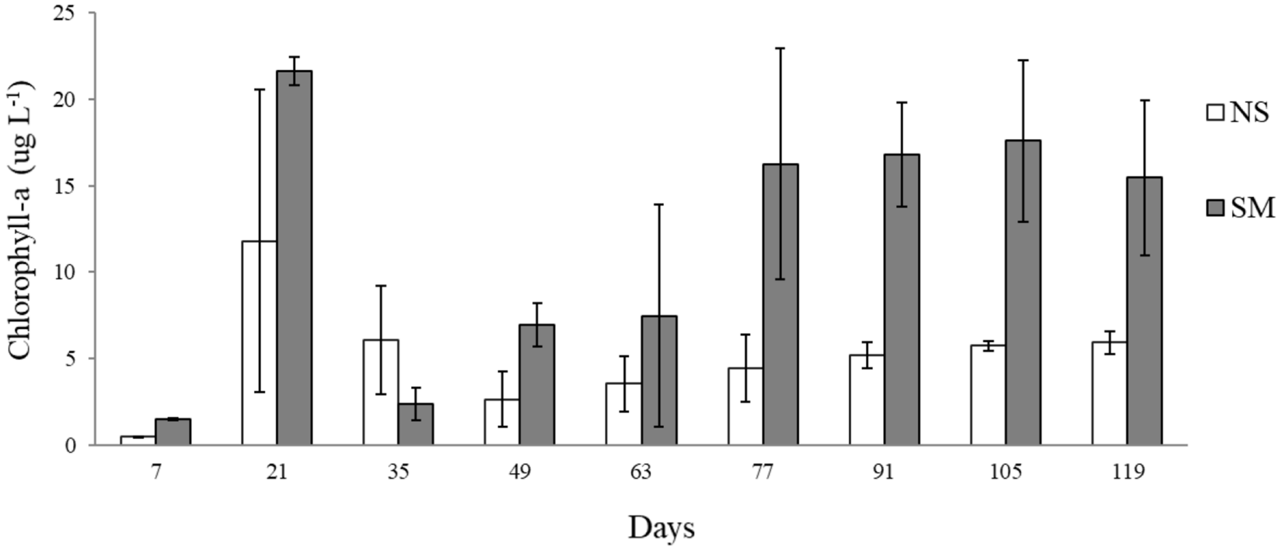

Fig. 2. Variations in the chlorophyll-a (Chl-*a*) content of tank water (NS = macrophytes without shrimp; SM = macrophytes with shrimp). Values represent mean ± SE.

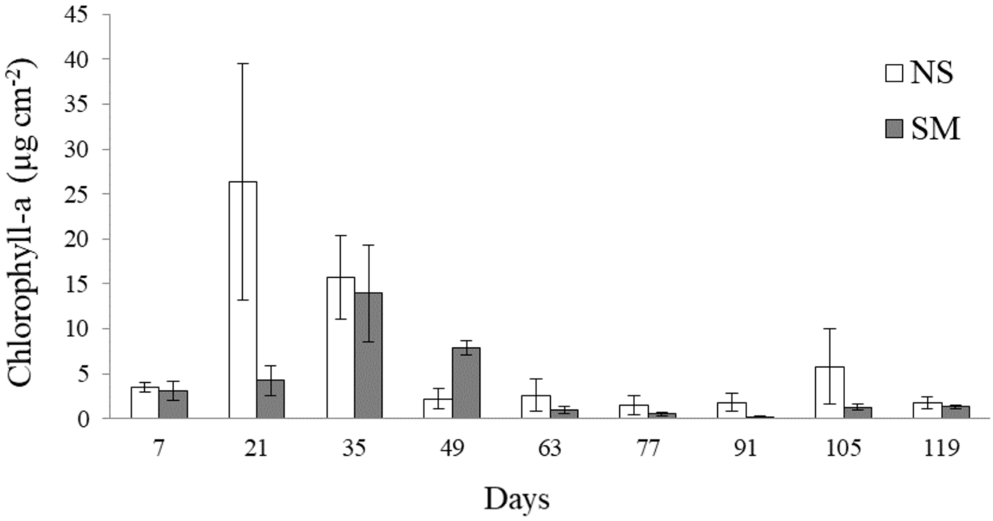

Fig. 3. Variations in periphyton Chl-*a* on the leaves of *V. denseserrulata* (NS = macrophytes without shrimp; SM = macrophytes with shrimp). Values represent mean ± SE.

3.3 Changes in the growth rate of *V. denseserrulata*

At the end of the experiment, the relative growth rates (RGR) of *V. denseserrulata* plants in tanks with shrimp (SM) were significantly higher than the treatment without shrimp (NS) (student *t*-test, $t = -5.485$, $df = 4$, $p = 0.005$). The mean RGR of *V. denseserrulata* was 17.3 ± 0.2 $mg\,g^{-1}\,d^{-1}$ in the SM treatment, while in the NS treatment the mean value was 14.1 ± 1.0 $mg\,g^{-1}\,d^{-1}$ (Fig. 4).

4 Discussion

This study demonstrates that the presence of Chinese swamp shrimps *N. d. sinensis* leads to a reduction in periphyton biomass on the surface of submerged macrophytes, an effect which is most likely a result of direct consumption of periphyton.

When Yam and Dudgeon (2005) analyzed the carbon and nitrogen stable isotope signatures of two other species of atyid shrimp (*Caridina cantonensis* and *C. serrata*) and their potential food sources (leaf litter, fine particulate organic matter, and periphyton), the results indicated that periphyton contributed > 60% to the biomass of *C. cantonensis* in unshaded streams between 35 and 60% to the biomass of *Caridina* spp. in shaded streams. There is very limited information about the feeding of *N. d. sinensis* in the literature, but an analysis of gut content by Jiang *et al.* (2010) revealed that the food taken by the species in a stream in central China comprised mainly detritus and benthic algae. In previously reported experiment lasting 30 days, Ye (2017) showed that *N. d. sinensis* reduced the density of periphyton on the surfaces of

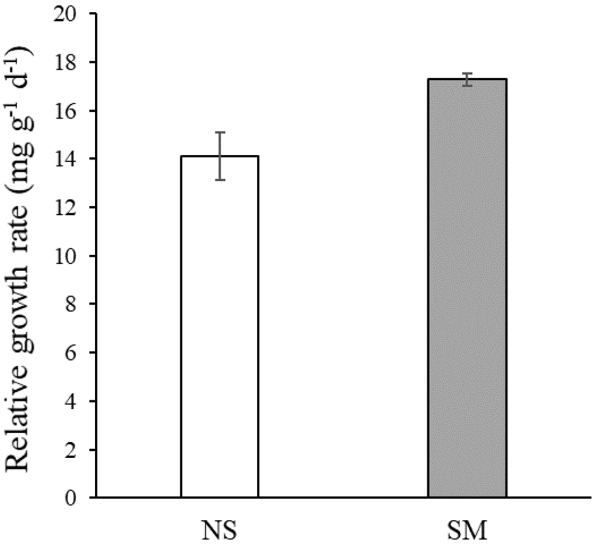

Fig. 4. The relative growth rate of *V. denseserrulata* in the experimental tanks (NS = macrophyte without shrimp; SM = macrophyte with shrimp), Values represent mean ± SE.

submerged macrophytes by > 70%. The negative effect of *N. d. sinensis* on periphyton growth agrees with studies of other atyid shrimps in the literature (Pringle *et al.*, 1993; Crowl *et al.*, 2001; Geddes and Trexler, 2003).

The presence of *N. d. sinensis* was seen to enhance the growth rate of submerged macrophyte *V. denseserrulata* under experimental conditions. Overgrowth of periphyton on leaf surfaces is known to reduce the light availability to macrophytes (Carignan and Kalff, 1980; Sand-Jensen and Borum, 1984), resulting in reduced growth and even loss of submerged plants (Daldorph and Thomas, 1995; Jones *et al.*, 2002; Li *et al.*, 2008). Asaeda *et al.* (2004) also showed that *N. d. sinensis* is able to enhance the growth of submerged macrophyte *Potamogeton perfoliatus* by removing the periphyton attached to the plants. The experiments of Li *et al.* (2008) showed that grazing by the snail *Bellamya aeruginosa* led to a decrease in periphyton biomass and a 6 to 8-fold increase in the growth rate of the submerged macrophyte *Vallisneria spiralis* relative to a snail-free control treatment. Furthermore, Jones and Sayer (2003) showed that in plant-dominated lakes, periphyton appears to have a stronger influence on plant growth than phytoplankton. Thus the removal of periphyton from the surface of *V. denseserrulata* by *N. d. sinensis* in the current experiment is likely to be the cause of the observed increase in plant growth rate.

An additional or alternative factor in the increased growth of *V. denseserrulata* in shrimp treatments may be linked to increased nutrient concentrations. Total nitrogen and total phosphorus concentrations were significantly higher in shrimp treatments than in tanks without shrimps. The presence of omnivorous shrimps is known to increase water nutrient concentrations through excretion and sediment resuspension (Takahashi and Ikeda, 1975; Pringle *et al.*, 1993), but since species of *Vallisneria* obtain most of their nutrient requirement from the sediments *via* well-developed root systems (Zhang *et al.*, 2010), the influence of nutrient in the water is likely to be limited. The increase in TN and TP in the water nutrients did not appear to exert a direct effect on periphyton biomass in our study. An earlier study by Geddes and Trexler (2003) recorded a positive correlation between the biomass of periphyton and the biomass of omnivorous shrimp (*Palaemonetes paludosus*) grazing on it, a phenomenon which was attributed to increased nutrient availability mediated by the shrimps. In our study, however, it seems the influence exerted by shrimps is *via* grazing, rather than nutrient regeneration.

Further analysis of Chl-*a* in the water in our mesocosms reveals significantly greater phytoplankton biomass in shrimp treatments than in non-shrimp treatments. The increase in phytoplankton is likely due to the elevated nutrient concentrations associated with *N. d. sinensi* presence. It is well-known from the literature that high biomasses of phytoplankton limit light penetration and that this shading effect is detrimental to submerged macrophyte growth in eutrophic waters (Jupp and Spence, 1977; Wetzel, 2001). In our study, however, the growth rates of submerged macrophytes in the shrimp treatments showed an increase rather than a decrease. As discussed previously, this increased growth is most likely a result of reduced periphyton due to shrimp grazing, and our results suggest periphyton exerts a more significant controlling effect on the growth of submerged macrophytes than phytoplankton in this case.

Our results have implications for the management and restoration of shallow lakes, which often involves the re-establishment and maintenance of submerged macrophytes essential in establishing clear water conditions. Our study shows that *N. d. sinensi* are able to reduce periphyton and increase the growth of submerged macrophytes. Stocking with *N. d. sinensi* may therefore be beneficial for the growth of submerged macrophytes, but the potential for increases in nutrient concentration, phytoplankton biomass and water turbidity must also be considered and further studies are needed to see if such effects of *N. d. sinensi* are density or water depth dependent.

In conclusion, our study showed that *N. d. sinensi* could reduce the biomass of periphyton on the leaves of the submerged macrophyte *V. denseserrulata,* while increasing the biomass of phytoplankton. Increasing growth rates of *V. denseserrulata* under these conditions suggest that periphyton exerts a stronger limiting effect on submerged macrophyte growth than phytoplankton in our experimental systems.

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