

Water clearance efficiency indicates potential filter-feeding interactions between invasive *Sinanodonta woodiana* and native freshwater mussels

Karel Douda  · Zuzana Čadková

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Abstract The Chinese pond mussel (*Sinanodonta woodiana* Lea, 1834) is a benthic filter-feeder that prefers soft-bottomed freshwater habitats and has successfully spread into both tropical and temperate water bodies outside its natural Southeast Asian range. Due to its preference for nutrient-rich waters with high levels of suspended food particles, the capacity of *S. woodiana* to influence natural seston concentrations is thought to be relatively low in comparison to that of other invasive bivalves. The experimental quantification of seston removal efficiency reported here demonstrates that *S. woodiana* is able to reduce seston loads to levels comparable to those by the control native freshwater mussel species *Unio tumidus* Philipsson, 1788. Moreover, increasing food depletion did not cause detectable changes in the filtration regime of *S. woodiana*, although the activity of native *U. tumidus* was significantly reduced. The seston clearance rate (volume of water cleared of particles per unit time) of *S. woodiana* averaged $9.3 \pm 4.0 \text{ mL g}^{-1} \text{ wet mass h}^{-1}$, which corresponds to the total daily volume of water filtered being up to several hundreds to thousands L m^{-2} at the maximal *S. woodiana* population densities reported in the literature. The observed filtration capacity of *S.*

woodiana and its current invasional spread into areas inhabited by endangered freshwater mussels call for more careful consideration of filter-feeding interactions with native mussels. The potential impacts of *S. woodiana* should be studied in more detail with respect to available food resources and long-term nutritional needs of native species and reflected in management strategies in the invaded range.

Keywords Clearance rate · Competition · Freshwater mussels · Invasive bivalve · Seston

Introduction

Feeding interactions, such as competition for food resources, is one of the most important mechanisms for the impacts of invasive species in invaded communities (White et al. 2006). While this mechanism is broadly acknowledged for some trophic guilds such as predators or plant herbivores, its less understood in a key trophic guild in freshwater ecosystems, filter-feeding collectors (Strayer and Malcom 2007).

The spread of filter-feeding non-native bivalve species represents one of the major threats to the function and biodiversity of freshwater ecosystems (Higgins and Vander Zanden 2010). Water filtration is among the mechanisms most frequently considered to be problematic in non-native ranges (Sousa et al.

K. Douda (✉) · Z. Čadková
Department of Zoology and Fisheries, Czech University
of Life Sciences Prague, Kamýčká 129, 165 21 Prague,
Czech Republic
e-mail: k.douda@gmail.com

2009, 2014), with potential effects on ecosystem functions (nutrient cycling) and biodiversity (e.g., species richness, evenness). Native freshwater mussels can be strongly affected by invasive dreissenid bivalves through heavy fouling (attachment) on their shells, which leads to the reduced influx and depletion of suspended food particles in the water entering the inhalant openings of the mussel (Haag et al. 1993; Sousa et al. 2011). While the impact of fouling is the most obvious case, it has been demonstrated that food competition between dreissenids and unionid bivalves can be important even in the absence of fouling (Strayer and Smith 1996), and some non-fouling invasive freshwater bivalves are also supposed to be important food competitors (Sousa et al. 2014; Ferreira-Rodríguez et al. 2016).

The Chinese pond mussel (*Sinanodonta woodiana* Lea 1834) is a benthic fast-growing filter-feeder of the family Unionidea (Mollusca: Bivalvia) that prefers soft-bottomed freshwater habitats and successfully spreads in both tropical and temperate water bodies outside its natural Southeast Asian range (Watters 1997). It has no capacity to attach to hard bottoms or other mussels' shells like the most problematic invasive bivalves. In its native range, *S. woodiana* is often the dominant species in most of its habitats, and extremely high population biomass of adult *S. woodiana* (up to 25 kg m⁻²) have been reported at some invaded European sites (Kraszewski and Zdanowski 2007).

The impact of invasive *S. woodiana* on the population dynamics of native freshwater mussels has not been comprehensively studied to date; nevertheless, several authors have described declines in native mussel species in association with the invasive spread of *S. woodiana* (Paunovic et al. 2006; Benkó-Kiss et al. 2013). It has been documented that *S. woodiana* competes with native mussels for hosts (Donrovich et al. 2017), but other effects are also likely. It has been hypothesized that *S. woodiana* might compete with native bivalve species for food and space or act through the modification of natural habitats (Watters 1997; Sousa et al. 2014). However, *S. woodiana* preference for nutrient-rich waters with high levels of suspended food particles (Kraszewski and Zdanowski 2007) place the species among unionid bivalves with high nutritional demands and restricted occurrence along a river or trophic gradient (Bauer 2001). In such an environment, the capacity of *S. woodiana* to

influence the seston concentration can be less significant in comparison with that of other invasive bivalves occurring in more oligotrophic conditions. On the other hand, this species has been observed living in sympatry with native mussel species, such as *Unio pictorum* (Linnaeus 1758), *Unio crassus* (Philipsson, 1788), *Unio tumidus* (Philipsson, 1788), *Pseudanodonta complanata* (Rossmässler, 1835), *Anodonta anatina*, and other mollusk species (Paunovic et al. 2006; Bódis et al. 2016). Obviously, the habitat preferences of *S. woodiana* overlap with those of several native European freshwater mussels, which can further increase the risk of filter-feeding interactions.

This short note reports on the findings of an experimental study based on the comparison of water clearance efficiency between European invasive (*S. woodiana*) and native (*U. tumidus*) unionid bivalve species. We quantified the seston removal efficiency of *S. woodiana* in a spatially limited mesocosm in order to investigate whether this species is able to reduce the seston loads to levels comparable to those by control native freshwater mussel species. We also tested whether increasing food depletion causes detectable changes in the filtration regime of the studied species. We discuss future research needs in this area and the consequences for the potential filter-feeding interactions and coexistence of endangered and invasive freshwater mussels.

Materials and methods

The experiment was conducted using individuals of invasive *S. woodiana* from a population in the non-native European range located in the Kyjovka River near Týnec (Czech Republic, 48°46'40"N, 17°0'51"E) and individuals of a native European species (*Unio tumidus*) as a control sampled from the adjacent Morava River near Lanžhot (Czech Republic, 48°41'18"N, 16°59'26"E). Both sampling locations are slow-flowing lowland river habitats with a maximal water depth of 1–2 m and mean annual flow rate of 0.82 (Kyjovka) and 61.1 (Morava) m³ s⁻¹. Quantification of the water clearance rate was performed using a modification of the method developed by Pusch et al. (2001). Mussels were transported to the experimental facility of the Czech University of Life Sciences Prague in Bechyně (Czech Republic) and

held in a 700-L flow-through shallow tank filled with natural river water (taken from the Lužnice River, 49°18'25"N, 14°30'15"E) for 2 weeks before the start of the experiment to allow acclimation to experimental conditions. Mussels were fed by replacing part of the tank water with fresh river water each sixth hour (25% of the water was pumped into the tank), and the water was continuously aerated using an airstone to guarantee a sufficient supply of natural seston.

The water clearance efficiency of individual mussels was measured in 18 experimental polyethylene chambers (450 × 300 × 150 mm, length × width × depth), each containing one plastic tray (120 × 150 mm) with a 30-mm layer of washed sand (2–10 mm particle size) as a substrate for mussels. The experimental chambers were filled with 7500 mL of fresh river water in order to carry out the study under the ambient conditions in the river with respect to the seston content and water quality (pH = 7.68, electrolytic conductivity = 257 $\mu\text{S cm}^{-1}$, temperature = 19.1 °C, O_2 = 8.65 mg L^{-1} , turbidity = 17.17 nephelometric turbidity units [NTU], total suspended solids [TSS] at 105 °C = 23.6 mg L^{-1} , TSS at 550 °C = 10.35 mg L^{-1}). An airstone was placed in each chamber to create a moderate flow of water to keep the seston in suspension. Immediately after filling the chambers with fresh river water, *S. woodiana* individuals (weight 309.3 ± 137.1 g, length 138.2 ± 26.2 mm, mean ± SD) were placed in six replicate chambers (one individual per chamber, half-buried into the substrate in their natural position), individuals of *U. tumidus* (weight 49.9 ± 7.8 g, length 72.8 ± 4.1 mm, mean ± SD) were placed in another six chambers, and the six remaining units were retained without mussels as a control. Thirty minutes after the placement of mussels, when it was confirmed that all tested individuals had their siphons extended as a sign of activity, the experiment began by measuring the actual values of water pH, electrolytic conductivity, temperature, O_2 and turbidity in all 18 experimental chambers on site using a Multi 3420 multiparameter analyzer and TURB 355 IR turbidimeter (WTW, Germany). Measurements were repeated after 60 min and then 6, 12, 24, 48, 72 and 198 h after the start of the experiment (Fig. 1). It was ensured that the mean (± SD) water pH (7.52 ± 0.21), electrolytic conductivity (258.6 ± 5.4 $\mu\text{S cm}^{-1}$), temperature (18.61 ± 0.49 °C) and dissolved O_2 concentration (8.69 ± 0.15 mg L^{-1}) remained stable during the experiment and did not differ among experimental treatments.

Turbidity measurements (NTU) were calibrated against the dry mass of the seston content before and during the experiment (24 calibration measurements in total) by filtration on glass fiber filters (flushed with deionized water, precombusted, preweighed, 0.7 μm pore size AP-40, Millipore, Merck, Ireland). We dried the filters at 105 °C for 6 h, cooled them in a desiccator for 35 min, weighed them (2 times to verify a constant weight) and then combusted them at 550 °C for 1 h, cooled them in a desiccator for 35 min, and reweighed them (2 times to verify a constant weight) to determine the total dry mass of the seston and organic matter content. The method blanks, processed in the same way as the experimental samples but flushed with deionized water instead of seston samples, represented 10% of the total number of samples. No significant changes were detected in the initial and final weights of the blanks. Mussels that had been used for the experiment were briefly wiped, and their live weight was recorded after the end of experiment; thus, all results regarding mussel body mass are given as the wet total mass (WTM, shell and soft tissue).

The decrease in seston concentration during the first 60 min of the experiment was used for the calculation of filtration activity parameters. The mean value of seston loss recorded in the control chambers (without mussels) was subtracted from the data before the analysis. The results for seston-removal activity are given as the retention rate of suspended matter: seston dry mass (DM) in mg removed from the water per gram of the total mussel wet mass during 1 h of filtration (expressed in $\text{mg DM g}^{-1} \text{WTM h}^{-1}$). We also calculated the clearance rate of the water volume: theoretical volume of water in milliliters cleared per gram of the total mussel wet mass during 1 h of filtration (expressed in $\text{mL g}^{-1} \text{WTM h}^{-1}$). Filtration activity parameters were compared between species using Kruskal–Wallis ANOVA tests.

To evaluate the levels of suspended solids to which the surrounding water can be effectively cleared by the filtration activity of the two mussel species, we compared the levels of suspended solids at different time points during the experiment using ANOVA followed by Tukey's HSD post hoc test with adjusted *p* values using the Bonferroni method.

The filtration activity of each individual was quantified visually during the experiment (with mussels with extended and open siphons being considered

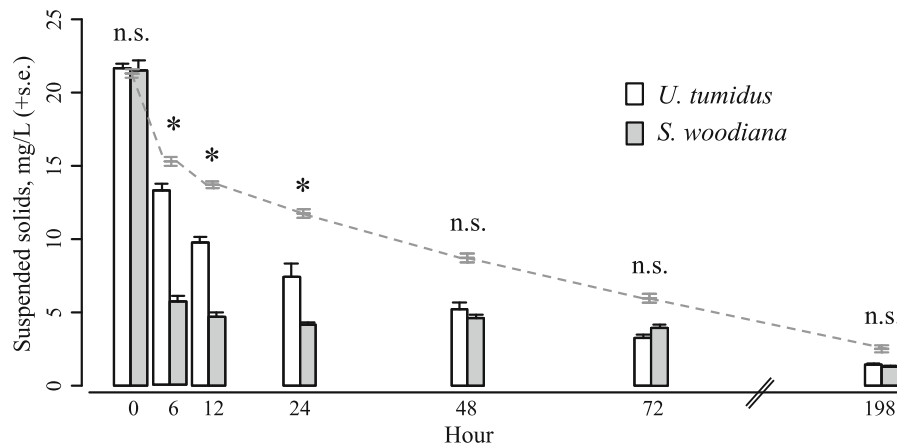


Fig. 1 Temporal progression of seston removal by invasive (*S. woodiana*) and native (*U. tumidus*) freshwater mussel species revealed in the clearance rate experiment. Bars represent mean (+ SE, $n = 6$ per species) values of total suspended solids (TSS) recorded at respective time points. The background rate

of seston decline is indicated by the dashed line (TSS in control chambers \pm SE, $n = 6$). TSS significantly differed from control chambers at all time points sampled after the start of the experiment, *indicates significant ($p < 0.05$) differences between species (Tukey's HSD test with Bonferroni correction)

active), and the proportions of active and non-active individuals of both species were compared between the initial (0–24 h) and advanced (48–198 h) phases of the experiment with the use of Fisher's exact test. All analyses were performed using the R 3.3.2 software package (R Development Core Team 2016).

Results and discussion

Retention rates of seston ranged between 0.09 and 0.38 mg DM g^{-1} WTM h^{-1} (mean: 0.21) for *S. woodiana* and between 0.02 and 0.68 mg DM g^{-1} WTM h^{-1} (mean: 0.33) for *U. tumidus*. Clearance rates ranged between 3.9 and 15.0 mL g^{-1} WTM h^{-1} (mean: 9.3) for *S. woodiana* and between 0.9 and 29.0 mL g^{-1} WTM h^{-1} (mean: 14.3) for *U. tumidus*. There were no significant differences in the retention or clearance rates between the invasive and native mussel species (Kruskal–Wallis ANOVA, Chi squared = 0.64, $df = 1$, $p = 0.43$), and both the retention and clearance rates of *S. woodiana* correspond to the values typical for European unionids (Pusch et al. 2001).

The calculated clearance rates revealed that the theoretical amount of water filtered by an individual adult *S. woodiana* mussel ranged between 26.9 and 85.7 L per day (58.3 ± 20.8 , mean \pm SD). Because

the maximal population density of *S. woodiana* usually reaches a few individuals per m^2 (biomass 2000–3000 $g m^{-2}$) in both lotic and lentic habitats, the total volume of filtered water by a *S. woodiana* population can be expected to reach several hundred $L m^{-2}$ daily. However, the population biomass of *S. woodiana* can reach up to 27,000 $g m^{-2}$ at some sites (Kraszewski and Zdanowski 2007), corresponding to the total amount of filtered water being more than 6000 $L m^{-2}$ daily in these cases.

In terms of the temporal progression of water clearance during the experiment, both species significantly decreased the seston levels in comparison with the control at all time points sampled after the start of the experiment (Tukey's HSD test, all $p < 0.05$). There was a steeper decline in seston concentration in *S. woodiana* chambers at the beginning of the experiment (Fig. 1), which can be attributed to the higher mass of *S. woodiana* individuals. As a result, the seston concentrations at 6, 12, and 24 h differed markedly between the species (Tukey's HSD test, all $p < 0.05$). Thereafter, the level of suspended solids stabilized at approximately 5 $mg L^{-1}$, and there was no difference in seston concentrations between the species from 48 h onward. The further reduction in seston levels between 48 and 198 h in all treatments can be attributed to sedimentation and the natural development of the periphyton communities, as

indicated by the comparable rate of seston decrease in the control group.

The quantification of filtration activity revealed that *U. tumidus* individuals were filtering at 95.8% of controls during the initial phase, but only 50.0% filtration activity was recorded during the advanced phase, and this difference was statistically significant (Fisher's exact test, $p < 0.001$). In contrast, there was no significant difference in filtration by *S. woodiana* individuals between the initial (91.7% filtering) and advanced (77.8% filtering) phases of the experiment (Fisher's exact test, $p = 0.38$). This result indicates that the seston concentration decreased to a level that influenced the filter-feeding activity of native *U. tumidus* but that invasive *S. woodiana* was less affected and did not change its filtration regime.

Overall, these results indicate potentially strong and diverse effects of *S. woodiana* filter-feeding activity, which should be studied using more detailed approaches, as filtration rates vary according to seston composition and seasonal factors (Kim et al. 2011; Marescaux et al. 2016). Our experimental approach is limited by the use of small-scale individual mesocosms with standardized conditions and did not address the effects of intra-specific interactions, different flow conditions, daily temperature changes or other potentially influential factors. Also, because the feeding and filtration activity of freshwater bivalves can be selective towards specific particle sizes or taxonomic groups (Lopes-Lima et al. 2014), the role of selective filtration in feeding interactions between *S. woodiana* and native unionids should be quantified in future works.

Additionally, our data indicate a need for more detailed quantification of nutrient assimilation, excretion and biodeposition rates, which would enable the inclusion of *S. woodiana* filtration activity into nutrient budget models (Cyr et al. 2016) and a better understanding of its role in invaded aquatic habitats.

It is important to note that potential filter-feeding interactions between the invasive *S. woodiana* and native unionids are not restricted to potential food competition and that the effects should not necessarily be presumed to always be negative for native species. Elevated seston concentrations are a widespread stressor in aquatic ecosystems and have been documented to be a direct cause of freshwater mussel reproductive failure (Gascho Landis et al. 2013). Because *S. woodiana* is tolerant of a wide range of

environmental conditions (Douda et al. 2012), including polluted and eutrophized water, it cannot be excluded that its filter-feeding activity can also have positive effects by facilitating the removal of excess suspended solids that can otherwise be highly problematic for native mussel reproduction (Gascho Landis et al. 2013). These potential interactions should be addressed in future studies, as positive facilitation caused by invasive species is a frequently overlooked phenomenon (Rodriguez 2006).

In conclusion, our results demonstrate that *S. woodiana* is able to reduce seston loads to levels comparable to those by control native freshwater mussel species (*Unio tumidus*) without detectable changes in its filtration regime. The current invasional spread of this species to areas inhabited by endangered freshwater mussels calls for more careful consideration of potential filter-feeding interactions with native mussels, which should be studied with respect to available food levels and long-term nutritional needs of particular species. Filtration activity effects should be included in the impact assessment of *S. woodiana* protocols and reflected in management strategies in its invaded range.

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