Title: The current distribution of the Jackson Lake spring snail and interactions with the invasive New Zealand mud snail

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Introduction

Endemic species make a unique contribution to global biodiversity. Unfortunately, only existing in one or a few locations, endemic species are particularly susceptible to extinction through any number of anthropogenic or natural disturbances. The second leading threat to global biodiversity today is the presence of invasive species (Carlton and Geller 1993, Wilcove et al 1998). Introduced into ecosystems where they have not evolved, invaders can successfully establish and threaten native biota, depending on the role they assume in a community. In addition, invasive species are one of the three leading threats to freshwater ecosystems throughout the United States and may be the most detrimental stressor to species west of the continental divide (Richter et al 1997).

The Jackson Lake spring snail (*Pyrgulopsis robusta*) may be facing extinction and has been petitioned for threatened species listing by the USFWS (Susan O'Ney, GTNP, personal communication). The Jackson Lake spring snail is a narrowly endemic prosobranch snail that occupies a spring stream within the Greater Yellowstone Ecosystem (GYE). However, the presence of the New Zealand mud snail (*Potamopyrgus antipodarum*), an invader in western U.S. rivers, may be threatening the survival of this population. The mud snail first appeared in Yellowstone National Park in 1994 (Madison River) and has now spread over 50 river miles within the GYE. In one stream (Polecat Creek) *Pyrgulopsis* has decreased in yearly samples since the invasive *Potamopyrgus* appeared (Dan Gustafson, Montana State University, personal communication) but remains abundant in a tributary of this stream. Some evidence exists, though, that the invasive mud snail is a superior competitor to the endemic spring snail in this tributary (Riley, Dybdahl and Hall, in review). In addition, the mud snail overlaps the entire known current distribution of the Jackson Lake spring snail.

The main objective of this project was to explore both the historic and current ranges of the Jackson Lake spring snail. In Part A, we examined general habitat characteristics that might provide insight into factors influencing the known current distribution in one tributary spring stream (hereafter referred to as Marmot Spring). In addition, we examined the presence of the New Zealand mud snail as a potentially limiting factor for Jackson Lake spring snail densities. Finally, we also examined the relationship among Jackson Lake spring snails and other potential native snail competitors. In Part B, we examined general habitat characteristics in the historic range of the Jackson Lake spring snail. In addition, we collected samples to look for the presence of the Jackson Lake spring snail.

Part A. Analysis of joint distribution with the New Zealand mud snail in the current range

Methods

In July of 2005, we collected eight benthic invertebrate samples from 5 sites in Marmot Spring, where distributions of *Potamopyrgus*, the New Zealand mud snail, and *Pyrgulopsis*, the Jackson Lake spring snail, overlap (Fig. 1, Table 1). Four samples at each site were collected with a surber sampler to measure snail densities on cobble substrates. The other four samples were collected with a core sampler to measure densities on vegetation. Core samples were sieved through a standard 500 micron sieve. Distance between sites was at least 100m. We preserved samples in 70% ethanol and returned to the lab for identification and enumeration of snails. These samples were compared to samples collected in July 2001, 2002 and 2003 using the same methodology. July 2003 cobble samples are not included in this report because they are currently being processed.

In July of 2005, at each of the 5 sites, we also collected 3 samples of periphyton to measure concentrations of algae and organic matter, indicative of food availability for these snails. Three samples at each site were analyzed for chlorophyll *a* content. Chlorophyll *a* represents live algae that was actively photosynthesizing at the time of collection. We also recorded temperature and substrate types for each site.

Within each year and each habitat type (macrophytes and cobbles), we performed a simple linear regression between *Potamopyrgus* densities and *Pyrgulopsis* densities. This analysis was used to determine if densities of the invasive and endemic species were positively or negatively related within each habitat. We also repeated the linear regression analysis within each year and each habitat type with two other native snails as predictor variables. We used this analysis to help understand baseline variability in community relationships across years. We would expect the relationship between *Pyrgulopsis* and other native snail species to potentially be more stable than the relationship with *Potamopyrgus* if *Potamopyrgus* is still in the process of invading and displacing species in this stream. We repeated these analyses for each year to determine if patterns were changing over time. We then used an ANOVA to examine food availability, as represented by chlorophyll *a*, across all sites and across two years. We examined the relationship between snail densities and algal food sources for one of those years, 2005, by performing a linear regression between chlorophyll *a* and snail abundance. Finally, we combined data from all years and used an ANOVA with site and year as factors to determine these effects on each snail species across all years. All statistical tests were performed on Systat 10 (SPSS 2000).

Results

General characteristics of Marmot Spring

Marmot Spring is a small, geothermal, headwater spring stream. Along the entire spring, the width does not exceed 12 meters and, in many locations, is much narrower. Water depth rarely, if ever, exceeds 0.5 meters. Substrates include cobbles, logs, macrophytes and macroalgae. Macrophytes include muskgrasses (*Chara* spp.), stoneworts (*Nitella*), *Elodea* and mosses. Cobble sizes range from pebbles to boulders, but most are smaller than 30 mm in diameter. Cobbles and macrophytes dominate the majority of this spring, and therefore were the two habitats emphasized in this study. Cobbles are prevalent in fast currents, while macrophytes dominate areas with slower flow. Riparian vegetation includes the common monkeyflower (*Mimulus guttatus*), common cow parsnip (*Heracleum sphondylium*), willow (*Salix* spp.), Columbia monkshood (*Aconitum columbianum*), reeds(*Phragmites* spp.) and spikerush (*Eleocharis* spp.).

Pyrgulopsis co-occurred with many invertebrate taxa within Marmot spring throughout the sampling periods, including three other snail species (*Physa spp., Fossaria spp.* and *Pyrgulopsis robusta*). The endemic *Pyrgulopsis* and the invasive *Potamopyrgus* are the most functionally similar and are the most closely related taxonomically (Subclass: Prosobranch, Family: Hydrobiidae). Marmot Spring and Polecat Creek comprise the entire known range of the endemic *Pyrgulopsis*. The other two native snails, *Physa* (Subclass: Pulmonate, Family: Physidae) and *Fossaria* (Subclass: Pulmonate, Family: Lymnaeidae) are found elsewhere in the GYE. All snails occupy a variety of habitats throughout Marmot Spring, including cobbles, logs, macrophytes and macroalgae (personal observation).

2001

In vegetation samples, *Pyrgulopsis* densities were positively related to *Potamopyrgus* densities (R^2 =0.415, p=0.001). On the other hand, *Pyrgulopsis* densities were negatively related to *Physa* densities (R^2 =0.198, p=0.026; Fig. 2). There was no relationship between *Fossaria* densities and *Pyrgulopsis* densities. In cobble samples, *Pyrgulopsis* densities were positively related to *Fossaria* and *Potamopyrgus* densities, but both relationships are likely driven by outliers in both data sets (R^2 =0.940, p=0.000, and R^2 =0.864, p =0.000, respectively; Fig. 3). There was no significant relationship between *Pyrgulopsis* densities and *Physa* densities.

2002

In vegetation samples, *Pyrgulopsis* densities were positively related to *Fossaria* densities (R^2 =0.305, p = 0.012). No other relationships were significant (Fig. 4). In cobble samples, *Pyrgulopsis* densities were positively related to *Potamopyrgus* and *Physa* densities (R^2 =0.702, p =0.000, and R^2 = 0.520, p = 0.000, respectively; Fig. 5). There was no relationship between *Pyrgulopsis* and *Fossaria* densities.

2003

In vegetation samples, *Pyrgulopsis* densities were not significantly related to densities of any other snail species (Fig. 6). We are currently still processing cobble samples from 2003.

2005

In vegetation samples, *Pyrgulopsis* densities were positively related to *Fossaria* densities (R^2 = 0.581, p = 0.002; Fig. 7). On the other hand, *Pyrgulopsis* densities were not related to *Physa* or *Potamopyrgus* densities in vegetation in 2005 (Fig. 7). In cobble habitats, *Pyrgulopsis* densities were positively related to *Physa* densities (R^2 = 0.360, p = 0.007; Fig. 8). No other relationships were significant.

Relationship to algal food sources

The amount of chlorophyll *a*, as an indicator of algal biomass, did not differ between 2003 and 2005. However, sites significantly differed in the amount of algae present (p=0.000) and there was a significant interaction between site and year, indicating that some sites declined between years while others increased (p=0.019, Fig. 9). Surprisingly, there was no relationship among chlorophyll *a* and 2005 snail densities on cobbles, whether examining individual species or total snail abundance (Fig. 9).

2001 – 2005

Snail densities were much lower on cobbles compared to vegetation (Figs. 10, 11). Average densities on cobbles never exceed 1200 individuals/m^2 for any species. On the other hand, densities in vegetation are much higher, with average densities of *Potamopyrgus* and *Pyrgulopsis* often exceeding an average of 5000 individuals/m^2 for any given year. In cobble habitats, *Potamopyrgus* densities differed significantly across years (p=0.013), and across sites (p=0.020), with sites responding differently among years, as indicated by a marginally significant site by year interaction (p=0.061). *Potamopyrgus* densities increased between 2001 and 2002, but then decreased between 2002 and 2005 (Figs. 10, 11). *Pyrgulopsis* densities, on the other hand, do not differ significantly among sites or years. There is a negative decreasing trend across years, but it is not significant. *Fossaria* densities differed across years, with a gradual increase from 2001 to 2002 and a drastic increase between 2002 and 2005 (p=0.000; Fig. 10). *Fossaria* densities differed across sites (p=0.025) and there was a marginally significant site by year interaction (p=0.071). *Physa* densities also increased across years (p=0.041), but there was no difference across sites and no significant interaction.

In vegetation, *Potamopyrgus* displayed a surprising trend, with densities significantly decreasing across years (p=0.044; Figs. 10, 11). Densities of *Potamopyrgus* also differed across sites (p=0.002) and there was a significant interaction between site and year (p=0.000). *Pyrgulopsis* densities also differed across years (p=0.000) and sites (p=0.001), with a significant interaction between site and year (p=0.003). *Pyrgulopsis* densities decreased from 2001 to 2003, but increased from 2003 to 2005 (Figs. 10, 11). *Fossaria* densities also differed across years (p=0.000) and sites (p=0.001), with a significant interaction between site and year (p=0.003). Finally, *Physa* densities have not changed across years, but there is a significant effect of site (p=0.001) because densities are consistently higher in sites 3 – 5 across all years.

Synthesis

Potamopyrgus densities on cobbles spiked in 2002, but have since decreased. This pattern is consistent across all sites (except for site 2, where a steady decline on cobbles has occurred). Overall, *Pyrgulopsis* densities on cobbles have declined from 2001 to 2005, although this result is not significant (Figs. 10, 11). This suggests that *Potamopyrgus* has not yet displaced *Pyrgulopsis* from cobble habitats in Marmot Spring, although we cannot rule out the fact that this could be happening. However, declines from 2002 to 2005 in *Potamopyrgus* densities indicate that decreases in *Pyrgulopsis* densities during this time frame cannot be attributed to increases in *Potamopyrgus* densities.

In vegetation, surprisingly, it appears that, overall, *Potamopyrgus* densities are declining in Marmot Spring (Fig. 10). Densities were relatively constant from 2001 to 2002, but declined drastically between 2002 and 2005. However, individual sites within the spring responded differently (Fig. 11). *Potamopyrgus* increased at some sites from

2001 to 2002, but have since declined to pre-2002 levels. Only site 1 experienced an increase in *Potamopyrgus* densities from 2003 to 2005; all other sites declined. *Pyrgulopsis* densities also declined in vegetation from 2001 to 2003, but increased from 2003 to 2005 (Fig. 10). The overall population density of *Pyrgulopsis*, though, is still much lower than 2001 levels. Across all sites, *Pyrgulopsis* densities have declined since 2001, with the exception of site 3 (Fig. 11). Site 3 spiked in *Pyrgulopsis* densities in 2005 and is responsible for the increase in overall densities from 2003 to 2005. This is the only site where densities increased significantly from 2003 to 2005.

All snail species, including *Pyrgulopsis* and *Potamopyrgus*, exhibit higher densities in vegetative habitat. This pattern could be related to the higher surface area of vegetation when compared to cobble habitats. A high surface area could increase food availability (epiphytic algae) and/or space for colonization. However, high densities of snails in vegetation could also be related to the fact that macrophytes are found in water with slower currents and/or potentially provide more protection from predators.

Increases in *Potamopyrgus* densities do not appear to be related to decreases in *Pyrgulopsis* densities over this time scale. In fact, in some years, densities of these two species are positively related (Table 2). This suggests that *Pyrgulopsis* and *Potamopyrgus* are present in similar microhabitats. Even though higher densities of both species are found in vegetation, cobble areas with high densities of *Pyrgulopsis* are likely to also have high densities of *Potamopyrgus*. Occupying similar microhabitats could suggest that these snails are competing for space and/or resources, but evidence of displacement has not yet occurred. Interestingly, Fossaria and Physa have increased drasticallVariability in densities for all four snail species between years suggests that long-term monitoring should continue to determine if changes in snail populations over a four-year period will accurately reflect increases or declines over a longer time scale.

Part B. Exploration of the historic range of the Jackson Lake spring snail

Methods

In July of 2005, we systematically sampled 6 sites around Elk Island in Jackson Lake where the presence of the Jackson Lake spring snail was recorded many years ago (Walker 1908, Beetle 1958). We focused efforts on sites where habitat characteristics indicated a higher likelihood of finding springs (i.e. different vegetation from surrounding area, etc.). One person snorkeled in deeper habitat farther from the shoreline (2 m deep or greater), collecting benthic samples with a kicknet or handpicking invertebrates from the substrate. Two other people used kicknets and sieves in shallow, near-shore areas of the same site to collect samples. GPS readings were recorded from each site, as well as basic habitat characteristics (i.e. presence of macrophytes, type of substrate). We preserved snails that were collected.

In July of 2005, we also systematically sampled 4 other likely sites around Jackson Lake, where springs or streams were flowing into the lake. The two sites chosen on the western side of Jackson Lake were: 1) three spring streams in North Moran Bay and 2) a stream south of Waterfalls Canyon. The sites chosen on the eastern side of Jackson Lake were: 1) Lizard Creek and the surrounding marsh area and 2) Arizona Creek. At each of the sites, we extensively sampled streams flowing into the lake as well as the shoreline along Jackson Lake. GPS readings and habitat characteristics were recorded. We preserved any snails that were collected.

Results and Synthesis

We failed to locate *Pyrgulopsis robusta* at any sites around Elk Island (Tables 3 and 4). The six Elk Island sites all contained large cobbles (typical of many shorelines in Jackson Lake) with a few macrophytes present at some protected sites within the bay areas. Many Elk Island sites showed signs of exposure during last year (i.e. terrestrial plants, such as thistles, growing underwater). We did not see signs of groundwater spring inputs, although scuba diving in this area might reveal springs that we could not detect. Spring inputs could potentially support a *Pyrgulopsis robusta* population deeper underwater.

We also failed to locate *Pyrgulopsis robusta* at the other four sites around Jackson Lake (Table 4). The North Moran Bay site was the most similar to habitat characteristics of the current range of *Pyrgulopsis*. This site consisted of three spring streams with similar riparian vegetation to Marmot Spring (i.e. *Mimulus* (monkeyflower) and *Heracleum* (cow parsnip)). In addition, one spring had high densities of another snail, *Stagnicola* spp. (Family: Lymnaeidae), suggesting that this site is capable of supporting a dense population of a similar species. The Lizard Creek site also had a dense population of *Stagnicola* as well as riparian vegetation that included *Mimulus*. The other two sites, Arizona Creek and south of Waterfalls Canyon are unlikely to support populations of *Pyrgulopsis robusta*.

Tables and Figures

Table 1. Marmot Spring sites, GPS locations and basic substrate types.

Site	East/West UTM Coordinates	North/South UTM Coordinates	Spring snails present?	Basic Habitat Characteristics
1	0522795 E	4886747 N	Yes	V: 70 % C: 30 % Temp: 23ºC
2	0522922 E	4886759 N	Yes	V: 40% C: 60% Temp: 24ºC
3	0523044 E	4886635 N	Yes	V: 50% C: 50% Temp: 24ºC
4	0523187 E	4886468 N	Yes	V: 50% C: 50% Temp: 25ºC
5	0523257 E	4886349 N	Yes	V: 40% C: 60% Temp: 25ºC

Notes: "V" represents aquatic vegetation, including macrophytes and macroalgae. Only a small amount of macroalgae was present at any given site and therefore was grouped with macrophytes. "C" represents cobble habitat. Other general characteristics of Marmot Spring are included in the text.

Table 2. Summary table of relationship between *Pyrgulopsis robusta* and three other snail species in two habitat types.

	Cobbles			Vegetation		
Year	PA	Foss	Phys	PA	Foss	Phys
2001	+	+	0	+	+	--
2002	+	0	+	0	+	0
2003	NA	NA	NA	0	0	0
2005	0	0	+	0	+	0

Notes: "PA" represents the invasive *Potamopyrgus antipodarum*, "Foss" is the native *Fossaria* spp. and "Phys" is the native *Physa* spp. 2003 data for cobble habitat is not available. A "0" is no relationship to *Pyrgulopsis* densities within that habitat for a particular year, while a "+" or a "--" represent a significant positive or a negative relationship, respectively.

Table 3. Elk Island sites GPS locations.

Site	**East/West UTM Coordinates**	**North/South UTM Coordinates**	**Spring snails present?**	**Basic Habitat Characteristics**
1: NE Elk Is., Bay Area	0526369	4857151	No	Cobbles and macrophytes
2: Channel between Dollar and Elk Is.	0526884	4857322	No	Cobbles with few to no macrophytes
3: Elk Is. Campground	0526942	4856337	No	Silt and cobbles with few to no macrophytes
4: South Bar Elk Is.	0526488	4855486	No	Cobbles
5: SW Elk Is.	0525998	4855668	No	Cobbles
6: North Bar Bay Elk Is.	0525760	4856903	No	Silt and cobbles with macrophytes

Table 4. Other Jackson Lake sites and GPS locations.

Site	**East/West UTM coordinates**	**North/South UTM coordinates**	**Spring snails present?**	**Basic habitat characteristics**
North Moran Bay	NA	NA	No	Three spring streams with similar riparian vegetation to Marmot Spring
South of Waterfalls Canyon	0523211	4860283	No	Higher gradient mountain stream with cobbles
Lizard Creek	0525055	4871984	No	Muddy stream and marsh area with some vegetation similar to Marmot spring
Arizona Creek	0527545	4868213	No	Large cobbles with very few macrophytes

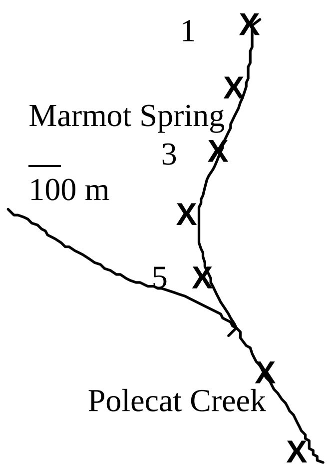

Fig. 1. Schematic of sampling sites in Marmot Spring.

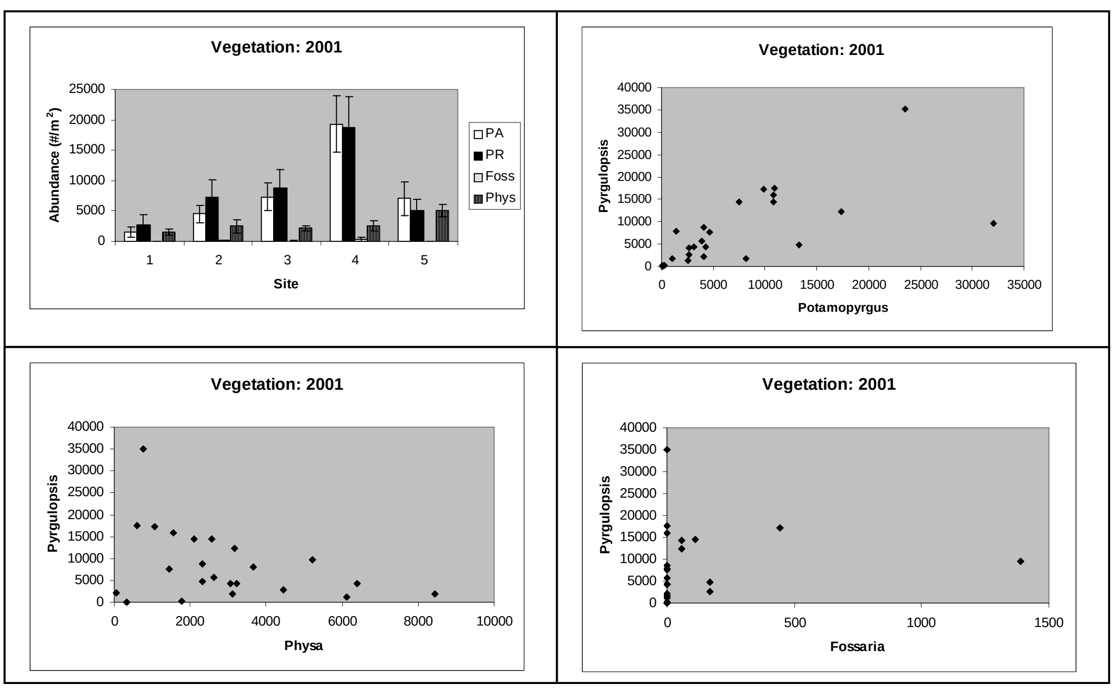

Fig. 2. 2001 snail densities in vegetation. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

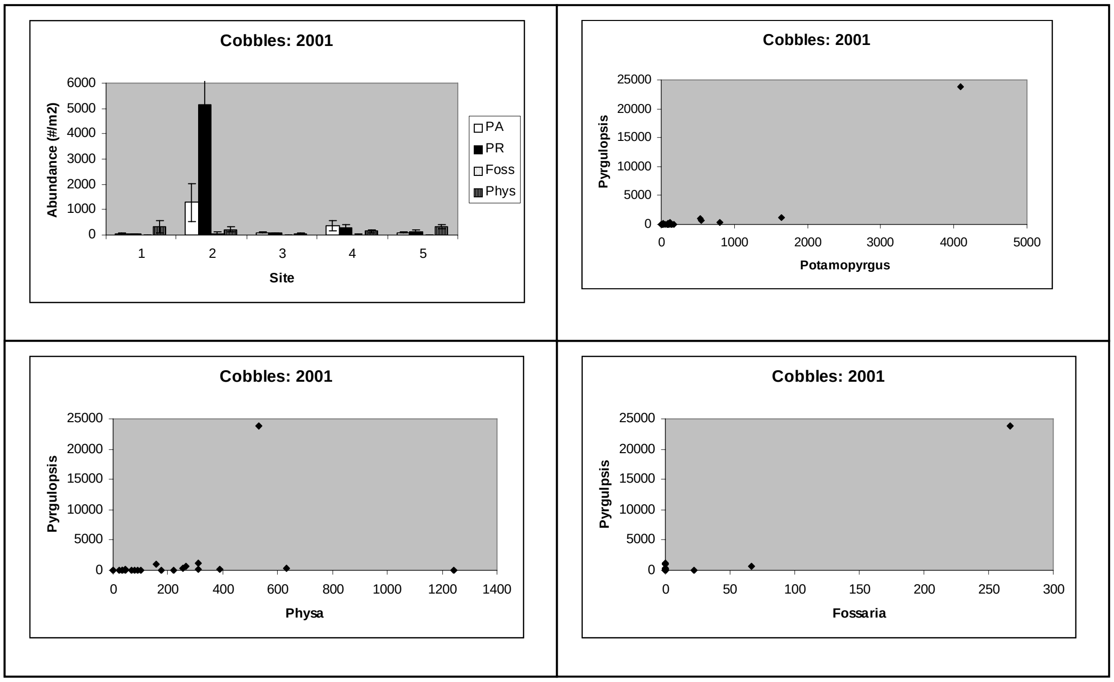

Fig. 3. 2001 snail densities on cobbles. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

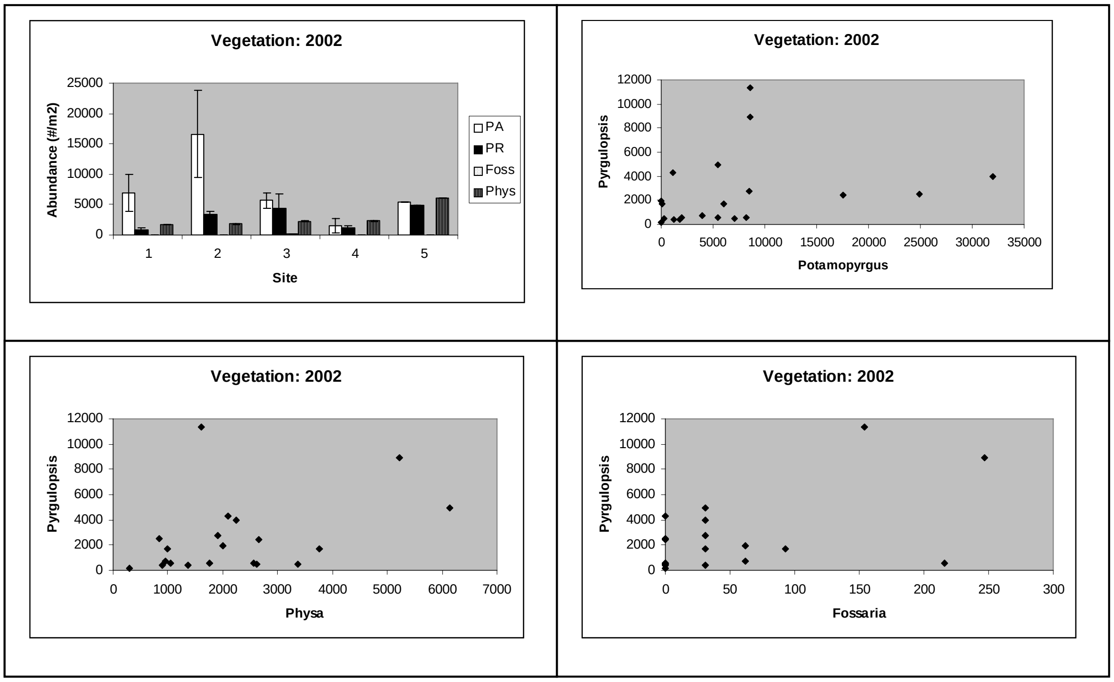

Fig. 4. 2002 snail densities in vegetation. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

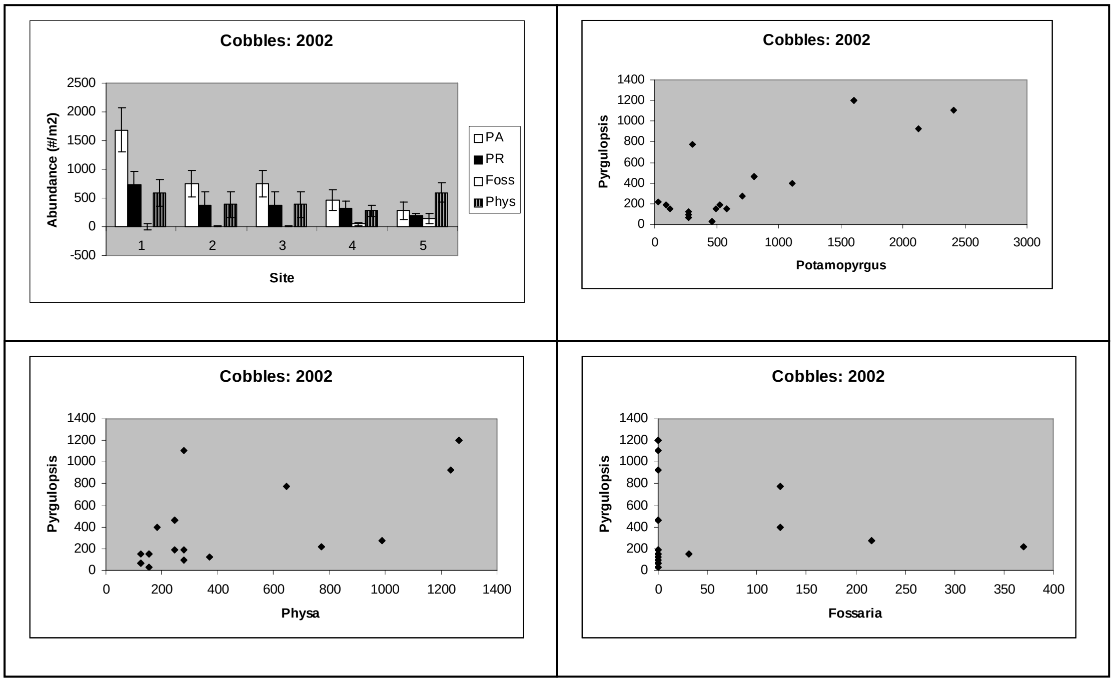

Fig. 5. 2002 snail densities on cobbles. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

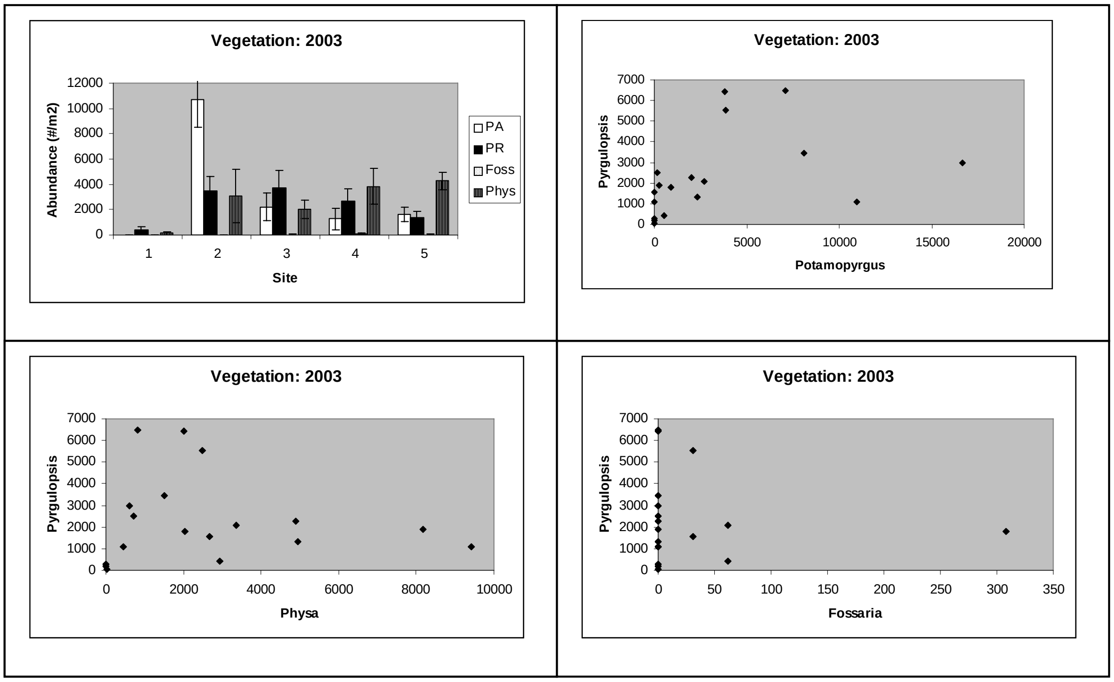

Fig. 6. 2003 snail densities in vegetation. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

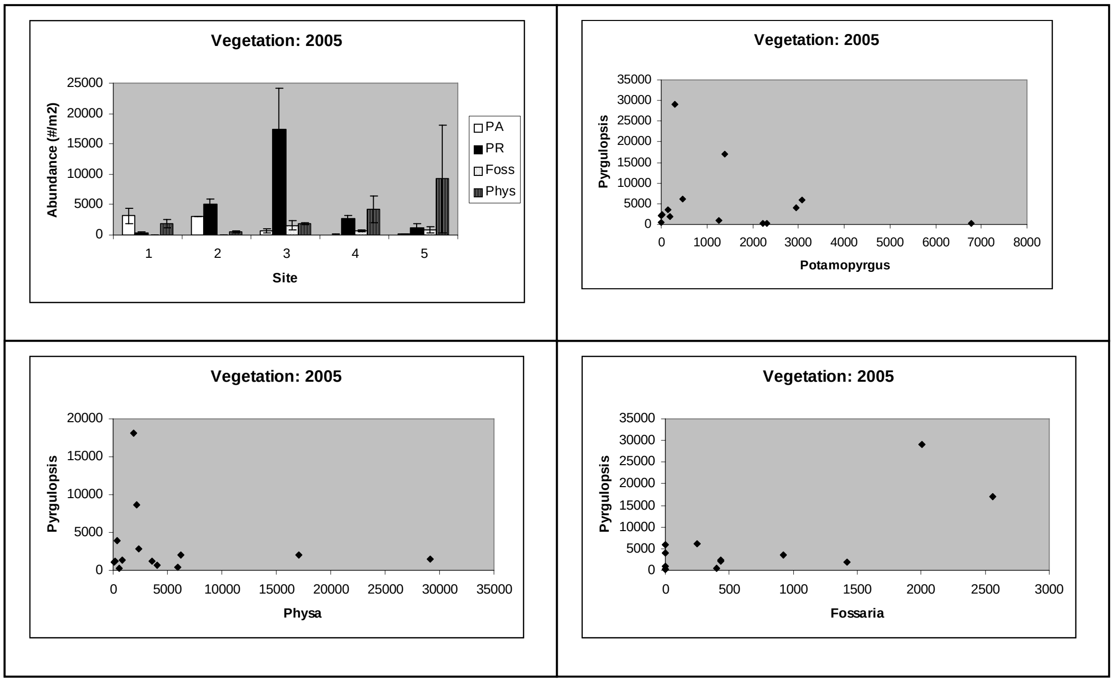

Fig. 7. 2005 snail densities in vegetation. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

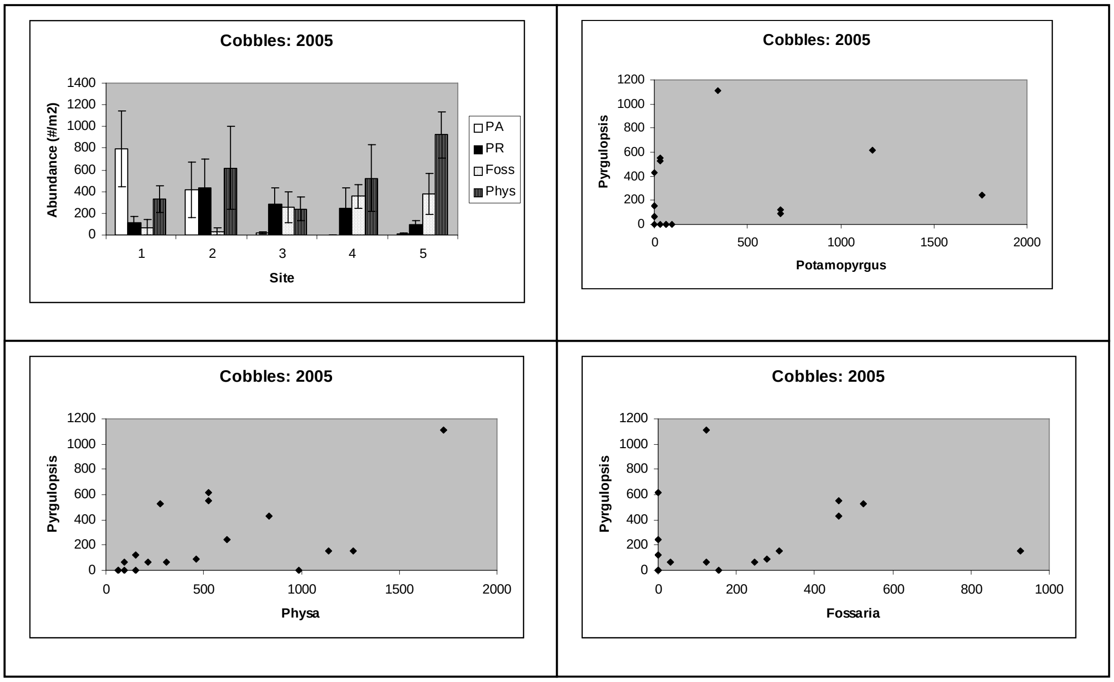

Fig. 8. 2005 snail densities on cobbles. The top left panel depicts average densities across the five Marmot Spring sites for all four snail species. Error bars are ±1 standard error. The abbreviations for snail species are as follows: PA – *Potamopyrgus antipodarum*, PR – *Pyrgulopsis robusta*, Foss – *Fossaria* spp., Phys – *Physa* spp. The top right panel is a regression of *Potamopyrgus* densities on the x-axis and *Pyrgulopsis* densities on the y-axis. The bottom two panels are also regressions of *Pyrgulopsis* densities against two native species densities (*Physa* and *Fossaria*, respectively).

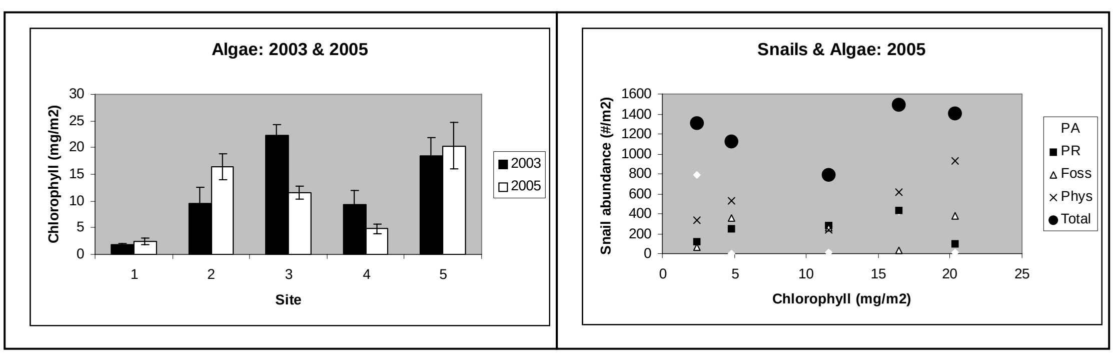

Fig. 9. Algal densities in 2003 and 2005 and relationship to snail abundance in 2005. The left panel depicts chlorophyll *a* abundance at each site in 2003 and 2005. The right panel depicts regressions between chlorophyll abundance and snail abundance on cobbles in 2005. Abbreviations are as above. “Total” represents total snail abundance and is the sum of the four species densities.

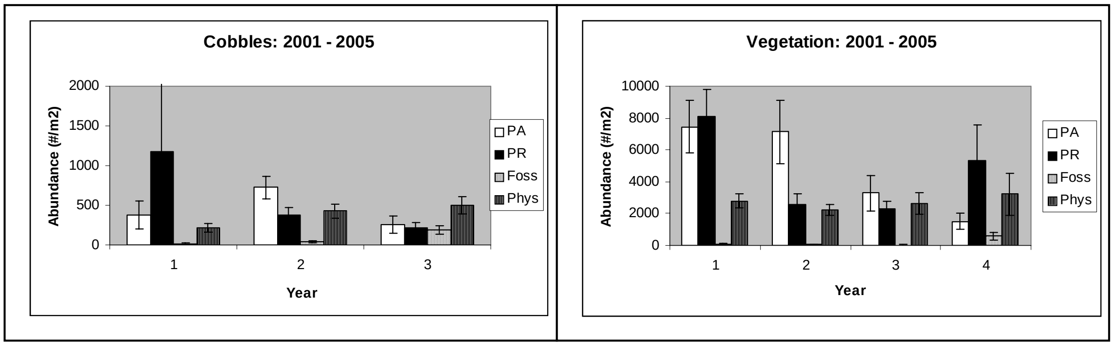

Fig. 10. Snail densities in two habitats across years. In the left panel, year 1 corresponds to 2001, year 2 to 2002 and year 3 to 2005. In the right panel, year 1 and 2 are the same, but year 3 corresponds to 2003 and year 4 corresponds to 2005. Data for cobbles is not available for 2003.

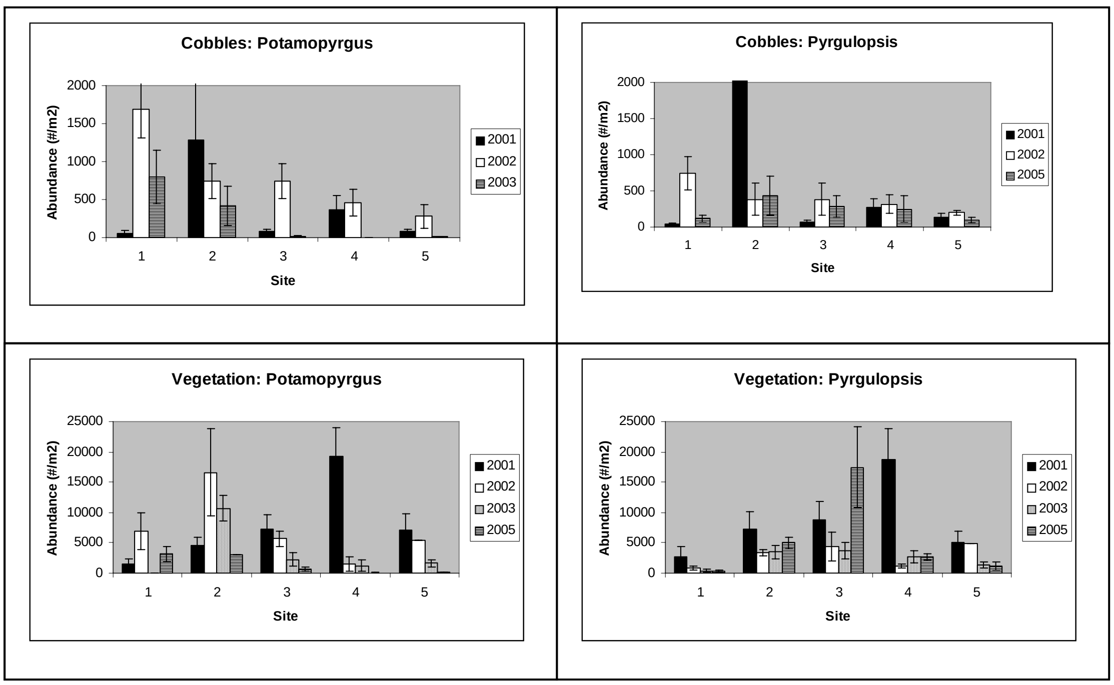

Fig. 11. Snail densities in two habitats across years at each site. Note on the top right panel that abundance of Pyrgulopsis at site 2 greatly exceeds the y-axis (average: 6000/m^2). Also note the large difference in abundance between scales of the y-axis for cobbles versus vegetative habitat.