

INTERACTIONS BETWEEN THE INVASIVE NEW ZEALAND MUDSNAIL (*POTAMOPYRGUS ANTIPODARUM*) AND A NATIVE SNAIL (*FOSSARIA BAKERILYMNAEA BULIMOIDES* GROUP) IN THE GREATER YELLOWSTONE

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✦ ABSTRACT

Understanding invasive species impacts is critical to determining how an ecosystem may function after an introduction. Invasive species can alter the structure and function of ecosystems, reduce biological diversity, and alter communities through predation, facilitation and competition. In the past 30 years, the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) has established in areas of conservation concern in the American West including Yellowstone National Park. To develop a greater understanding of the impact of *P. antipodarum* on the native co-occurring snail, *Fossaria* (*Bakerilymnaea*) *bulimoides* group, we conducted two experiments to assess the interactions occurring between these snails. We found that *F. bulimoides* growth was reduced by all interactors, but especially by *P. antipodarum*. In addition, growth of *F. bulimoides* was much more affected by high biomass of snails than *P. antipodarum*. *P. antipodarum* grew more in the presence of interactors and their growth was facilitated by the presence of the native snail *F. bulimoides*.

✦ INTRODUCTION

Invasive species can be important drivers of change in ecosystems by altering structure and function and by promoting loss of biological diversity (Wilcove et al. 1998, Dukes and Mooney 2004, Chapin et al. 2000, Baskin 1998). Invasive species also change invaded communities through predation

(reviewed in Davis 2009; Lockwood et al. 2007), facilitation (Bruno et al. 2005) and competitive interactions (reviewed in Bruno et al. 2005, Davis

2009, Lockwood et al. 2007). Among invasive and native herbivores, experimental manipulations facilitate examination of the types of interactions that can occur between invasive and native species. Hence, experiments can provide insight into the mechanisms that may underlie the success of the invader (Byers 2000, Riley et al. 2008, Cross and Benke 2002).

The invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) has gained attention from government agencies and scientists because of the snail's ability to reach astounding numbers in some sites in short periods of time (Hall et al. 2003, Levri et al. 2007). *P. antipodarum* possess several characteristics that may have facilitated their success as invaders. First, all invasive *P. antipodarum* are asexual parthenogens, a trait that contributes to rapid population growth (Wallace 1992, Schreiber et al. 1998) and facilitates establishment: the introduction of an individual snail has the potential to initiate a new population. Second, the presence of opercula allow mud snails to survive periods of desiccation, which may increase their probability of spread by humans or other animals. Third, *P. antipodarum* was introduced to the western U.S. without coevolved parasites or predators to help regulate population size as they do in the native range of New Zealand.

Potamopyrgus antipodarum is an herbivorous snail that consumes plant and animal detritus, epiphytic and periphytic algae, including diatoms and green algae (Haynes and Taylor 1984). These invasive snails have been shown to compete with native herbivores including other snail species, and potentially a variety of other macroinvertebrates (Fenchel and Kofoed 1976; Riley et al. 2008; Cada 2004; Kerans et al. 2005). Additionally, when *P. antipodarum* are abundant, they may reduce resources for other grazing macroinvertebrates. For example, Hall and colleagues (2003) found that *P. antipodarum* consumed 75% of gross primary productivity in a stream in the western U.S. Also, if *P. antipodarum* reduce growth and reproduction of native invertebrates through competition, food resources for animals higher in the food web, such as fish, may be limited. Negative effects on native herbivores are also expected when *P. antipodarum* are abundant because snails can be strong interactors by linking primary producers with secondary consumers in stream ecosystems (Hawkins and Furnish 1987). However, effects of *P. antipodarum* on native species are not always negative (Schreiber et al. 2002, Brenneis et al. 2010, Brenneis et al. 2011). Therefore, it is critical to conduct experiments that permit us to assess whether *P. antipodarum* is likely competing, facilitating, or having no effect on native species.

We conducted two experiments to determine whether *P. antipodarum* interacts with a native snail from an invaded ecosystem in the western U.S. Specifically, we asked whether competition or facilitation was occurring under: 1) an ambient low biomass of the native and invasive species, and 2) under identical higher biomass that represented the total ambient biomass of both snail species in the source stream.

◆ METHODS

Study system

The New Zealand mudsnail (*Potamopyrgus antipodarum*) is native to New Zealand but has become a worldwide invader. In North America, the snail was first discovered in the Snake River, Idaho in 1987 (Bowler, 1991). In most of the western United States, only one clone of the snail is present (Dybdahl and Kane 2005). In the western U.S., the snail has spread to areas of conservation concern including the Madison and Yellowstone River basins in the Greater Yellowstone ecosystem. We chose the native snail, *Fossaria (Bakerilymnaea) bulimoides* group, because the two snails occur in the same habitats and

consume similar resources. We conducted two experiments to determine the type of interactions occurring between these two snails. For our experiments, we measured ambient snail densities and collected snails from Polecat Creek, a small tributary of the Snake River with geothermal inputs and a high occurrence of the invasive snail (20,000-500,000 snails/m²; Hall et al. 2006). This stream is located just south of Yellowstone National Park in the John D. Rockefeller National Parkway in Northwest Wyoming. Because *P. antipodarum* occur at a high biomass in this stream, if interactions between the native and invasive snail occur, they should be evident at this biomass.

Experimental design

We conducted two laboratory experiments to determine how snail growth was affected by biomass level (low vs. high) and identity of interactors (heterospecifics vs. conspecifics). Our first experiment examined the type of interaction that was occurring (competition, facilitation, none) between *P. antipodarum* and *F. bulimoides* under low ambient biomass of each snail species. We used different but realistic levels of low ambient biomass of each species to assess interactions at the actual biomass at which each species occurs. Because *P. antipodarum* is invasive they occur at much higher ambient biomass than the native. Hence, our second experiment examined how snail growth was affected when the snails interacted at an equal, higher biomass of both species. This experiment allowed us to assess whether one snail species had a competitive advantage over the other when interacting at the same biomass.

To assess low ambient snail biomass of each species (for Experiment 1) and total ambient snail biomass (for Experiment 2), we haphazardly collected 10 substrate samples across the width of Polecat creek in June 2009. We used a 6" diameter stove pipe corer to collect snails. We separated organic matter and invertebrates from rocks and sediment by elutriating the sample and collecting on a 250 μm sieve following Hall et al. (2006). The samples were preserved in 70% ethanol and processed at the University of Wyoming. *P. antipodarum* were measured with a dissecting microscope using an ocular micrometer and *F. bulimoides* were measured using calipers. We used mass length regressions (Hall et al. 2006, Riley, unpublished data) to determine the ambient biomass (mg/m²) of each snail species in each sample. We used the average of all ten stove pipe samples to calculate the total ambient snail biomass (Experiment

2) and the average of the lowest five samples to calculate the low ambient snail biomass for each species (Experiment 1).

For both laboratory experiments we collected *P. antipodarum* and *F. bulimoides* at Polecat Creek in late June and July 2009. We collected *P. antipodarum* by sweeping kick nets through beds of algae and sorted juvenile targets and adult interactors using sieves. Juvenile snails (average size 2.18 mm) fell through the larger sieve (~2.5 mm) but stayed above the 1 mm sieve. Adult interactors (average size 3.7 mm) stayed above the larger sieve. We collected *F. bulimoides* by hand picking snails off of rocks and the stream bank and we used calipers to select the desired size class. To maximize the number of interactors in the experiments, we used juvenile *F. bulimoides* for both targets and interactors. Because *F. bulimoides* can grow to a much larger adult size than *P. antipodarum*, using juveniles allowed us to have many more individuals for an equivalent biomass than if we had used larger adults.

To determine the number of snails needed in each experimental chamber, we scaled the total ambient snail biomass and the low ambient biomass down to the area of periphyton-covered unglazed tiles (1 tile = 0.00516 m²) that we used in each experiment (Experiment 1: three tiles, Experiment 2: two tiles). Periphyton-covered tiles were the source of food during the experiments. We only measured growth of “target”, juvenile snails. *P. antipodarum* targets had an average shell length of 2.18 mm for both experiments, and *F. bulimoides* targets were 2.24 mm and 4 mm in shell length for experiments 1 and 2 respectively. In each chamber there were also “interactors”, conspecifics or heterospecifics, depending on the treatment.

Both experiments were conducted at the University of Wyoming in 2.4-l aquaria with constantly oxygenated recirculating, filtered water. The aquaria were housed in a room with controlled light (12:12-h light:dark cycle) and temperature (18 C°), which are similar to mid-summer day lengths and temperatures in Polecat Creek. We used full spectrum lights to achieve low ambient light levels from Polecat Creek (the brightest light levels that we could achieve in the aquaria). Lights were placed directly over the experimental aquaria to maintain adequate light levels for periphyton growth.

To colonize tiles with periphyton, we placed unglazed tiles in Polecat creek and allowed periphyton to grow for three weeks prior to the experiments. The tiles were placed on platforms in

the stream, which prevented grazing by benthic invertebrates (Lamberti and Feminella 2007). We transported the tiles back to the University of Wyoming the same day that they were removed from the stream. Eight triplets and pairs of tiles (Experiments 1 and 2 respectively) with varying degrees of periphyton growth were scrubbed to measure initial levels of chlorophyll *a* concentration and ash free dry mass (AFDM). Chlorophyll *a* was measured using fluorometry and AFDM was measured by filtering the remaining slurry onto filter paper, drying at 105°C for 24 hours and weighing the sample following methods from Steinman et al. (2006). Although tiles varied somewhat in the amount of periphyton, we attempted to control for this by pairing tiles with more and less periphyton.

Experiment 1

To assess the type of interactions that occurred between the invasive *P. antipodarum* and the native snail *F. bulimoides*, we used an experiment with asymmetrical controls and a fixed factorial design (Underwood 1997). Each target species experienced intraspecific and interspecific interactions with two levels of biomass (low and high). A control was also included in the experiment for each species and contained a low biomass of one snail species. The four treatments and controls were independently replicated four times for each target species. In this experiment, low target biomass was the low ambient biomass of either *P. antipodarum* or *F. bulimoides* (1P: 1227.18 mg/m² or 1F: 279.69 mg/m²) in Polecat Creek (Table 1). The biomass of interactors was 1P or 1F for the low and 2P or 2F for the high biomass treatments (Table 1). For each replicate, snails were placed in an aquarium with three periphyton-colonized tiles as a food source and allowed to grow for three weeks. After three weeks, all animals were removed from each replicate and preserved in 70% ethanol. We measured the shell length of all target individuals (*P. antipodarum* under the dissecting microscope using an ocular micrometer and *F. bulimoides* with calipers). We omitted all animals that died during the experiment from the analysis. Additionally, the remaining periphyton on the tiles was scrubbed and measured for AFDM and chlorophyll *a* using the same methods described above.

Experiment 2

In contrast to the first experiment, in the second experiment the two snail species (*F. bulimoides* and *P. antipodarum*) interacted at a higher, identical biomass, the mean total ambient

snail biomass found in Polecat creek in June 2009 (6666.67 mg/m²). Similar to Experiment 1, we measured the growth of each target species in

interspecific and intraspecific interactions and at low and high biomass (Riley et al. 2008). In Experiment 2, low target biomass was half (.5) of the total

Table 1. Experimental design by Underwood (1997) to determine whether competition occurs between *F. bulimoides* and *P. antipodarum*. “F” represents the low ambient biomass of the native snail *F. bulimoides* (279.69 mg/m²) and “P” represents the low ambient biomass of the invasive snail *P. antipodarum* (1227.18 mg/m²). In the experiment, biomass was scaled to the area of the three tiles (.0074 m²) in each aquarium.

Target Species	Biomass treatment	Interaction type	Target biomass	Native biomass	Invasive biomass
<i>F. bulimoides</i>	Control (1F)	control	1F	-	-
<i>F. bulimoides</i>	Low (2F)	Intraspecific	1F	1F	-
<i>F. bulimoides</i>	High (3F)	Intraspecific	1F	2F	-
<i>F. bulimoides</i>	Low (1F+1P)	Interspecific	1F	-	1P
<i>F. bulimoides</i>	High (1F+2P)	Interspecific	1F	-	2P
<i>P. antipodarum</i>	Control (1P)	control	1P	-	-
<i>P. antipodarum</i>	Low (2P)	Intraspecific	1P	-	1P
<i>P. antipodarum</i>	High (3P)	Intraspecific	1P	-	2P
<i>P. antipodarum</i>	Low (1P+1F)	Interspecific	1P	1F	-
<i>P. antipodarum</i>	High (1P+2F)	Interspecific	1P	2F	-

Table 2. Experimental design used to measure interactions at equal biomass between two snail species *F. bulimoides* and *P. antipodarum* (Riley et al. 2009). In this design, “x” is the mean total ambient snail biomass (6666.67 mg/m²) and includes contributions from both snail taxa. Biomass for this experiment was scaled to the area of two tiles (0.00516 m²) in each aquarium.

Target Species	Biomass treatment	Interaction type	Target biomass	Native biomass	Invasive biomass
Control (no snails)	-	-	-	-	-
<i>F. bulimoides</i>	Low (1x)	Intraspecific	.5x	.5x	-
<i>F. bulimoides</i>	High (3x)	Intraspecific	.5x	2.5x	-
<i>F. bulimoides</i>	Low (1x)	Interspecific	.5x	-	.5x
<i>F. bulimoides</i>	High (3x)	Interspecific	.5x	-	2.5x
<i>P. antipodarum</i>	Low (1x)	Intraspecific	.5x	-	.5x
<i>P. antipodarum</i>	High (3x)	Intraspecific	.5x	-	2.5x
<i>P. antipodarum</i>	Low (1x)	Interspecific	.5x	.5x	-
<i>P. antipodarum</i>	High (3x)	Interspecific	.5x	2.5x	-

ambient biomass (x). We used this low biomass to ensure that the effects of intraspecific competition between targets were negligible. The biomass of the interactors was .5x for the low and 2.5x for the high biomass treatments (Table 2). We also included controls with tiles and no snails. Controls were used to compare the grazing effects between species by comparing levels of chlorophyll *a* and AFDM between controls and low and high intraspecific treatments. For each replicate, snails were placed in an aquarium with two periphyton-colonized tiles and were allowed to grow for three weeks.

After three weeks, all animals were removed from each replicate and preserved in 70% ethanol. We measured the shell length of all target individuals in the same manner as the previous experiment. To assess the level of algae removed by grazing in each replicate, we also scrubbed the tiles to measure chlorophyll *a* and AFDM and analyzed these metrics

of periphyton biomass following Steinman et al. (2006).

Statistical analysis

For both experiments, the response variable was biomass-specific growth rates (SGR) calculated as, $\ln(M_f/M_i)/t$, where M_f is the final mass of the snail, M_i is the initial mass and t is time (e.g. Cross and Benke 2002, Hall et al. 2006, Sterner and Elser 2002). We converted shell length to ash free dry mass using mass-length regressions (Hall et al. 2006 for *P. antipodarum* and Riley, unpublished data for *F. bulimoides*). For Experiment 1, we compared SGR with two analyses for each target species separately (Underwood 1997). First, we used a one-factor ANOVA to determine whether competition occurred by comparing all experimental treatments to the controls. Second, we excluded the controls and conducted a nested two-way ANOVA, with

interaction type, biomass level, and replicate nested within both factors.

To compare SGR of target snails in Experiment 2, we used separate two-way ANOVA's for each target species. Similarly to Experiment 1, the factors were biomass level, interaction type, and replicate nested within biomass level and interaction type. For all ANOVAs, the data were normally distributed and variances were homogeneous.

To compare grazing effects between target species and treatments in Experiment 2, we measured AFDM and chlorophyll *a* from all experimental tiles. We used a one-way ANOVA to determine whether chlorophyll *a* and AFDM differed between the ungrazed controls and the treatments. For each metric of periphyton biomass, we used a three-way ANOVA with target species, biomass level, and interaction type with replicate nested within biomass level and interaction type as factors. Because of unequal variances, we log transformed chlorophyll *a* and AFDM values. All analyses were performed using the statistical software R (R Development Core Team 2009).

◆ RESULTS

Experiment 1

To assess whether competition occurred under low ambient biomass of each species, we compared the controls to all experimental treatments combined for each target species separately. Surprisingly, we found that *P. antipodarum* were facilitated by the presence of interactors ($F = 4.1321$, $p = 0.043$; Figure 1a). In contrast and as expected, *F. bulimoides* grew significantly less in the presence of heterospecifics and conspecifics ($F = 7.1437$, $p = 0.009$; Figure 1b).

We omitted the controls from rest of the analyses. For *F. bulimoides*, we found that both interaction type and biomass level significantly

affected SGR. As expected, SGR was 34% lower under high biomass than low biomass. Surprisingly, SGR was 32% lower with *P. antipodarum* than with conspecifics (Table 3, Figure 2a). The interaction type by biomass term was not significant (Table 3) and there was no effect of replicate nested within biomass and interaction type (Table 3). Similarly to *F. bulimoides*, SGR of *P. antipodarum* was 18% lower in the high biomass than low biomass treatments (Table 2; Figure 2b). But in contrast to *F. bulimoides*, SGR of *P. antipodarum* was marginally higher with heterospecifics than with conspecifics (Table 3; Figure 2b). The interaction type by biomass term was not significant (Table 2, Figure 2a) but, replicates within each biomass and interaction type treatment differed (Table 3).

Experiment 2

In contrast to Experiment 1, in Experiment 2 snails interacted at a higher identical biomass, the mean total ambient snail biomass in Polecat Creek. SGR of *F. bulimoides* did not differ between biomass or interaction type treatments nor did replicates within each treatment differ (Table 4; Figure 3). The absence of effects resulted from negligible growth of *F. bulimoides* in this experiment (SGR (d-1) at Low biomass = 0.0029, High biomass = 0.0010).

In contrast, SGR of *P. antipodarum* was over fourteen times higher than *F. bulimoides* in the high biomass treatment (Figure 3). SGR of *P. antipodarum* was also higher at low biomass and with heterospecifics but not uniformly across biomass treatments (Table 4, Figure 3).

Chlorophyll *a* ($\mu\text{g}/\text{m}^2$) was significantly lower on tiles grazed by *F. bulimoides* ($F. bulimoides = 3412.6 \mu\text{g}/\text{m}^2$, $P. antipodarum = 5845.8 \mu\text{g}/\text{m}^2$) and was also lower in interspecific interactions. In contrast, AFDM (mg) did not differ between target species but was lower on tiles from high biomass treatments. For AFDM, there was also a significant interaction between target and biomass interaction type (Table 5).

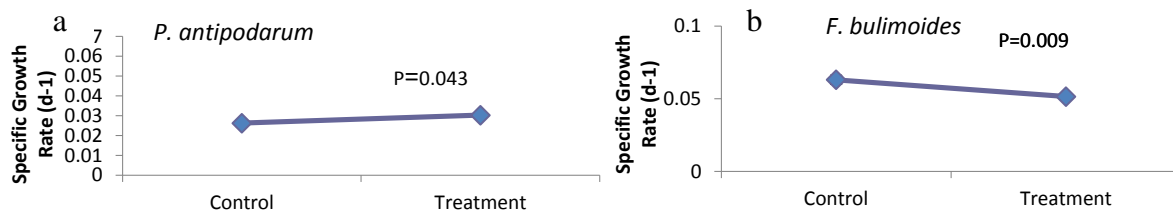


Figure 1. Specific growth rate in the control group, where snails were maintained at low ambient biomass without interactors (Table 1) compared to the treatment group, where all treatments were combined (low and high biomass and interspecific and intraspecific interactions) for a) *Potamopyrgus antipodarum*, and b) *F. bulimoides* sp..

Table 3. Results of 2-way ANOVA of SGR for each species by treatment for Experiment 1. Replicate is nested within biomass and interaction type. Stars denote statistically significant effects.

	<i>F. bulimoides</i>			<i>P. antipodarum</i>		
	Mean squares	F value	P value	Mean squares	F value	P value
Biomass	0.004	15.062	0.000*	0.001	5.531	0.019*
Interaction type	0.003	14.036	0.000*	0.001	3.634	0.058
Biomass by interaction type	0.000	1.230	0.272	0.000	0.309	0.579
Replicate	0.000	0.702	0.594	0.001	4.102	0.003*

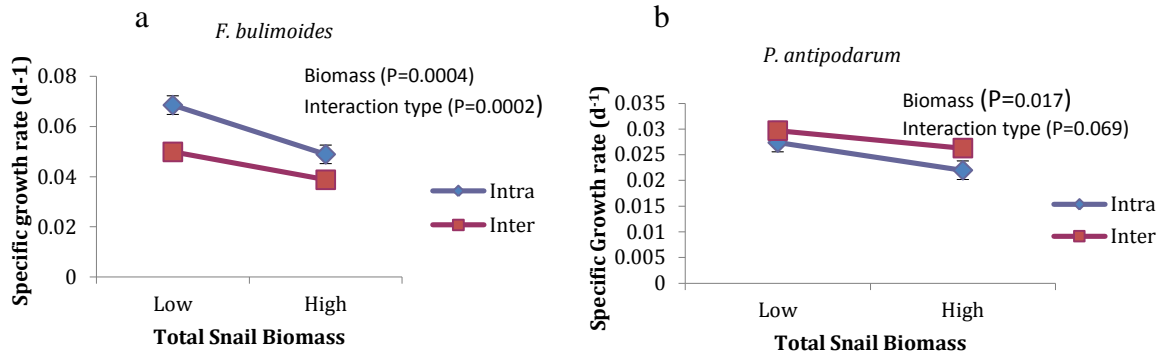


Figure 2. Specific growth rate in low and high biomass treatments in intraspecific interactions (with conspecifics) and in interspecific interactions (with heterospecific) for a) *F. bulimoides* and b) *P. antipodarum* in Experiment 1

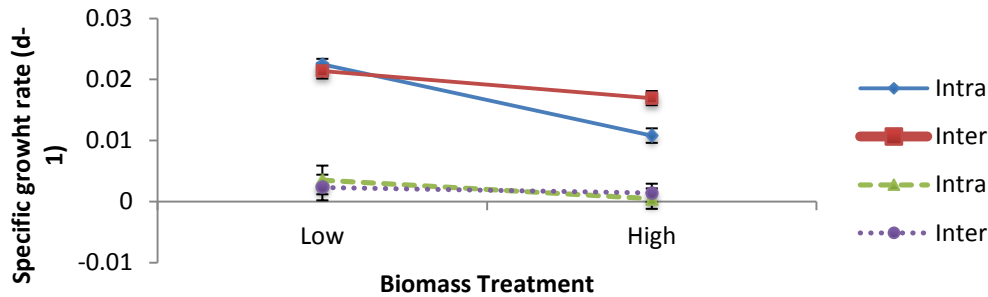


Figure 3. Specific growth rate in low and high biomass treatments in intraspecific interactions (with conspecifics) and in interspecific interactions (with heterospecific) for *F. bulimoides* (dashed lines) and *P. antipodarum* (solid lines) in Experiment 2.

Table 4. Results of 2-way ANOVAs of SGR for each species by treatment for Experiment 2. Replicate is nested within biomass and interaction type. Stars denote statistically significant effects.

	<i>F. bulimoides</i>			<i>P. antipodarum</i>		
	Mean squares	F value	P value	Mean squares	F value	P value
Biomass	0.000	1.094	0.298	0.007	63.800	1.592e-14*
Interaction type	0.000	0.049	0.826	0.001	5.576	0.019*
Biomass by interaction type	0.000	0.317	0.575	0.001	10.973	0.001*
Replicate	0.000	0.294	0.881	0.001	8.951	6.377e-7*

Table 5. Chlorophyll *a* ($\mu\text{g}/\text{m}^2$) and ash free dry mass (AFDM, mg) using a three-way ANOVA with targets, biomass level, and interaction type and replicate nested within biomass level and interaction type as factors. Stars denote statistically significant effects.

	Chlorophyll <i>a</i>			AFDM		
	Mean squares	F value	P value	Mean squares	F value	P value
Target	1.458	8.653	0.013*	0.019	0.144	0.712
Biomass	0.021	0.122	0.734	1.409	10.845	0.007*
Interaction type	1.331	7.897	0.017*	5.485	42.335	4.388e-5*
Target:biomass	0.302	1.793	0.208	0.042	0.325	0.580
Target:interaction type	0.444	2.635	0.133	2.091	16.142	0.002*
Biomass:interaction type	0.059	0.351	0.565	0.349	2.693	0.129
Target:biomass:interaction type	0.112	0.665	0.432	0.276	2.129	0.173
Target:biomass:interaction type:rep	0.245	1.456	0.276	0.242	1.864	0.167

◆ DISCUSSION

Experiment 1

As we expected, the native snail *F. bulimoides* grew less when they interacted with conspecifics or heterospecifics (treatments), than in the absence of interactors (controls). In contrast, *P. antipodarum* possessed higher growth rates in the presence of interactors (treatments) than without interactors (controls). *F. bulimoides* likely possessed lower growth in the presence of interactors because of resource limitation. However, it is not clear why *P. antipodarum* possessed higher growth in the presence of interactors.

As expected, within the treatments both species grew faster at a low biomass of interactors. However, *F. bulimoides* grew significantly more in the presences of conspecifics whereas *P. antipodarum* grew faster with heterospecifics. These results are probably driven by the unequal ambient biomass of the two species (Table 1). Because *P. antipodarum* is an invasive species, the low ambient biomass for *P. antipodarum* is over four times greater than the low ambient biomass of *F. bulimoides* in Polecat Creek. However, this result suggests that at a low ambient biomass of each species, growth rates of *F. bulimoides* are suppressed by the invasive snail. Conversely, the invasive snail *P. antipodarum* grew more in the presence of the native snail than with conspecifics, probably because conspecifics occur at a much higher biomass than *F. bulimoides*.

Experiment 2

When snails interacted at the total mean ambient biomass of both species combined, *F. bulimoides* essentially failed to grow. Growth of *P. antipodarum* was over fourteen times higher than *F. bulimoides* in the high biomass treatment and over seven times higher in the low biomass treatment. Because *F. bulimoides* exhibited such little growth, we found no effect of biomass or type of interactors on growth of *F. bulimoides*. In contrast, and as expected, *P. antipodarum* exhibited higher growth rates in the low biomass treatment and also grew more with heterospecifics than with conspecifics at a high biomass of *F. bulimoides*. This result suggests that *F. bulimoides* may facilitate the growth of *P. antipodarum*. A similar result was found in experiments with *P. antipodarum* and the native snail *Pyrgulopsis robusta* (Riley et al. 2008). Growth of *P. antipodarum* was greater with heterospecifics than with conspecifics at high biomass (Riley et al. 2008). The mechanism underlying the facilitation of *P. antipodarum* by native snails in the Greater Yellowstone Ecosystem is not known.

The results of this experiment show that when *F. bulimoides* occur at the mean ambient biomass of both species (1x in Table 2) their growth nearly ceases. This result suggests that *F. bulimoides* are much more sensitive to high biomass of other snails, either conspecifics or heterospecifics, than the invasive *P. antipodarum*. This result also implies that when there is an identical biomass of both species, the invasive *P. antipodarum* can grow 7-14 times faster than the native.

Interestingly, the analysis of chlorophyll *a* suggests that *P. antipodarum* maintained high growth rates despite consuming less periphyton than the native snail *F. bulimoides*. This result suggests that *P. antipodarum* possesses higher assimilation efficiencies for nutrients than *F. bulimoides*. There are two reasons why this result was unexpected. First, because mass-specific ingestion rates are higher for smaller animals than for larger animals (Peters 1983, Karasov and Martinez del Rio 2007), we expected consumption could be higher for *P. antipodarum* than for the much larger *F. bulimoides*. Second, other studies indicate that *P. antipodarum* is a superior grazer to many macroinvertebrates (Krist and Charles, in review) and controls periphyton abundance more than other grazers (Biggs and Lowe 1994).

◆ IMPLICATIONS

The results from both experiments indicate that *F. bulimoides* grow better at a lower biomass of conspecific and heterospecific snails. Perhaps growth of *F. bulimoides* is more sensitive to biomass than *P. antipodarum* because *F. bulimoides* have low assimilation efficiencies. If this is the case, then *F. bulimoides* may require more food and larger areas to graze to meet dietary requirements for growth and reproduction.

P. antipodarum grew more in the presence of interactors and specifically were facilitated by the presence of *F. bulimoides*. This result may have serious consequences for native snail species by increasing the success of *P. antipodarum* when *F. bulimoides* or *Pyrgulopsis robustus* (Riley et al. 2008) are common. Over time, as population sizes of *P. antipodarum* increase, our results suggest that growth rates of *F. bulimoides* will decrease. Consequent declines in the population growth rate of *F. bulimoides* may eventually lead to extirpation of this native snail species in populations where *P. antipodarum* are invasive (occur at a high biomass). Additionally, a decrease in native fauna may have negative effects at higher trophic levels, when predators do not thrive on a diet of *P. antipodarum* (Vinson and Baker, 2008). Finally, results from our experiments show the possible interactions between *P. antipodarum* and *F. bulimoides* under controlled conditions, but may not reflect what is actually occurring in Polecat Creek.

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