Periphyton growth on allochthonous input in streams may lead to higher individual growth rates of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*)

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ABSTRACT

The aquatic, invasive New Zealand mud snail (*Potamopyrgus antipodarum*) exploits a variety of food sources. Here we examine the change in growth of snails that fed on periphyton colonizing leaf litter, wood, rock, and a control. Juveniles were grown in the lab on *Spirulina* algae powder (control) or periphyton grown on rock, leaf litter, or wood. Length was measured at the beginning of the experiment and after eight weeks. Snails grown on leaf litter increased in length more than twice as much as the control and the snails in the rock treatment, and the snails grown on wood showed an increase in length more than twice as much as snails in the rock treatment. This suggests that allochthonous material may contribute to a more nutritious food source for New Zealand mud snails and possibly aid in their invasion success.

The diet of an introduced species can be an important factor in its invasiveness (Courant *et al.*, 2017). An invader that can exploit a broad array of food sources may experience different levels of success depending on the food source. The New Zealand mud snail (NZMS), *Potamopyrgus antipodarum* (Gray 1853) is a generalist feeder and a world-wide invader found in various freshwater habitats in at least 40 countries and six different continents (Geist *et al.*, 2022, Alonso *et al.*, 2023). In its native range in New Zealand, the snail exists in mixed populations of sexual and asexual individuals, but in invasive populations, NZMS reproduce asexually by parthenogenesis resulting in nearly all female populations (Proctor *et al.*, 2007; Dybdahl and Kane, 2005). The high reproductive rate of NZMS can result in extremely high secondary production (Hall *et al.*, 2006) resulting in population densities in some locations exceeding 500,000 m^{-2} (Geist *et al.*, 2022). The success of the NZMS has been attributed to several factors including its high reproductive rate (Geist *et al.*, 2022), parthenogenetic reproduction (Geist *et al.*, 2022), predator avoidance mechanisms (Levri and Clark, 2015; Levri *et al.*, 2017b), and tolerance of a wide variety of ecological conditions (Proctor *et al.*, 2007; Alonso and Castro-Díez, 2008, 2012; Geist *et al.*, 2022).

NZMS have been found to have numerous negative effects on aquatic ecosystems. These include disproportionately consuming primary production, the domination of the nitrogen cycle, outcompeting native species, and even resulting in reduced condition to trout that consumed them (Vinson and Baker, 2008; reviewed in Proctor *et al.*, 2007; Alonso and Castro-Díez, 2008, 2012; Geist *et al.*, 2022; Alonso *et al.*, 2023). These effects have resulted in it being considered a substantial threat to many areas (Proctor *et al.,* 2007).

NZMS are capable of surviving on a wide variety of food sources including detritus, algae, and periphyton growing on multiple sources including rocks, leaf litter, and submerged aquatic vegetation (Dorgelo, 1991; Dorgelo and Leonard, 2001; Liess and Lange, 2011). This variation allows the snail to exploit numerous habitats including vegetation, woody debris, leaf litter, mud, silt, and rocky areas in both lakes and streams (Proctor *et al.*, 2007). NZMS utilize food resources in a way that helps them to outcompete native species (Riley and Dybdahl, 2015) and limit the growth of their competitors (Riley *et al.,* 2008). By grazing the snail can also alter the periphyton assemblage in streams to favor diatoms which can increase rates of nitrogen fixation (Arango *et al.,* 2009), and the snail appears to be a more effective grazer than some native

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Key words: invasive, gastropod, allochthonous inputs, periphyton, streams.

Citation: Ghannam S, Levri EP. Periphyton growth on allochthonous input in streams may lead to higher individual growth rates of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*). *J. Limnol. 2023;82:2092.*

Edited by: Fabrizio Stefani, *CNR-IRSA Water Research Institute, Brugherio, Italy.*

Received: 9 August 2022.
Accepted: 25 May 2023.

Licensee PAGEPress, Italy
J. Limnol., 2023; 82:2092
DOI: 10.4081/jlimnol.2023.2092

species (Hansen *et al.,* 2016) resulting in a greater impact on the periphyton community (Krist and Charles 2012). The diet of the NZMS has been demonstrated to influence its individual growth rate with diets of epilithic periphyton resulting in higher growth rates than detritus-based diets (Bilka and Levri, 2013; Levri *et al.*, 2017a). However, periphyton communities colonize both autochthonous (materials found in the stream such as rocks and sediment) and allochthonous material (material found in the stream that came from outside sources such as leaf litter and woody debris). The periphyton communities could differ depending on the substrate which could in turn result in food sources for the snails of different nutritional and/or energetic value. Here we compare the growth rates of juvenile NZMS that fed upon periphyton colonizing on rock, leaf litter, and wood.

We hand collected New Zealand mud snails on May 28th, 2021, from Spring Creek, Centre County, PA at 40.8507; -77.8224. We placed the snails in four 1-liter plastic containers filled with stream water and fed them *Spirulina* algae powder *ad libitum*. We changed the water three times per week using water taken from Spring Creek on the Penn State Altoona campus.

We used four different food treatments in the experiment. The control was a standard diet of *Spirulina* powder which was 1 ml of a solution of approximately 0.5 g of *Spirulina* powder suspended in 50 mL of water. The remaining treatments were periphyton grown on rock, wood, or Elm (*Ulmus americana*) leaf litter. To provide periphyton covered rocks for the experiment, we added rocks and water from Spring Run stream on the Penn State Altoona campus to two plastic 10-liter containers. The rocks were maintained for four weeks by adding stream water to the containers to maintain a constant water level and keeping the rocks in the same orientation, remaining the same side up at all times. We placed the rock containers on a windowsill to allow for exposure to sunlight in order to allow for periphyton growth. We also collected wood and elm leaf litter (whole leaves) from Spring Run. Elm leaves were selected because they were locally abundant, and we had observed NZMS foraging on them at other locations. They were rinsed to remove any animals from them. The wood was cut into small disc-shaped pieces using a jigsaw, and the leaf litter was cut into pieces of approximately the same surface area as the wood discs. The leaf litter and the wood pieces were placed into 10-liter plastic containers filled with stream water on the windowsill to allow for periphyton growth for 4 weeks. We rotated the 10-liter plastic containers every other day to attempt to control the amount of light each received. We measured the diameters of the wood disc-shaped pieces, elm leaf pieces, and rocks using calipers. The average diameter of the wood was 28.5 mm (standard error = 0.41 mm). The average diameter of the rocks was 31.3 mm (standard error = 0.63 mm), and the average diameter of the leaves was 28.2 mm (standard error = 0.99 mm).

We began the experiment on September 24th, 2021. For all of the non-*Spirulina* treatments, we added the rocks, wood, and leaf litter to 200 mL clear plastic cups filled with 150 ml of stream water. The rocks, leaf litter and wood were placed in the same orientation (same side up) as they were in the larger container. We used 25 cups in each treatment with one snail per cup.

We isolated a total of 100 juvenile snails (offspring of the snails originally collected), between 0.5 mm and 1.0 mm in length, with 25 of each assigned to each treatment. We then measured each snail to the nearest 0.1 mm using an ocular micrometer in a dissecting microscope and then placed one snail into each cup. We used an analysis of variance to test that the mean initial size of snail was not different between treatments. Each treatment was placed on a separate tray near the window to allow for exposure to sunlight. We rotated the trays three times per week to attempt to control for amount of sunlight and position. We monitored the water level in each cup daily throughout the experiment with water being added as needed to maintain 150 ml. In the control treatment, we added 1 ml of water mixed with *Spirulina* powder three days per week. No additional food was added to the remaining treatments. We provided oxygen using aeration for five seconds per cup three times per week for all treatments, and we maintained the experiment for 59 days before the snails were removed from the cups and measured for length a second time. The length of approximately 59 days was chosen based on previous experiments where that amount of time was found to be sufficient for the snails to at least double in size while they are juveniles (Levri *et al.*, 2017a; Levri *et al.,* 2020). We calculated the change in length of each snail in millimeters, and we used SPSS statistical software to perform a univariate analysis of variance to test for the effects of treatment on the log of change in length. The data were log-transformed to meet the homogeneity of variances assumption of the statistical test which was tested using a Levene's test of equality of error variances. We then performed a Tukey HSD *post-hoc* test to compare the means between treatments with p-values correcting for the number of tests. At the conclusion of the experiment, we were not able to find some of the snails in the cups, and, in some cups, we found empty shells. It is possible that some snails crawled out of the cups (this is rare, but it does happen), and other snails that were not found could have died early in the experiment at a time when the shells were very small and brittle and may have been crushed so as not to be seen. 14 out of 25 snails survived in the control, 15/25 survived in the leaf treatment, 17/25 survived in the rock, and 17/25 survived in the wood treatment. All of the non-surviving snails were removed from the analysis.

We found a significant effect of treatment on change in length (F=9.89, df=3, p<0.001) (Fig. 1). Pairwise contrasts indicated that the leaf treatment resulted in significantly greater growth compared to control and rock treatments (Fig. 1, Tab. 1). The wood treatment grew significantly larger than the rock treatment but not the control. The wood and leaf treatments did not differ in mean length increase, and the control and rock treatments also did not differ in length increase (Fig. 1, Tab. 1).

NZMS can be found on a variety of freshwater substrates (Proctor *et al.*, 2007). Each of these substrates have the potential to accumulate periphyton biofilms which the snails seem to readily consume. The quality of food can be assessed by determining the growth rate of individuals, and the food quality can influence invasive species (Dorgelo and Leonards, 2001). NZMS feed on different food sources, including algae, bacteria, detritus, and fungi (Liess and Lange, 2011). Because it appears that the snails seem to show preference in nature for different substrates, we compared their growth rates when feeding on biofilms from three different common substrates in their invaded range in the eastern US, rock, wood, and leaf litter.

In this experiment, we found that feeding on biofilms associated with allochthonous input of wood or leaf litter resulted in greater growth of NZMS than periphyton grown on rock, and snails grown on leaf litter grew more than snails on the control diet. This suggests that allochthonous substrates may provide a better biofilm diet than periphyton grown on rock surfaces. Previous work has demonstrated that NZMS grow at a faster rate when consuming periphyton on rock compared to detritus or a *Spirulina* powder control (Bilka and Levri, 2013; Levri *et al.*, 2017a). In this experiment, we did not find a difference between the control and the periphyton on rock treatment. It is not clear why that did not occur. It is possible that the amount of *Spirulina* used in this experiment was greater than in the previous experiments. In those experiments as well as this one, more *Spirulina* was used than the snails would be able to consume. It is also possible that the amount or quality of periphyton was lower in the present experiment. However, we did notice periphyton communities on the rocks. The wood treatment was also not significantly different from the control; however, the trend was in the direction of periphyton on wood resulting in a greater growth rate than the control. It is possible that a larger sample size would have resulted in a significant difference, or the quality and amount of *Spirulina* could have resulted in similar growth rates to the wood or rock treatments.

The elm leaf litter treatment resulted in significantly greater snail growth than rock or the control. Both the leaf and wood treatments resulted in greater growth than the rock treatment. This suggests that leaf and wood allochthonous input may provide additional energy or nutrients to the snails in the form of the periphyton communities that grow on them, or the snails may be able to consume some of the leaf or wood debris. Recent work from Bovee and Tiegs (2023) suggests that NZMS may be forage directly on leaf litter. This could make leaf litter an especially profitable food source as the snails would be able to consume both the leaves and the periphyton community. The difference in food on the leaf and wood compared to the rock would likely be the presence of decomposers (bacteria and fungi) that would not be found on the rock in this case. The rocks here were cultured in the lab so there would be little if any allochthonous organic material settling on them. Thus, the bacterial and fungal compositions of the diet on the leaves and wood may lead to greater growth of the snails. If it is the decomposition of the allochthonous material feeding the periphyton communities that is causing the increased growth, then one would expect that materials that degrade faster should result in greater growth rates. This could be tested in future studies by comparing allochthonous materials that degrade at different rates such as different species of leaf litter. The

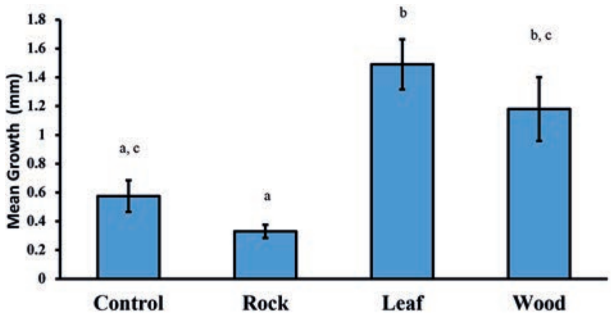

Fig. 1. The effect of the substrate type on the mean total growth in millimeters. The error bars are standard errors. Similar letters above the bars indicate that the groups are not statistically significantly different from each other in pairwise contrasts.

Tab. 1. Results from a Tukey HSD post-hoc test to compare means of change in length between each treatment. P-values in bold indicate statistical significance.

Comparison	Mean difference	p
Control *vs* rock	0.168	0.617
Control *vs* wood	-0.306	0.140
Control *vs* leaf	-0.508	**0.004**
Rock *vs* wood	-0.477	**0.004**
Rock *vs* leaf	-0.676	**<0.001**
Leaf *vs* wood	0.202	0.462

results presented here suggest that aquatic systems, such as headwater streams or other forested waterbodies that provide relatively more organic allochthonous material, may better support NZMS than other sources.

ACKNOWLEDGEMENTS

We would like to thank Mark Oswalt, Kassie Evans, Kalie Wallace, and Kara Wright for their help in the lab. We would also like to thank Maureen Levri for comments on previous versions of this manuscript. This work was funded by grants from Penn State Altoona and supported by the Schreyer's Honors Program at Penn State University.

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