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Gastropods in lower Snake River and three of its tributaries and the effects of competition with the New Zealand mud snails (Potamopyrgus antipodarum)

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Gastropods in the Lower Snake River and three of its tributaries and the effects of competition with the New Zealand Mud Snails (*Potamopyrgus antipodarum*).

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Master's Thesis

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Project Summary

The purpose of this study was to determine the distribution of New Zealand mud snails (*Potamopyrgus antipodarum*) in the lower Snake River and three tributaries and to determine if this invasive snail is competing with native gastropods. *Potamopyrgus antipodarum* is a successful invader in much of the Western United States and has been shown to impact nutrient cycling and community structure in invaded ecosystems. This study is divided into two chapters: the first chapter focuses on the current density and genera richness of native gastropods and the distribution of *P. antipodarum* in the Lower Snake River and three tributaries near Lewiston, Idaho; while the second chapter explores the possibility that *P. antipodarum* may be competing for food resources with the native pebble snail, *Fluminicola*. The field survey of native gastropods serves the dual purpose of determining the level of invasion of *P. antipodarum* in the Lower Snake River and surrounding tributaries as well as providing a baseline survey of native gastropod density and genus richness. Limited studies of the pre-invasion distribution and abundance of native gastropods exist making this baseline survey an important study which may provide insights into how native gastropod populations change as levels of *P. antipodarum* increase. Conflicting results from competition experiments between native gastropods and *P. antipodarum* has resulted in an ambiguous understanding of the impacts *P. antipodarum* may be having on native gastropods. The second chapter of this study looks at the grazing rates of *Fluminicola* under intra- and inter-specific competition to aid in the understanding of how *P. antipodarum* may be impacting native gastropods.

Chapter 1

Density and genus richness of native gastropods and the occurrence of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in the Lower Snake River and three tributaries.

Abstract

The New Zealand mud snail, *Potamopyrgus antipodarum*, is an invasive gastropod that can impact native gastropods in the United States. However, limited knowledge on the native snail community prior to invasion by *P. antipodarum* makes assessing these impacts difficult. A baseline survey was conducted to determine the density and genus richness of gastropods in four rivers near Lewiston, Idaho that are downstream of the current invasion area of *P. antipodarum*. A total of nine genera from five families were found among the fifteen sites surveyed including *P. antipodarum*. Sites ranged from zero to seven genera of gastropods with a mean gastropod richness of 2.875 genera per site. Average site densities of gastropods ranged from zero to 625.33 snails m^{-2} with the highest river-specific mean density found in the Grand Ronde River with 251.66 gastropods m^{-2}.

We collected abiotic and periphyton biomass data to determine which factors were correlated with genus richness and gastropod density. Both periphyton biomass (as ash-free dry mass) and calcium ion concentrations were positively correlated with snail density while no significant correlations were found between the independent variables and genus richness. General linear modeling suggests water velocity and river have significant effects on both gastropod density and genus richness. We analyzed body length as total shell length of each genus of gastropods among rivers and found that three of the four dominant genera had significant differences in body size among rivers. Among river variations in body size may be attributed to low calcium concentrations, low chlorophyll *a* levels, and low pH which can increase metabolic demands on gastropods.

Introduction

Freshwater gastropods inhabit a wide variety of freshwater habitats and often form narrow endemic ranges (Lydeard et al., 2004; Strong et al., 2008) with many species restricted to a single drainage or an isolated spring (Brown et al., 2008). In North America, over 70% of freshwater snails are listed as imperiled or presumed extinct (Lysne et al., 2008; Evans & Ray, 2010). Habitat loss, water pollution and the introduction of invasive species are the main factors attributed to the reduction in snail biodiversity (Strong et al., 2008). It is imperative that ecologists and resource managers gain insights into the distribution and population dynamics of native gastropods as well as understand the impacts invasive species have on native gastropods in freshwater ecosystems.

Gastropods perform a crucial role in aquatic ecosystems as consumers of periphyton, macrophytes, and detritus and as prey for an array of organisms. Gastropods are important grazers of periphyton (Brown et al., 1994; Dillon, 2000; Munoz et al., 2000) and have been shown to preferentially graze diatoms and other algae (Connor & Edgar, 1982; Cattaneo & Kalff, 1986; Liess & Kahlert, 2007; Krist & Charles, 2012). Gastropods can reduce chlorophyll *a* levels in streams by over 35% (Cross & Benke, 2002; Riley et al., 2008). Cross & Benke (2002) found that the absence of snails from experimental stream channels resulted in 12 times the chlorophyll *a* and twice the ash-free dry mass for periphyton than treatments with snails. In snail density experiments, increased snail density resulted in decreased algal biomass (Osenberg, 1989; Liess & Kahlert, 2007). Gastropod populations can be food limited with direct relationships between periphyton production and gastropod density (Osenberg, 1989; Hill, 1992).

Birds, fishes, amphibians, crayfish and large macroinvertebrates all consume gastropods (Dillon, 2000). Gastropods provide greater than 85% of the autumn diet of some ducks (Ross et

al., 2005) and many birds supplement their diet with calcium rich foods including gastropods during egg laying (Petrie, 1996; Scheuhammer et al., 1997; Reynolds & Perrins, 2010). The presence of fishes has been shown to negatively impact snail population density (Dillon, 2000). Pumpkinseed sunfish, *Lepomis gibbosus,* are molluscivorous fishes with gastropods comprising over 70% of adult dietary biomass (Garcia-Berthou & Moreno-Amich, 2000). Tiger salamander (*Ambystoma tigrinum*) and Eastern newt (*Notophthalmus viridescens*) larvae consume large amounts of gastropods and gastropod biomass was the second most important food source for these amphibians (Dillon, 2000). Crayfish are an important source of mortality for gastropods and in mesocosm experiments have been shown to reduce snail biomass by over 90% (Johnson et al., 2009). Snail densities have also been shown to be negatively impacted by leech and dragonfly larvae predation (Brönmark, 1992; Turner & Chislock, 2007). Snails are a critical link between primary productivity and secondary consumers in aquatic food webs.

Gastropod richness and abundance can also be influenced by abiotic factors including conductivity, pH, calcium ion levels, and river flow. Gastropods generally require habitats with high conductivity, calcium ions, and pH (Dillon, 2000). Growth and reproduction in gastropods is influenced by conductivity and environmental calcium levels (Kefford & Nugegoda, 2005; Zalizniak et al., 2009). Low levels of calcium and other ions results in decreased shell strength, reduced locomotion, and increased metabolic demands in gastropods (Hunter et al., 1967; Dalesman & Lukowiak, 2010). A direct correlation between calcium concentrations and gastropod species richness has been repeatedly demonstrated (Dillon, 2000). Calcium concentrations may also indirectly result in higher gastropod abundance by increasing primary producer biomass resulting in higher food resources for gastropods (Dillon, 2000; Harris et al., 2011). The pH of aquatic systems is connected to the availability of ions that are critical to

gastropod survival (Dillon, 2000) and pH below 5.0 results in absence of gastropod from aquatic systems (Scheuhammer et al., 1997). Gastropods in lotic environments are also restricted by stream velocity as higher velocities (greater than 0.20 m s^{-1}) result in detachment and increased mortality which may reduce population sizes (Lysne & Koetsier, 2006).

Invasive species can dramatically alter the native community by reducing biodiversity and changing ecological processes (Alonso & Castro-Diez, 2008). The effects of invasive species on aquatic ecosystems are often irreversible and lead to reductions in biodiversity due to predation and competition with native species (Lysne et al., 2008; Strayer, 1999). Invasive gastropods impact native ecosystems by altering carbon and nitrogen levels (Hall et al., 2003; Arango et al., 2009), consuming large amounts of primary producer biomass (Riley et al., 2008; Strayer, 2010), and changing native macroinvertebrate community composition (Kerans et al., 2005; Riley et al., 2008; Cross et al., 2010; Brenneis et al., 2011).

The New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1853; Gastropoda, Hydrobiidae), is a freshwater prosobranch snail native to New Zealand. *Potamopyrgus antipodarum* was first found in the United States in the middle reaches of the Snake River in 1987 (Bowler, 1991; Brown et al., 2008) where it rapidly spread to watersheds along the Snake River from Idaho Falls west to Hell's Gate State Park (Benson, 2011). Further expansion is expected as *P. antipodarum* currently occupies only a small fraction of possible habitats in North America (Loo et al., 2007; Strayer, 2010).

The continued expansion of *P. antipodarum* is occurring at alarming rates and by multiple vectors (Zaranko et al., 1997; Kerans et al., 2005). In a ten year period, *P. antipodarum* extended its range by over 640 km along the Snake River, Idaho (Zaranko et al., 1997). Passive drifting in the water column, floating on aquatic vegetation, transport by recreational boats,

dispersal by fish and birds, and active upstream movement are all methods of spread used by *P. antipodarum* (Bowler, 1991; Zaranko et al., 1997; Sepulveda & Marczak, 2011). *Potamopyrgus antipodarum* can also be transported internally by fish that are unable to digest these snails and defecate the unharmed snails to new locations in the watershed (Zaranko et al., 1997; Brown, 2007; Bruce et al., 2009; Brenneis et al., 2011). The invasion success of *P. antipodarum* is attributed to its high fecundity (Zaranko et al., 1997; Weetman et al., 2006), parthenogenetic reproduction (Zaranko et al., 1997; Alonso & Castro-Diez, 2008), high resistance to predation and parasitism (Alonso & Castro-Diez, 2008; Adema et al., 2009), and tolerance to severe environmental conditions (Zaranko et al., 1997; Alonso & Castro-Diez, 2008).

In the wake of rapid declines of non-marine mollusks (Lydeard et al., 2004), it is critical to understand how introduced species are impacting native gastropod populations. However, limited knowledge on the native snail community prior to invasion by *P. antipodarum* makes assessing these impacts difficult. We conducted a baseline survey to determine the genus richness, gastropod density, and body size of gastropods in areas of the Lower Snake River, Grande Ronde River, Asotin Creek, and the Clearwater River. These rivers are near the know range of *P. antipodarum* invasion in the Snake River watershed and are likely to be invaded in the near future.

We hypothesize that number of genera and gastropod density will be higher in areas with high levels of periphyton biomass, high levels of conductivity (greater than 200 µS/cm) and calcium ion levels (greater than 20 mg/L), and low water velocity (less than 15 m/s). Body length is expected to be different between rivers for some genera due to differences in abiotic factors (especially conductivity and calcium ion concentrations which are essential for gastropod survival), and periphyton biomass (which reflects food availability). We also predict that *P.*

antipodarum will be present at low densities as the areas surveyed are at the leading edge of the invasion front for *P. antipodarum*.

Methods

Survey Sites

We conducted our survey for gastropods in the Lower Snake River and three tributaries: the Clearwater River, Grande Ronde River and Asotin Creek (Figure 1). The Clearwater River is the largest tributary of the Snake River with a drainage basin of 24,980 km^2 that joins the Snake River at Lewiston, Idaho (USGS, 2012). The Clearwater River is a mountain fed river that runs through central Idaho and has a low mean summer water temperature of 12.7ºC and a mean annual discharge of 430 m^3 s^{-1} (USGS, 2012). The Grand Ronde River is a warm river than run through the arid lands of northwest Oregon and southwest Washington. The Grand Ronde River has a mean annual discharge of 85 m^3 s^{-1} (USGS, 2012) and joins the Snake River approximately 50 km south of Lewiston, Idaho. Asotin Creek is a small tributary with a mean annual discharge of 1.5 m^3 s^{-1} (USGS, 2012) with a thick riparian zone located at the north end of the city of Asotin, Washington (10 km south of Lewiston, Idaho). The Snake River is a large river with a mean annual discharge of 1,500 m^3 s^{-1} (USGS, 2012) running through Idaho, Oregon, and Washington and covers 1,735 km from its headwaters in Wyoming (Fore & Clark, 2005). The Snake River is a highly impacted river with 13 hydroelectric dams located from the confluence with the Columbia River through the river's central reach in Southern Idaho (Sanderson et al., 2009). We sampled fifteen locations (Figure 1) for gastropods, periphyton, and abiotic factors in the late summer and fall of 2012.

Gastropod Sampling

We collected gastropods from three channel transects along a 50 meter shore transect at each site. Plots occurred at three water depths: 10 cm, 20 cm, and 30 cm along each channel transect resulting in a total of nine plots for each site. We visually inspected each rock and hand collected all gastropods located within a quarter meter plot frame. Gastropods were preserved in 70% alcohol immediately after collection. Specimens were counted, identified to the genus level using Brown (2001), and measured for body length (here after length) as total shell length (from the apex to the bottom of the aperture of the shell) to the nearest 0.01 mm using digital calipers.

Periphyton Biomass

The biomass of periphyton was determined by both chlorophyll *a* and ash-free dry mass (AFDM) methods. A grid system on the plot frame was used to randomly collect four rocks for each transect. We cleaned each rock by scraping and brushing the periphyton off the rock and rinsing the periphyton into a bucket. Each sample was then transferred to specimen container and immediately put on ice. We placed the clean rock into a labeled plastic bag and surface area was determined in the lab using the foil wrapping method as described by Bergey & Getty (2006). All samples were processed within 24 hours. In the lab, we homogenized and brought periphyton samples to one liter before using fluorometry to determine chlorophyll *a*. Three subsamples of 7 ml were placed into fluorometry test tubes and run in the fluorometer. We used the average of the three subsamples to determine each rock's level of chlorophyll *a* (µg/L).

Ash-free dry mass was determined in accordance with Hauer & Lamberti (1998). Briefly, we stained a subsample (200 mL) of the homogenized periphyton (see previous paragraph) through a pre-measured glass fiber filter with a pore size of 1.5 µm (VWR International grade

691). Filters with periphyton samples were then dried at 60º C for at least 24 hours. We massed the dried filter to determine dry mass prior to ashing the dried filters in a muffle furnace at 450 º C for 1 hour to remove organic matter. The filter was reweighted to determine AFDM. We conducted all measurements on an analytical balance to the nearest 0.1 mg. AFDM was calculated by subtracting the dry filter mass from the ash-free dry filter mass and then dividing by the surface area of the rock (see previous paragraph).

Abiotic Factors

We measured temperature, pH, conductivity, turbidity, and dissolved oxygen just upstream and downstream of the shore transect at each site using YSI 6000 series environmental probe. All measurements using this probe were made mid-morning (10 to 11a.m.) to decrease variability among sites due to time of day fluctuations. We used Hach 600 series water quality kits to determine nitrogen and phosphorus levels for water samples taken from each channel transect. Calcium ion levels were also determined from the water samples using a Vernier calcium ion selectivity probe. We used a water flow meter to determine water velocity for each plot.

The substrate for each site was assessed for total surface area using the stone shape equation method as described by Bergey & Getty (2006). Twelve randomly selected rocks (four from each transect) were selected using a grid system on the plot frame. We traced each rock onto water-proof plastic sheets and recorded the height of the rock using hand calipers to the nearest 0.05 mm. In the lab, the maximum length and width of each rock was determined from the traced image and the surface area of each rock was calculated using the following equation:

$$SA = 1.15(LW + LH + WH)$$

where SA is the surface area, L is the length, W is the width, and H is the height of the rock at its longest distance (Bergey & Getty, 2006).

Statistical Analyses

The data collected from this survey was used to identify possible correlative factors affecting gastropod density and genus richness. We used a combination of multiple linear regressions (MLRs), general linear models (GLMs) and ANOVAs (Quinn & Keough, 2002; Zar, 2010) to identify potentially influential factors. MLRs and GLMs were developed to identify the environmental variables which had a significant effect on total gastropod density, the density of individual genera, and gastropod richness. We transformed the data using natural log, square root, inverse, and cubed values to meet normality. Pearson correlation matrix of independent variables was used to determine if independent variables were collinear (Quinn & Keough, 2002). Acceptable MLRs and GLMs were those with one to three predictors; with p-values less than 0.05; with the highest r-squared values; and with tolerance values greater than 0.1 (Miles & Shevlin, 2001; Quinn & Keough, 2002). We conducted forward and backward step-wise regressions to confirm the best regressions for the data. Logit regressions were conducted for each genus using absence or presence of the genus as the dependent variable to determine if any independent variable correlated to genus presence in a non-density dependent manner.

We collected water velocity, plot depth, and river for each plot and these data were analyzed to determine their influence on gastropod density or genus richness. Due to unequal variance among treatments and a the lack of normality in the data, we used Kruskal-Wallis tests to determine if snail density or genus richness were significantly different due to river flow, plot depth, or river of origin. Wilcoxon's pair wise comparisons with a Bonferroni adjustment to

compensate for family-wide error were then conducted to determine which sites were significantly different from one another (Quinn & Keough, 2002). We also constructed general linear modeling using water velocity, plot depth, and rivers to determine if any interaction effect existed between these three independent variables and gastropod density or genus richness. To determine which aspects of a river may be influencing differences in gastropod density or genus richness between rivers, we conducted one-way ANOVA tests on each of the independent variables among rivers.

We analyzed gastropod length to determine if length of gastropods varied significantly between the four rivers. A ranked one-way ANOVA was performed on the data for each genus. All significant ANOVA results were then tested for pair wise comparisons using Tukey's test (Quinn & Keough, 2002). We conducted all statistical analyses using SYSTAT version 13.

Results

A total of 4,824 gastropods from nine genera in five families were collected during our survey including the invasive snail, *P. antipodarum*. The five families included Hydrobiidae, Ancylidae, Lymnaeidae, Physidae, and Planorbidae. Dominant genera included *Fluminicola*, *Physa*, *Ferrissia,* and *Vorticifex* (Table 1) with *Fluminicola* being the dominant genus at eight sites and having the highest abundance (30.89%) for the survey overall. Site gastropod richness ranged from zero to seven genera with a mean richness of 2.9 genera per site. Two locations, one on the Clearwater River and one on the Snake River, possessed no gastropods while the most northern site on the Snake River (at the confluence with Asotin Creek) had the highest number of genera. *P. antipodarum* were found at two locations, one in Asotin Creek and the other at the confluence of Asotin Creek and the Snake River. Density of gastropods among sites ranged from

zero to 625.33 gastropods m^{-2} (Table 1). The highest river mean density was in the Grand Ronde River (251.66 gastropods m^{-2}) and the lowest river mean density was in the Clearwater River (5.44 gastropods m^{-2}).

Linear regressions for the data indicated no correlations between the dependent variables and gastropod richness. Gastropod density was positively correlated with AFDM ($p = 0.002$) and calcium ion concentration ($p = 0.008$) and accounted for 54.8% of the variation in gastropod density among sites ($p = 0.003$, $F = 9.488$, $r^2 = 0.548$). Both forward and backward stepwise regressions resulted in the same multiple linear regression found when manually improving linear regressions. The only independent variables that showed co-linearity were calcium ion concentrations and conductivity (Table 2). All single genus density regressions and logit regressions for absence or presence of a genus were not significantly correlated to any of the dependent variables.

Comparisons between water velocity, plot depth, and river (based on plot data) found that only river was a significant independent variable in models predicting genus richness and gastropod density. Genus richness was higher in the Grand Ronde River than Asotin Creek ($p < 0.01$) and higher in the Grand Ronde River than the Clearwater River ($p < 0.01$; Figure 2). The Grand Ronde had higher gastropod density than all other rivers ($p < 0.02$) and gastropod density was also higher in Asotin Creek than the Clearwater River ($p < 0.01$; Figure 3).

General linear modeling for water velocity, plot depth, and river found an interaction effect between river and water velocity for both number of genera ($p = 0.03$) and density of gastropods ($p = 0.02$; Table 3). Asotin Creek had the highest average water velocity (0.56 m s^{-1}), highest genus richness, and moderate gastropod density while rivers with low average river velocity (less than 0.06 m s^{-1}) had lower number of genera and moderate to low gastropod

densities. Moderate stream flows (0.29 m s^{-1}) were associated with the highest density and moderate genus richness in the Grand Ronde River. Individual plots with high genus richness (3 or more genera) were found to have water velocity of less than 0.20 m s^{-1}. Gastropod density and water velocity was highly variable with high gastropod density (greater than 100 individuals m^{-2}) occurring in plots with river flows between zero and 0.74 m s^{-1}.

We analyzed the independent variables among rivers to determine which factors may account for the significant river effect on genus richness and gastropod density (Table 4). Of the physiochemical and periphyton biomass variables we assessed, temperature ($p < 0.01$), pH ($p = 0.02$), chlorophyll *a* ($p < 0.01$) and calcium ion concentrations ($p < 0.01$) were significantly different among rivers (Figure 4). Phosphates also showed a significant relationship among rivers ($p = 0.04$; Table 4), however, Turkey's pairwise comparisons showed no significant relationships between pairs. Temperature was higher in the Grand Ronde River than both Asotin Creek and the Clearwater River ($p < 0.03$). We also found higher temperatures in the Snake River compared to the Clearwater River ($p < 0.01$). The Clearwater River had lower pH levels than the Grand Ronde River and Asotin Creek ($p < 0.05$). Chlorophyll *a* levels were significantly different among all rivers except Asotin Creek and the Snake River ($p < 0.05$) with the highest levels of chlorophyll *a* found in Asotin Creek and the lowest levels in the Clearwater River. The Clearwater River was also lower in calcium ions compare to all other rivers ($p < 0.01$).

Three of the four dominant genera were found to have significant differences in length among rivers (Table 5; Figure 5). *Fluminicola* were longer in the Snake River than all other rivers ($p < 0.02$). *Vorticifex* were shorter in the Clearwater River than both the Snake and Grand Ronde Rivers ($p < 0.01$). *Physa* were longer in the Clearwater River than in Asotin Creek ($p = 0.04$) while no significant differences in length were found for the limpet *Ferressia*.

Discussion

Our survey indicates the presence of nine genera from five families including the invasive snail, *P. antipodarum*. In a survey of mollusks from the Bruneau River, a large tributary of the Snake River in southwestern Idaho, the same five families of gastropods were documented (Lysne & Clark, 2009). A comparison of the genera between our survey and the Lysne & Clark (2009) survey showed eight gastropod genera in common including the four most abundant genera in our study and *P. antipodarum*. Two gastropods found in the Bruneau River that were absent from our survey locations were the invasive *Radix auricularia* and the native *Planorbella.* Our survey results included the native limpet *Fisherola* which was absent from the Bruneau River (Lysne & Clark, 2009). Lysne & Clark (2009) found eleven species in ten genera of gastropods indicating that our survey results using only genus level identification are comparable to surveys in this area that identify gastropods to the species level.

We found that gastropod density was directly correlated with both AFDM and calcium ion concentrations. Our survey assessed periphyton biomass using both chlorophyll *a* and AFDM. These variables were not strongly co-linear (Table 2) and both measures of biomass showed a positive trend with gastropod density, however, the relationship between chlorophyll *a* and gastropod density was not significant ($p = 0.06$). The majority of freshwater gastropods are grazers of aufwuchs which is composed of a matrix of bacteria, algae, fungi, and protozoans attached to benthic substrates (Aldridge, 1983). AFDM accounts for all of the organisms in periphyton (living and dead) while chlorophyll *a* measures only actively photosynthesizing organisms (Hauer & Lamberti, 1996). The significant correlation for AFDM and gastropod density in our study may indicate that gastropods are utilizing non-phototsynthic members of the periphyton and detritus as a food source. In a study of two prosobranch snails in the Ohio River,

dietary analysis showed detritus as the main food source, especially as water depth increased (Greenwood & Thorp, 2001). Stable isotope analyses suggest a mixed diet of detritus and microalgae for different species of gastropods with large variation between individuals (Doi et al., 2010; Sitnikova et al., 2012).

Alternatively, the significant correlation of AFDM and the near significant correlation of chlorophyll *a* to gastropod density in our study may indicate high consumption of photosynthetic members of the periphyton to the point of lowering the standing stock of diatoms and algae. Gastropods preferentially graze diatoms and algae (Connor & Edgar, 1982; Cattaneo & Kalff, 1986; Liess & Kahlert, 2007) which may result in a lower proportion of photosynthetic organisms in periphyton. Of course, both of these alternatives assume competition is occurring between gastropods and that aufwuch is a limiting resource. Several studies have found food resources to be limited among gastropods (Osenberg, 1989; Hill, 1992; Cross & Benke, 2002), however further study would be required to determine if competition is occurring at our study locations and to determine the extent to which periphyton is a limited resource for gastropod density in the Lower Snake River and its tributaries.

Calcium ion levels and overall conductivity are important for growth and reproduction in freshwater gastropods which obtain up to 80% of their calcium ions directly from the water (Kefford & Nugegoda, 2005; Zalizniak et al., 2009). As calcium concentrations in the environment are reduced, freshwater gastropods begin to lose ions to the environment resulting in decreased shell strength, reduced locomotion, and increased metabolic demands (Hunter et al., 1967; Zalizniak et al., 2009; Dalesman & Lukowiak, 2010). Passive transport of calcium ions is limited below 20 mg l^{-1} for most freshwater gastropod species and requires substantial energy to actively move calcium ions into the organism resulting in decreased survival (Dalesman &

Lukowiak, 2010). Forty percent of the sites we sampled had calcium concentrations below 20 mg l^{-1} with the lowest calcium concentrations found in the Clearwater River (mean of 8.9 mg l^{-1}). Similar results for calcium ion concentrations were found in a survey of the Snake River and its tributaries (Mann et al., 2010). Mann and colleagues (2010) found mean summer calcium ion levels of 29.7 and 4.0 mg l^{-1} for the Lower Snake River and Clearwater River respectively. Our results indicate that calcium may be a limiting factor for gastropod density in the Clearwater River and in some areas of the Snake River and its other tributaries.

We found that temperature, pH, chlorophyll *a* and calcium ion concentrations were significantly different among rivers and may explain the differences in the number of genera and densities of gastropods among rivers. The Clearwater River had significantly low temperatures, pH, chlorophyll *a,* and calcium ion levels than the other rivers. These results may explain the low levels of both number of genera and densities of gastropods found in the Clearwater River as high pH and calcium levels are associated with higher gastropod diversity (Dillon, 2000; Hoverman et al., 2011) and low chlorophyll *a* levels may indicate low algae biomass which can result in limited food resources for gastropods (Osenberg, 1989; Hill, 1992).

A significant river and water velocity interaction effect was observed for genus richness and gastropod density where water velocity was positively correlated with genus richness and gastropod density. These results are counterintuitive as native snails of the Snake River have been shown to have detachment velocities between 0.17 and 0.20 m s^{-1} in laboratory experiments (Lysne & Koetsier, 2006). In our study, high gastropods densities (greater than 100 individuals m^{-2}) were associated with water velocities between zero and 0.74 m s^{-1}. These results may reflect the differences in substrates between laboratory experiments (smooth PVC pipe; Lysne &

Koetsier, 2006) and natural stream bottoms (medium to large cobble) which can provide refuges for snails (Sepulveda & Marczak 2011).

The length of three of the four dominant genera of snails indicates differences in gastropod size between rivers. The hydrobiid, *Fluminicola* was significantly larger in the Snake River than all the other rivers. Larger *Fluminicola* were found at the two most southern sites on the Snake River where chlorophyll *a* levels (> 20 $\mu g\ l^{-1}$) and calcium ion concentrations were high (> 20 $mg\ l^{-1}$). Arakelova & Michel (2009) suggested that snail growth was faster on an algae diet compared to a detritus diet due to the higher caloric content of algae. The higher levels of chlorophyll *a* at the two southern sites of the Snake River may provide more energy for *Fluminicola* growth resulting in larger snails at these sites. The high levels of calcium ions would also reduce the metabolic demands on snails in the Snake River due to the ability to passively transport calcium ions (Dalesman & Lukowiak, 2010). It is also possible that the high abundance of *Fluminicola* in the Grand Ronde River (Table 1) resulted in higher levels of competition among individuals resulting in shorter lengths. Interspecific and intraspecific competition between hydrobiid snails can result in slower growth rates (Gorbushin, 1996). The lower snail density (Table 1) in the Snake River may have reduced the effects of competition allowing increased growth and longer body size in *Fluminicola* in the Snake River.

The length for *Vorticifex* was significantly larger in the Grand Ronde and Snake Rivers than the Clearwater River. The small size of *Vorticifex* in the Clearwater River may be attributed to the low calcium concentrations, low chlorophyll *a* levels, and the low pH of the river which can increase metabolic demands on snails (Dalesman & Lukowiak, 2010). However, the smaller length of *Vorticifex* in the Clearwater River may also be a result of small sample size (n=6). The

larger length of *Physa* in the Clearwater River than in Asotin Creek may also be attributed to the limited number of *Physa* found in the Clearwater River (n=7).

Our survey confirmed the presence of the invasive snail, *Potamopyrgus antipodarum*, in the Lower Snake River. *P. antipodarum* was found in two sites at the confluence of Asotin Creek and the Snake River at low densities (< 1 snail m^{-2}). *P. antipodarum* may negatively impact native gastropod populations by competing for preferred habitat, reducing the reproductive success of native gastropods, attracting fish predators, and increasing native predators of endemic snails (Bowler, 1991; Zaranko et al., 1997). In the Snake River, *P. antipodarum* can reach densities of 40,000 individuals m^{-2} and account for 85% of the snail community (Zaranko et al., 1997). Riley et al. (2008) investigated the impacts *P. antipodarum* had on *Pyrgulopsis robusta*, an endemic snail in Polecat Creek in Wyoming. They found that *P. antipodarum* negatively influenced the growth rates of *P. robusta* while the presence of *P. robusta* positively influenced the growth of *P. antipodarum* (Riley et al., 2008). *P. antipodarum* also reduced the growth of the threatened Bliss Rapids snail, *Taylorconcha serpenticola,* in laboratory experiments (Richards & Shinn, 2004).

However, other studies have found no impact or positive associations between native snail populations and *P. antipodarum*. Lysne & Koetsier (2008) found that *P. antipodarum* did not impose competitive pressure on the native snail, *Valvata utahensis*. In fact, at low densities (240 individuals m^{-2}), the presence of *P. antipodarum* increased the growth rate of *V. utahensis* (Lysne & Koetsier, 2008). Cope & Winterbourn (2004) conducted laboratory experiments with *P. antipodarum* and *Physella acuta* and found that *P. antipodarum* did not significantly affect growth in *P. acuta* and facilitated egg production in *P. acuta*. These contradictory results on the influence of *P. antipodarum* on the growth of other snails warrant further study.

Conclusions

Documenting the density and richness of freshwater gastropods is critical to the conservation of these highly imperiled taxa (Lydeard et al., 2004; Strong et al., 2008). In the Snake River, many gastropods are threatened by anthropogenic affects including impoundments and invasive species (Lysne & Koetsier, 2006; Richards & Arrington, 2008). Our survey is one of the few baseline gastropod surveys conducted in the Lower Snake River and its tributaries prior to the establishment of the invasive gastropod, *Potamopyrgus antipodarum.* Our results suggests the native gastropod genus richness is influenced by water velocity and river of origin while gastropod density is influenced by calcium ion concentrations, periphyton biomass as AFDM, water velocity, and the river of origin.

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Table 1. Genus richness and total gastropod density (gastropods m^{-2}) by site location. Genus density (gastropods m^{-2}) of the four most abundant gastropods and the invasive *Potamopyrgus antipodarum* are given by site.

River	Site	Genus Richness	Total Gastropod Density (m^2)	Genus Density	*Fluminicola*	*Physa*	*P. antipodarum*	*Ferrissia*	*Vorticifex*
Clearwater									
	CW1	3	11.11		8	1.78	-	-	1.33
	CW2	1	5.33		5.33	-	-	-	-
	CW3	4	5.33		2.22	1.33	-	-	1.33
	CW4	0	0.00		-	-	-	-	-
Average		2.0	5.44		3.89	0.78	-	-	0.67
Grand Ronde									
	GR0	5	540.9		204.89	-	-	278.22	40.00
	GR1	5	366.67		285.78	-	-	14.22	36.89
	GR2	1	93.33		92.89	-	-	-	-
	GR3	1	5.77		5.78	-	-	-	-
Average		3.0	251.66		147.33	-	-	73.11	19.22
Asotin Creek									
	AC0	4	44.88		0.44	69.33	-	0.44	0.44
	AC1	3	189.77		0.44	258.22	0.89	-	-
Average		3.5	117.33		0.44	163.78	0.44	0.22	0.22
Snake									
	S1	7	625.33		5.33	166.22	0.44	164.44	271.56
	S2	0	0.00		-	-	-	-	-
	S3	1	0.44		0.44	-	-	-	-
	S4	3	70.66		36.44	-	-	4.89	-
	S5	4	196.00		14.22	-	-	126.67	51.11
Average		3.0	178.49		11.29	33.24	0.09	59.20	64.53

Table 2. Pearson's Correlation Matrix for independent variables showing strength of co-linearity. Bold numbers indicate strong co-linearity between independent variables. Ash-free dry mass is abbreviated by AFDM while SA represents surface area.

	Temperature	pH	Conductivity	Dissolved Oxygen	Chlorophyll *a*	AFDM	Nitrate	Phosphate	Rock SA	Calcium ions
Temperature	1.00									
pH	0.44	1.00								
Conductivity	-0.56	-0.21	1.00							
Dissolved Oxygen	0.31	0.25	0.51	1.00						
Chlorophyll *a*	0.20	0.41	-0.66	-0.40	1.00					
AFDM	-0.04	-0.17	-0.24	-0.43	-0.20	1.00				
Nitrate	0.11	-0.00	-0.19	0.16	0.16	-0.19	1.00			
Phosphate	-0.01	0.03	0.65	0.65	-0.63	-0.23	-0.02	1.00		
Rock SA	-0.40	-0.35	-0.19	-0.43	0.20	-0.03	0.26	-0.43	1.00	
Calcium ions	0.39	0.36	**-0.82**	-0.59	0.68	0.41	-0.14	-0.62	-0.16	1.00

Table 3. Analysis of variance of genera richness and gastropod density for river, water velocity, and depth for Snake River Gastropod Survey. The degress of freedom (df), sum of squares (SS), mean squares (MS), f-ratio (F) and p-value (P) are given for each statistical test. Bold numbers indicate significant p-values.

Source of Variation	df	SS	MS	F	P
Genera Richness					
Depth	2	1.28	0.64	0.39	0.68
River	3	55.15	18.38	11.11	**<0.01**
Water Velocity	1	0.27	0.27	0.16	0.69
Depth X Water Velocity	2	1.40	0.70	0.42	0.656
River X Water Velocity	3	15.87	5.29	3.20	**0.03**
River X Depth	6	3.19	0.53	0.32	0.93
River X Depth X Water Velocity	6	3.97	0.66	0.40	0.88
Error	111	183.64	1.65		
Gastropod Density					
Depth	2	130890.32	65445.16	1.08	0.34
River	3	1896642.09	632214.03	10.45	**<0.01**
Water Velocity	1	35391.22	35391.22	0.59	0.45
Depth X Water Velocity	2	22573.02	11286.51	0.19	0.83
River X Water Velocity	3	664994.05	221664.68	3.66	**0.02**
River X Depth	6	213035.78	35505.96	0.59	0.74
River X Depth X Water Velocity	6	267757.26	44626.21	0.74	0.62
Error	111	6715956.57	60504.11		

Table 4. Analysis of variance of independent variables by river. Only independent variables that met parametric assumptions of normal distribution and equal variance were included in analysis. The degress of freedom (df), sum of squares (SS), mean squares (MS), f-ratio (F) and p-value (P) are given for each statistical test. Bold numbers indicate significant p-values.

Variation in Independent Variables by River	df	SS	MS	F	P
Temperature	3	0.69	0.23	11.62	**<0.01**
pH	3	0.06	0.02	5.37	**0.02**
Dissolved Oxygen	3	6.98	2.33	1.46	0.28
Chlorophyll a	3	7.09	2.36	32.07	**<0.01**
Ash-free Dry Mass	3	0.23	0.08	0.98	0.49
Nitrate	3	56263.42	18754.47	0.64	0.60
Phosphate	3	0.07	0.02	4.02	**0.04**
Calcium ions	3	4.04	1.35	10.44	**<0.01**

Table 5. Analysis of variance of body length as total shell length for the four most abundant genera by river. The degress of freedom (df), sum of squares (SS), mean squares (MS), f-ratio (F) and p-value (P) are given for each statistical test. Bold numbers indicate significant p-values.

Variation in TSL by River	df	SS	MS	F	P
Flumicola	3	848.68	282.89	6.94	**<0.01**
Vorticifex	3	256.58	85.53	7.34	**<0.01**
Physa	3	70.83	35.42	4.42	**<0.05**
Ferrissia	2	2.04	1.02	0.93	0.42

Chapter 1 - Figure Legend

Figure 1. Map of fifteen site locations along the Snake River and three tributaries.

Figure 2. Gastropod genera richness for each of the four rivers. Letters represent significant differences among rivers. Error bars represent standard error

Figure 3. Gastropod density for each river. Letters represent significant differences among rivers. Error bars represent standard error

Figure 4. Differences among rivers for temperature (A), pH (B), chlorophyll *a* (C), and calcium ion concentrations (D). Rivers are abbreviated CW (Clearwater River), GR (Grand Ronde River), AC (Asotin Creek) and S (Snake River). Letters represent significant differences among rivers. Error bars represent standard error

Figure 5. Body length as total shell length for *Fluminicola* (A), *Vorticifex* (B), and *Physa* (C). Rivers are abbreviated CW (Clearwater River), GR (Grand Ronde River), AC (Asotin Creek) and S (Snake River). Letters represent significant differences among rivers. Error bars represent standard error.

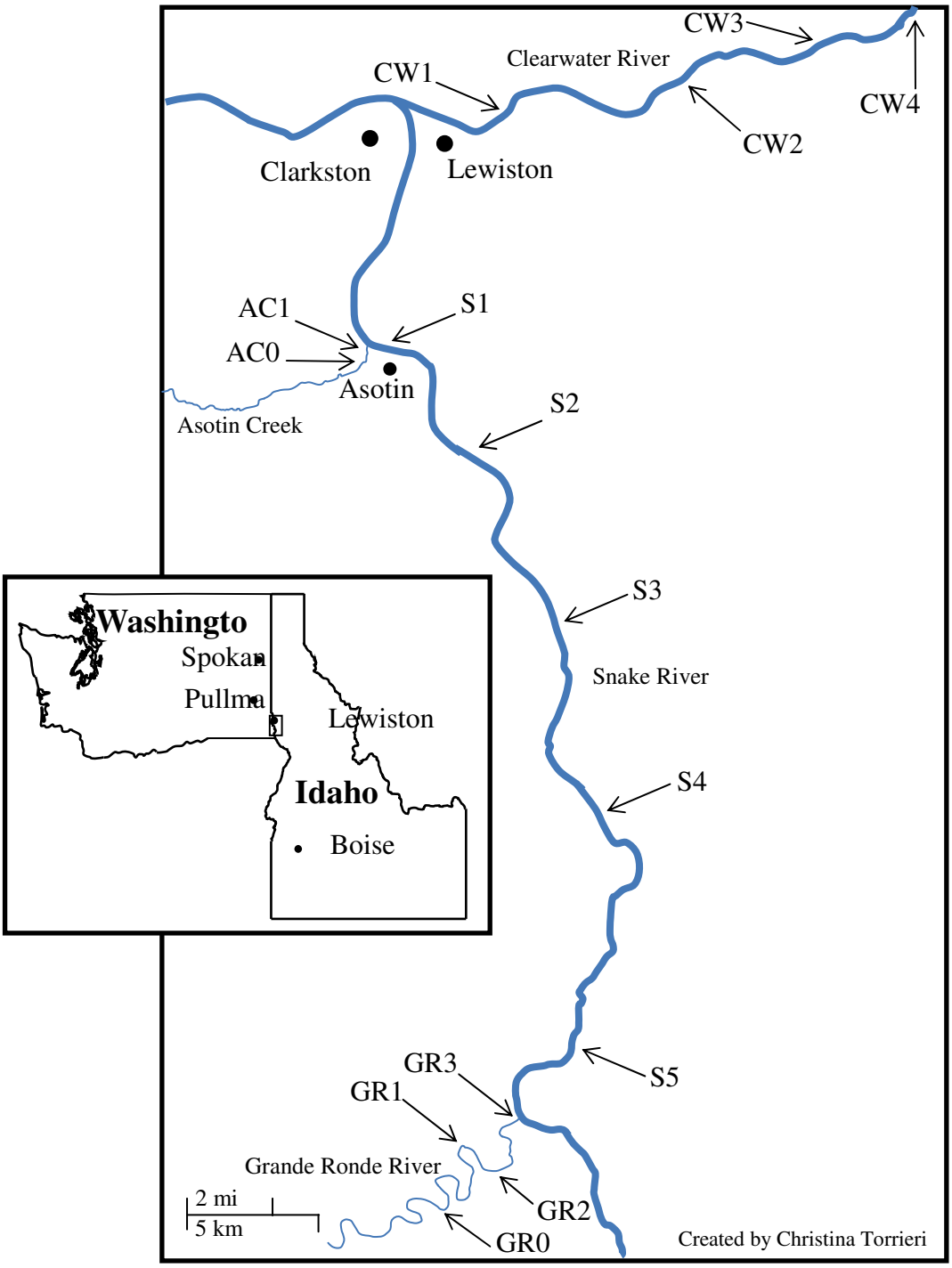
CW3
Clearwater River
CW1
CW4
CW2
Clarkston
Lewiston
AC1
S1
AC0
Asotin
Asotin Creek
S2
S3
Washingto
Spokan
Snake River
Pullma
Lewiston
S4
Idaho
Boise
GR3
S5
GR1
Grande Ronde River
2 mi
5 km
GR2
GR0
Created by Christina Torrieri

Figure 1.

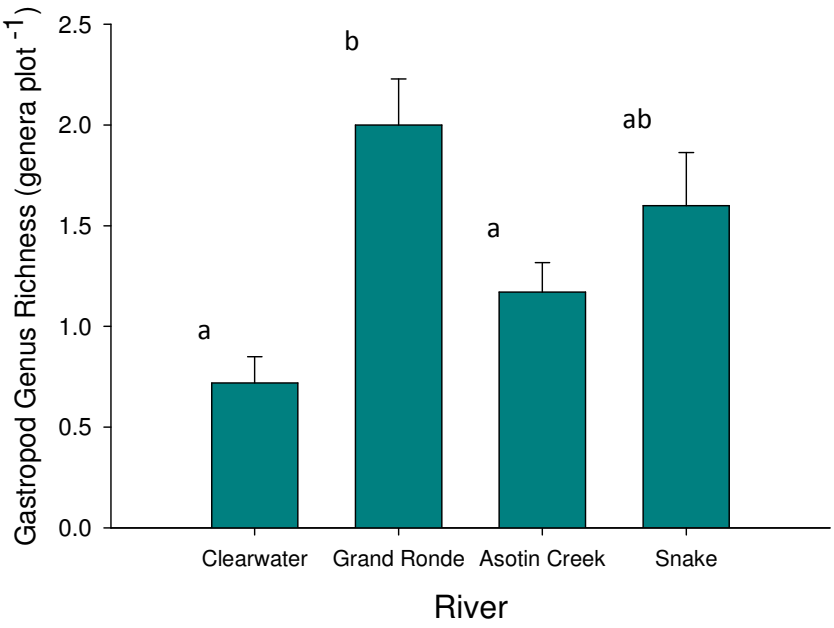

Figure 2.

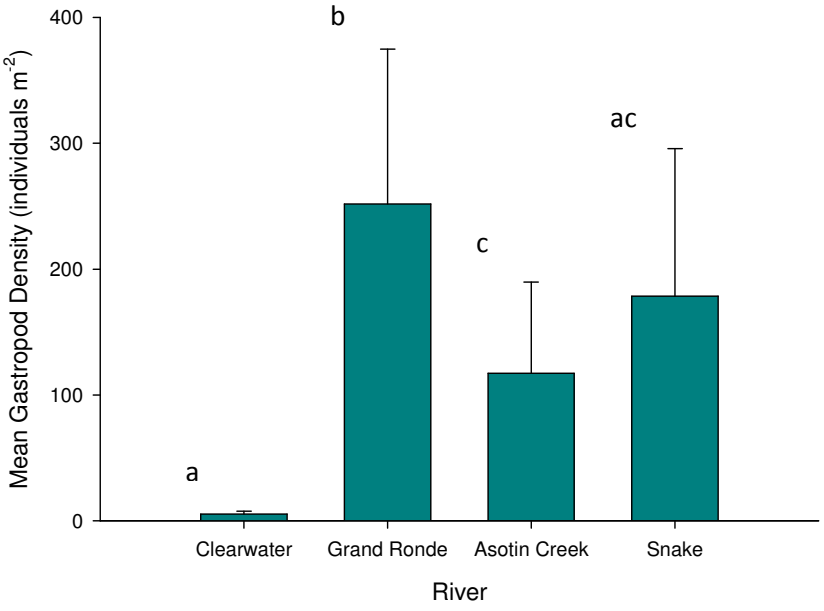

Figure 3.

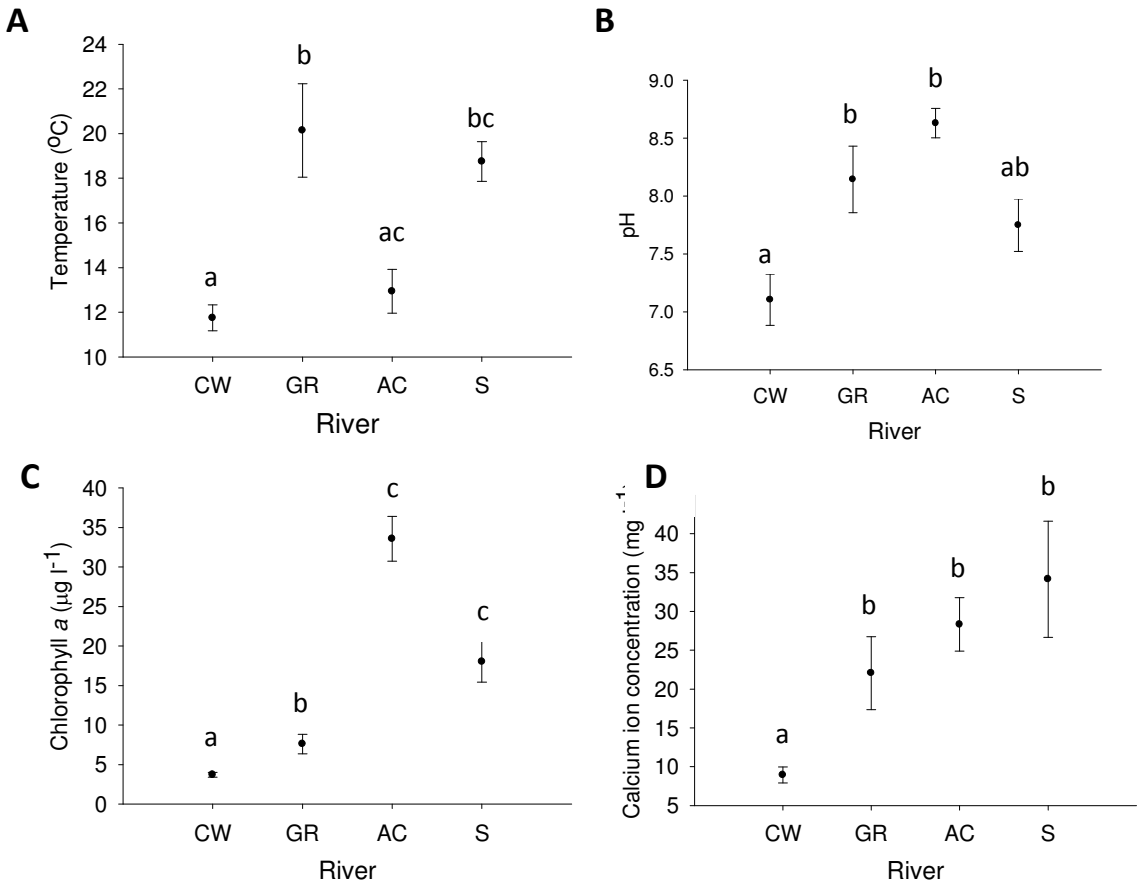
A
Temperature (°C)
24
22
20
18
16
14
12
10
a
b
ac
bc
CW
GR
AC
S
River
B
pH
9.0
8.5
8.0
7.5
7.0
6.5
a
b
b
ab
CW
GR
AC
S
River
C
Chlorophyll a (µg l-1)
40
35
30
25
20
15
10
5
0
a
b
c
c
CW
GR
AC
S
River
D
Calcium ion concentration (mg
40
35
30
25
20
15
10
5
a
b
b
b
CW
GR
AC
S
River

Figure 4.

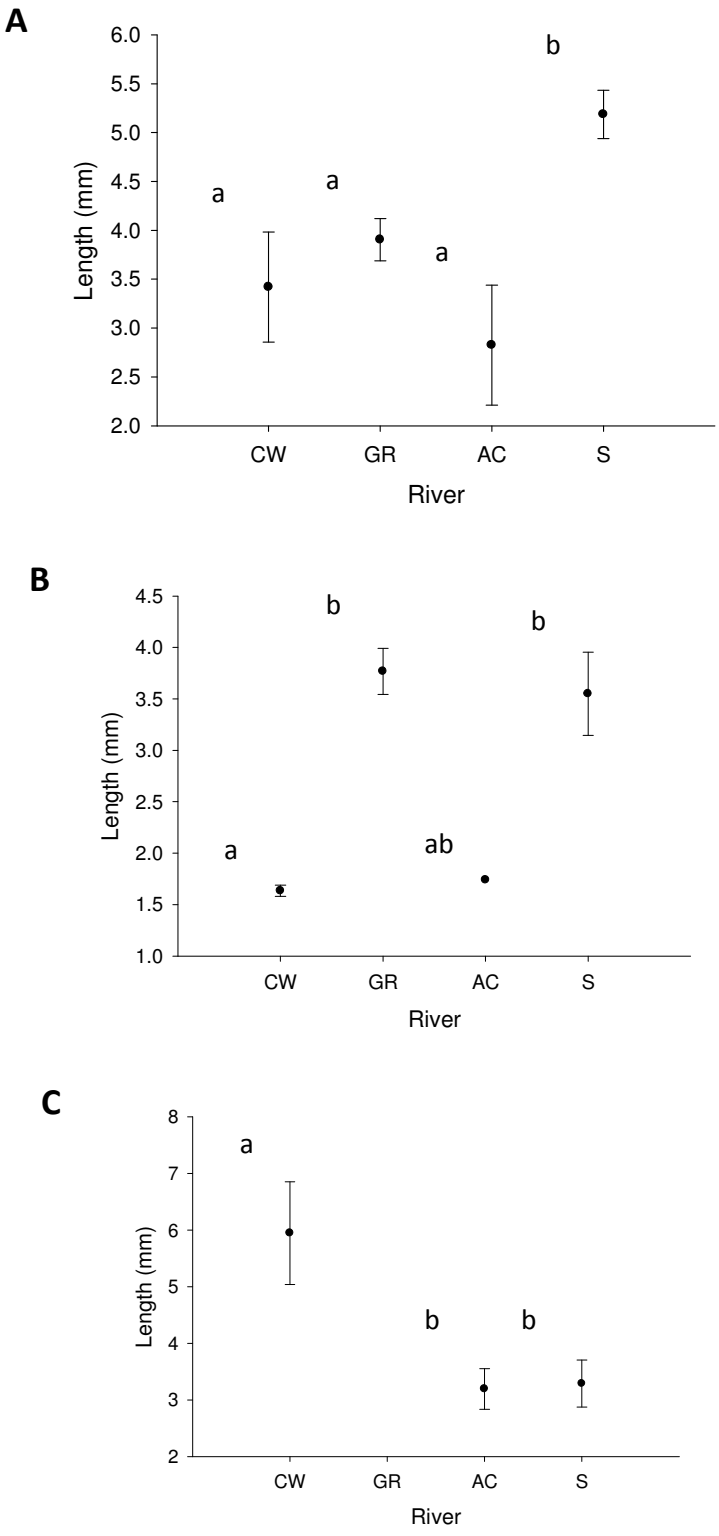
A
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
Length (mm)
a
a
a
b
CW
GR
AC
S
River
B
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Length (mm)
a
b
ab
b
CW
GR
AC
S
River
C
8
7
6
5
4
3
2
Length (mm)
a
b
b
CW
GR
AC
S
River

Figure 5.

Chapter 2

Grazing Trials and Competition between the native snail, *Fluminicola*, and the New Zealand mud snail, *Potamopyrgus antipodarum*.

Abstract

The New Zealand mud snail, *Potamopyrgus antipodarum*, is an invasive gastropod that can impact native macroinvertebrate population, including native gastropods. However, conflicting results from competition experiments between native gastropods and *P. antipodarum* has resulted in ambiguous understanding of the impacts *P. antipodarum* may be having on native gastropods. We conducted grazing trials with the native gastropod, *Fluminicola* under interspecific and intraspecific competition to aid in the understanding of how *P. antipodarum* may be impacting this native gastropod. Two different interspecific grazing trials were conducted; one for six hours in ambient light and the other for 24 hours in darkness. The intraspecific competition experiment was conducted for 24 hours in darkness. For each experiment snail mass, total fecal mass, gram-specific fecal mass, grazing rate, and remaining algal biomass on tiles (as chlorophyll *a* levels) were calculated. The interspecific grazing trial did not show effects of grazing while the intraspecific grazing experiment showed grazing effects with higher densities of *Fluminicola* resulting in higher grazing rates. These results may indicate that intraspecific competition among *Fluminicola* is stronger than interspecific competition between *Fluminicola* and *P. antipodarum*.

Introduction

Competition for limited food resources can occur in benthic macroinvertebrates in lotic environments (Hill, 1992; Cross & Benke, 2002). Gastropods and other periphyton grazers can experience exploitative competition when high population densities result in food resource depletion (Osenberg, 1989; Hill, 1992; Cross & Benke, 2002). Experiments with gastropods indicate an inverse relationship between gastropod density and periphyton biomass (Osenberg, 1989; Munoz et al., 2000; Liess & Kahlert, 2007) as well as lower grazing rates in gastropods at higher densities (Brown et al., 1994; King-Lotufo et al., 2002).

Interspecific and intraspecific competition are known to occur among gastropods. Lower growth and reproductive rates are often found in gastropod populations experiencing both interspecific and intraspecific competition (Brown, 1982; Hill, 1992; Cross & Benke, 2002), however, in some interspecific interactions only one species is negatively impacted (Gorbushin, 1996). Yet, coexistence of sympatric gastropods can be found in many locations and may be regulated by differences in life history, resource partitioning, or higher influences of intraspecific competition (Cross & Benke, 2002; Arakelova & Michel, 2009).

Invasive gastropods alter native communities and can impact native freshwater gastropods through competition and habitat alteration (Strayer, 1999). Invasive gastropods can directly compete with native gastropods for resources including space and food (Byers, 2000; Cope & Winterbourn, 2004; Lysne et al., 2008; Riley et al., 2008). Native gastropods can also experience indirect competition by invasive gastropods through alteration of nutrient cycling (Hall et al., 2003; Tibbets et al., 2010) and increased risk of predation by fishes drawn to the high densities of often inedible invasive gastropods (Bowler, 1991).

The New Zealand mud snail, *Potamopyrgus antipodarum,* is a hydrobiid snail that can reach high densities in invaded areas (Kerans et al., 2005; Hall et al., 2006). Individual snails are capable of parthenogenic reproduction at 3-3.5mm in size with two or more generations produced each year resulting in annual fecundity exceeding 230 offspring (Zaranko et al., 1997; Weetman et al., 2006). *P. antipodarum* feeds primarily on periphyton and prefers filamentous green algae, diatoms, and cyanobacteria (Dorgelo & Leonards, 2001; Arango et al., 2009). *P. antipodarum* can impact native ecosystems by altering carbon and nitrogen levels (Hall et al., 2003; Arango et al., 2009), consuming large amounts of primary producer biomass (Riley et al., 2008; Strayer, 2010), and changing native macroinvertebrate community composition (Kerans et al., 2005; Cross et al., 2010; Brenneis et al., 2011; Moore et al., 2012).

P. antipodarum has been shown to impact growth rates in native gastropods. Riley and colleagues (2008) investigated the impacts *P. antipodarum* had on *Pyrgulopsis robusta*, an endemic snail in Polecat Creek in Wyoming. *P. antipodarum* was found to negatively influence the growth rates of *P. robusta* while the presence of *P. robusta* positively influenced the growth of *P. antipodarum* (Riley et al., 2008). Competition between *P. antipodarum* and the native snail *Fossaria* indicate that at equal biomass, *P. antipodarum* reduces the growth of *Fossaria* (Thon, 2010). Further, Thon (2010) found that the presence of *Fossaria* facilitated the growth of *P. antipodarum*. In laboratory experiments, *P. antipodarum* also reduced the growth of the threatened Bliss Rapids snail, *Taylorconcha serpenticola* (Richards & Shinn, 2004). However, Lysne and Koetsier (2008) found that *P. antipodarum* did not impose competitive pressure on the native snail, *Valvata utahensis*. In fact, at low densities (240 individuals m^{-2}), the presence of *P. antipodarum* increased the growth rate of *V. utahensis* (Lysne & Koetsier, 2008).

These contradictory results on the influence of *P. antipodarum* on the growth of other gastropods warrant further study. We conducted laboratory experiments to determine the difference in grazing rates between the native snail *Fluminicola* and *P. antipodarum*. Interspecific grazing experiments were conducted using a fixed number of individuals of *Fluminicola* at three densities of *P. antipodarum*. Additionally, we conducted intraspecific grazing trials with *Fluminicola* to determine which type of competition was more detrimental to *Fluminicola* grazing rates. We predicted that (1) higher densities of *P. antipodarum* would result in lower grazing rates and (2) higher snail biomass regardless of snail composition would reduce periphyton biomass (as chlorophyll *a* levels).

Methods

Specimen Collection and Housing

Ceramic grazing tiles (5 cm x 5 cm) were placed in low-sided crates and suspended at the surface of the Turnbull Lab Pond (natural wetland pond) at Turnbull Laboratory for Ecological Studies for one month prior to being placed in Bold's growth media (James, 1978) in the laboratory. Grazing tiles were placed under strong (2,250 lux), cool-white lighting on a 16:8 light:dark cycle for two weeks before grazing trials. The native snail, *Flumincola*, was hand collected from Grand Ronde River approximately 3 km upstream from the confluence with the Snake River. The invasive snail, *P. antipodarum*, was hand collected from Riley Creek in the Hagerman Fish Hatchery, Hagerman, Idaho. Snails were housed in species specific aquaria at 16-18 ºC with aeration and a 12:12 light:dark cycle. Snails were fed ground spinach twice a week for the three weeks prior to grazing trials. All snails were starved for 24 hour prior to grazing trails to allow gut clearance.

Interspecific Snail Grazing Experiments

Snail competition experiments were conducted to determine if *P. antipodarum* influences grazing rates of *Fluminicola* under different density treatments. For each experiment, ceramic tiles were removed from growth media and the periphyton was removed from the sides and back of each tile using a small brush to give a total grazing surface area of 25 cm^2. A single tile was randomly placed on the bottom of a 500 mL plastic container filled with 200 mL of pond water. We placed three densities of *P. antipodarum* with a constant number of *Fluminicola* and grazing trials were conducted following Brown *et al* 1994.

For the six hour trial, we placed one *Fluminicola* with one, four, or eight *P. antipodarum* (Table 1). Single individuals of each species served as controls for snail grazing while no snails were added to containers to serve as negative controls for periphyton biomass (lost due to handling). Previous experiments indicate that water borne substance produced by *P. antipodarum* may influence the growth of other snail species (Cope and Winterbourn 2004). To investigate this possibility, we created an additional treatment with one *Fluminicola* and no *P. antipodarum*, but with half the pond water replaced with water from the *P. antipodarum* stock tank. This treatment served as the conditioned water treatment. We prepared five replicates for each treatment. Snails were randomly selected and placed into plastic containers. The six hour trials were conducted at ambient light levels.

For the 24 hour trial, we place five *Fluminicola* with five, ten, or fifteen *P. antipodarum* (Table 1). Negative controls with no snails were used to determine periphyton biomass without grazing. We did not use single individual treatments for each species due to limited numbers of both native and invasive snails. We also created a condition water treatment as stated in the

previous paragraph, but with five *Fluminicola* and no *P. antipodarum*. Eight replicates for each treatment were prepared. We randomly selected and placed snails into plastic containers. The 24 hour trial was conducted in darkness to aid in snail grazing (Liess and Lange 2011).

Intraspecific Snail Grazing Experiments

To determine if intraspecific competition occurs in *Fluminicola*, we conducted a third experiment with three densities of the native snails (Table 1). We randomly selected one, three, or eight *Fluminicola* and placed these snails into containers with periphyton covered tiles. A treatment without snails added to containers served as negative controls for periphyton biomass. We prepared five replicates for each treatment and allowed snails to graze for 24 hours in darkness.

At the end of each experiment, we removed all the snails and determined snail wet mass using an analytical scale. The tiles were removed and scrubbed into 1000 mL of distilled water to determine remaining algae biomass as chlorophyll *a* using fluorometry. We strained fecal pellets from the water using pre-weighted glass fiber filters as described in Brown *et al* (1994). We dried filters in drying oven at 60º C overnight prior to reweighting filters to determine fecal mass. We conducted all measurements on an analytical balance to the nearest 0.1 mg.

Statistical Analyses

Due to the non-parametric nature of the data set, we used ranked one-way ANOVA tests to determine differences in snail mass (SM), total fecal mass (TFM), gram-specific fecal mass (g-sFM), grazing rates (GR), and chlorophyll *a* levels for each of the experimental treatments

(Quinn & Keough, 2002; Zar, 2010). All statistical analyses were conducted using SYSTAT version 13.

Results

Interspecific Snail Grazing Experiments

In the six hour experiments SM, TFM, and g-sFM showed significant treatment effects (Table 2). The single *P. antipodarum* (1P) treatment had lower SM ($p < 0.01$) than the conditioned water treatment (1F:0PCW), the one *Fluminicola* and four *P. antipodarum* treatment (1F:4P), and the one *Fluminicola* and eight *P. antipodarum* treatment (1F:8P; Figure 1a). SM was higher ($p < 0.02$) in the 1F:8P treatment than the single snail controls (1F and 1P) and the equal one to one snail treatment (1F:1P; Figure 1a). TFM was lower in both 1F and 1P than the 1F:8P treatment ($p = 0.03$; Figure 1b). When fecal mass was normalized to snail mass (g-sFM), the 1P treatment had higher g-sFM than all of the other treatments (Figure 1c). Significant treatment effects were absent on chlorophyll *a* and GR (Figure 1d).

TFM and chlorophyll *a* were the only dependent variables with significant treatment effects for the 24 hour grazing trails (Table 2; Figures 2a-d). SM, g-sFM, and GR did not have significant treatment effects. The five *Fluminicola* and fifteen *P. antipodarum* treatment (5F:15P) had higher TFM than the control ($p = 0.01$). Chlorophyll *a* was lower in the control treatment than in the other treatments ($p < 0.02$).

Intraspecific Snail Grazing Experiments

In the *Fluminicola* intraspecific experiments significant treatment effects were seen to affect SM, TFM, g-sFM, and GR (Table 2). SM was significantly different among all treatments

($p < 0.01$) with a positive linear relationship between SM and snail density (Figure 3a). However, TFM only show a significant treatment effect between the single *Fluminicola* treatment (1F) and the eight *Fluminicola* treatment (8F; $p = 0.02$) with the higher snail density having higher TFM (Figure 3b). The same pattern was seen in GR with lower grazing rates in the 1F treatment when compared to the 8F treatment ($p = 0.02$; Figure 3d). *Fluminicola* showed higher g-sFM in the 1F treatment compared to the 8F treatment ($p < 0.01$; Figure 3c). No significant difference in chlorophyll *a* was observed among treatments.

Discussion

The results of our interspecific grazing experiments indicate that the highest density treatments had higher fecal production, however, when TFM was normalized to SM only the 1P treatment in the six hour trial was significantly different from the other treatments. A comparison between 1P and 1F treatments from the six hour interspecific grazing trial shows that *P. antipodarum* consumed 4.8 times more periphyton based on g-sFM than *Fluminicola* (Table 3). These results suggest that *P. antipodarum* may be the dominant grazer and may possibly out-compete *Fluminicola*.

P. antipodarum can consume large amounts of periphyton, but reduces chlororphyll *a* to similar or near similar levels as native macroinvertebrate grazers (Krist & Charles, 2012) and native snails (Riley et al., 2008). These results suggest that *P. antipodarum* competes with native grazers for periphyton, but does not account for the dominance of *P. antipodarum* in invaded systems (Riley et al., 2008). Possible explanations for the dominance of *P. antipodarum* despite equal periphyton consumption are that *P. antipodarum* has higher grazing and assimilation rates, has lower metabolic maintenance costs, or changes the periphyton community to species that are

less edible for native grazers (Riley et al., 2008; Krist & Charles, 2012). The small size of *P. antipodarum* compared to other macroinvertebrates may infer higher ingestion rate of algae as smaller animals usually have higher ingestion rates than larger animals (Krist & Charles, 2012). In laboratory experiments, *P. antipodarum* can have higher grazing rates, but lower assimilation efficiency than the mayfly, *Deleatidum sp*., across several periphyton densities (Broekhuizen et al., 2002). Yet, if *P. antipodarum* has lower metabolic demands than other grazers, the discrepancy between ingestion rate and assimilation rate may not negatively impact population growth rates for *P. antipodarum*. High densities of *P. antipodarum* in areas of equal periphyton grazing may also be attributed to the removal of edible algae by *P. antipodarum* which may restrict grazing in native species. Krist & Charles (2012) found that *P. antipodarum* altered the periphyton community more than native grazers and the new periphyton community consisted of small and adnate species resistant to grazing. Further research is needed to determine the underlying cause of competitive dominance in *P. antipodarum*.

Growth rates in snails have been shown to change with increased snail density and composition (Gresens, 1995; Cross & Benke, 2002; Cope & Winterbourn, 2004). Field and laboratory experiments with two coexisting species of *Elimia* found decreased growth rates at higher snail densities regardless of species composition (intraspecific verses interspecific competition; Cross & Benke, 2002). In contrast, experiments with two coexisting mud snails *(Hydrobia sp.)* found asymmetrical growth rates when interspecific competition occurred (Gorbushin, 1996). *Hydrobia ventrosa* showed reduced growth rates when housed with congeners while *Hydrobia ulvae's* growth rates increased in the presence of *H. ventrosa* (Gorbushin, 1996). Although our experiments showed no significant effects for GR in the interspecific trials, this may reflect the lack of significance between most treatments for SM than

a true lack of interspecific competition. Treatment groups with greater differences in SM may provide better insight into differences in interspecific competition between *Fluminicola* and *P. antipodarum* as competition has been found between *P. antipodarum* and other native snails (Bowler, 1991; Richards & Shinn, 2004; Riley et al., 2008; Filippenko, 2011).

The CW treatment in the 24 hour grazing trail showed no effect which suggests that any chemical signals produced and released into the water by *P. antipodarum* may not interfere with grazing in *Fluminicola*. Brown et al. (1994) also found no influence of water conditioning on intraspecific grazing rates using *Physella virgata*. In water treatment experiments between *P. antipodarum* and *Physella acuta*, Cope & Winterbourn (2004) found no effect of water conditioning on growth in *P. antipodarum*. However, *P. acuta* grown in *P. antipodarum* conditioned water did show increased shell growth compared to *P. acuta* grown in water conditioned by conspecifics (Cope & Winterbourn, 2004). The increased growth of *P. acuta* in water conditioned by *P. antipodarum* suggests the presence of metabolites or other chemical signals released by *P. antipodarum* which may induce growth and possibly earlier reproduction in *P. acuta* when *P. antipodarum* is present (Cope & Winterbourn, 2004).

Chlorophyll *a* levels were lower for the control without snails than any of the snail treatments during the 24 hour interspecific grazing experiment. These results may be an artifact of the experimental design in that low periphyton covered tiles may have been inadvertently placed into the control treatments or may reflect the fast generation time associated with some diatoms and other members of the periphyton. Snail grazing can increase growth in neighboring algae at small spatial scales presumably due to increased substrate availability and increased nutrients released as snail waste (Kawata et al., 2001). This may account for the increased levels of chlorophyll *a* in our snail treatments despite grazing. However, the absence of light for the

duration of the experiment leads us to believe that difference in chlorophyll *a* for our experiment is an artifact of experimental design.

Intraspecific competition in *Fluminicola* showed an increase in both FM production and GR at high densities. Our results contradict prior research in snail grazing under intraspecific competition. The snail *Physella virgata* can experience reduced grazing rates as density of conspecific increases (King-Lotufo et al., 2002). Brown et al. (1994) also found density-dependent reductions in grazing rates for grazing experiments using *P. virgata*. In both experiments, the increase in density resulted in interference behavior (shell-shaking) between snails that may have depressed grazing rates even when periphyton levels were not limited (Brown et al., 1994; King-Lotufo et al., 2002). Periphyton levels were not a limiting resource in our grazing trials and we did not observe interference behavior in *Fluminicola* which may explain the lack of decline in GR in our trials.

In conclusion, our results indicate no effects on interspecific competition between *Fluminicola* and *P. antipodarum*. However, individual consumption based on g-sFM shows that *P. antipodarum* consumes 4.8 times more periphyton than *Fluminicola* and therefore may be the dominant consumer. Metabolites or other chemicals in water condition by *P. antipodarum* did not affect grazing in *Fluminicola*. Although intraspecific competition showed an effect on high densities of *Fluminicola*, this result appears to indicate that grazing was increased at high densities. Overall, further research into the competitive interactions between *Fluminicola* and *P. antipodarum* are necessary to determine how *P. antipodarum* invasions will impact this native species.

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Table 1. Experimental design for inter- and intra- specific grazing trials. The number of *Fluminicola* (F) and *P. antipodarum* (P) is indicated before each letter for each group. Conditioned water treatments (CW) contained 50% *P. antipodarum* stock tank water mixed with pond water. Positive controls were not used in either of the 24 hour trials (NA).

Experiment	# of Replicates	Controls		Experimental Groups
		Negative	Positive	
Inter-specific				
Six hour	5	0F0P	1F; 1P	1F1P; 1F4P; 1F8P; 1F0PCW
24 hour	8	0F0P	NA	5F5P; 5F10P; 5F15P; 5F0PCW
Intra-specific				
24 hour	5	0F	NA	1F; 3F; 8F

Table 2. Analysis of Variance for the four dependent variables for each grazing trial. The degress of freedom (df), sum of squares (SS), mean squares (MS), f-ratio (F) and p-value (P) are given for each statistical test. Bold numbers indicate significant p-values.

Source of Variation	df	SS	MS	F	P
Inter-specific Competition					
Six hour Experiment					
Total Snail Mass (g)	5	1502.8	300.6	9.69	**<0.01**
Total Fecal Mass (g)	6	1046.8	174.5	2.48	**<0.05**
Grazing Rate (mg/hour)	5	673.9	134.8	2.60	0.05
g-specific Fecal Mass (g)	5	1128.0	225.6	4.84	**<0.01**
Chlorophyll a (µg/L)	6	932.4	155.4	2.16	**<0.01**
24 hour Experiment					
Total Snail Mass (g)	3	528.3	176.1	2.24	0.11
Total Fecal Mass (g)	4	12.73.5	318.4	3.04	**0.03**
Grazing Rate (mg/hour)	3	294.6	98.2	1.25	0.31
g-specific Fecal Mass (g)	3	291.3	97.1	1.12	0.36
Chlorophyll a (µg/L)	4	2144.5	536.1	5.89	**<0.01**
Intra-specific Competition					
24 hour Experiment					
Total Snail Mass (g)	2	250.0	125.0	50.00	**<0.01**
Total Fecal Mass (g)	3	285.4	95.1	4.55	**0.02**
Grazing Rate (mg/hour)	3	285.4	95.1	4.55	**0.02**
g-specific Fecal Mass (g)	2	180.7	90.4	10.97	**<0.01**
Chlorophyll a (µg/L)	3	156.1	52.0	1.64	0.22

Chapter 2 - Figure Legend

Figure 1. Snail mass (A), fecal mass (B), gram-specific fecal mass (C) and grazing rate (D) for six hour interspecific competition experiment between different ratios of *Fluminicola* (F) and *P. antipodarum* (P). Conditioned water treatments are abbreviated as CW. Different letters between treatments denote significant differences. Error bars represent standard error.

Figure 2. Snail mass (A), fecal mass (B), gram-specific fecal mass (C) and grazing rate (D) for 24 hour interspecifc competition experiment between different ratios *Fluminicola* (F) and *P. antipodarum* (P). Conditioned water treatments are abbreviated as CW. Different letters between treatments denote significant differences. Error bars represent standard error.

Figure 3. Snail mass (A), fecal mass (B), gram-specific fecal mass (C) and grazing rate (D) for 24 hour intraspecifc competition experiment for different densities of *Fluminicola* (F). Different letters between treatments denote significant differences. Error bars represent standard error.

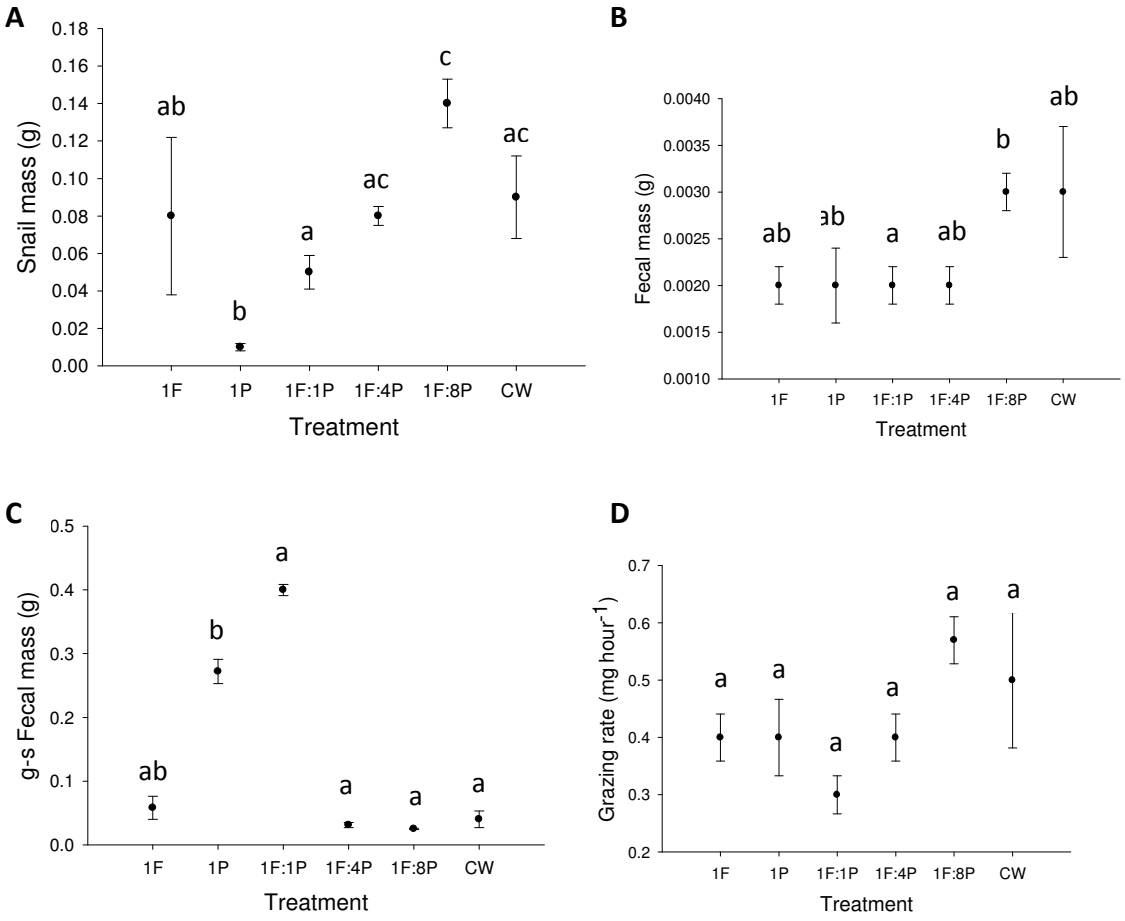
A
Snail mass (g)
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
ab
b
a
ac
c
ac
1F
1P
1F:1P
1F:4P
1F:8P
CW
Treatment
B
Fecal mass (g)
0.0040
0.0035
0.0030
0.0025
0.0020
0.0015
0.0010
ab
ab
a
ab
b
ab
1F
1P
1F:1P
1F:4P
1F:8P
CW
Treatment
C
g-s Fecal mass (g)
0.5
0.4
0.3
0.2
0.1
0.0
ab
b
a
a
a
a
1F
1P
1F:1P
1F:4P
1F:8P
CW
Treatment
D
Grazing rate (mg hour-1)
0.7
0.6
0.5
0.4
0.3
0.2
a
a
a
a
a
a
1F
1P
1F:1P
1F:4P
1F:8P
CW
Treatment

Figure 1.

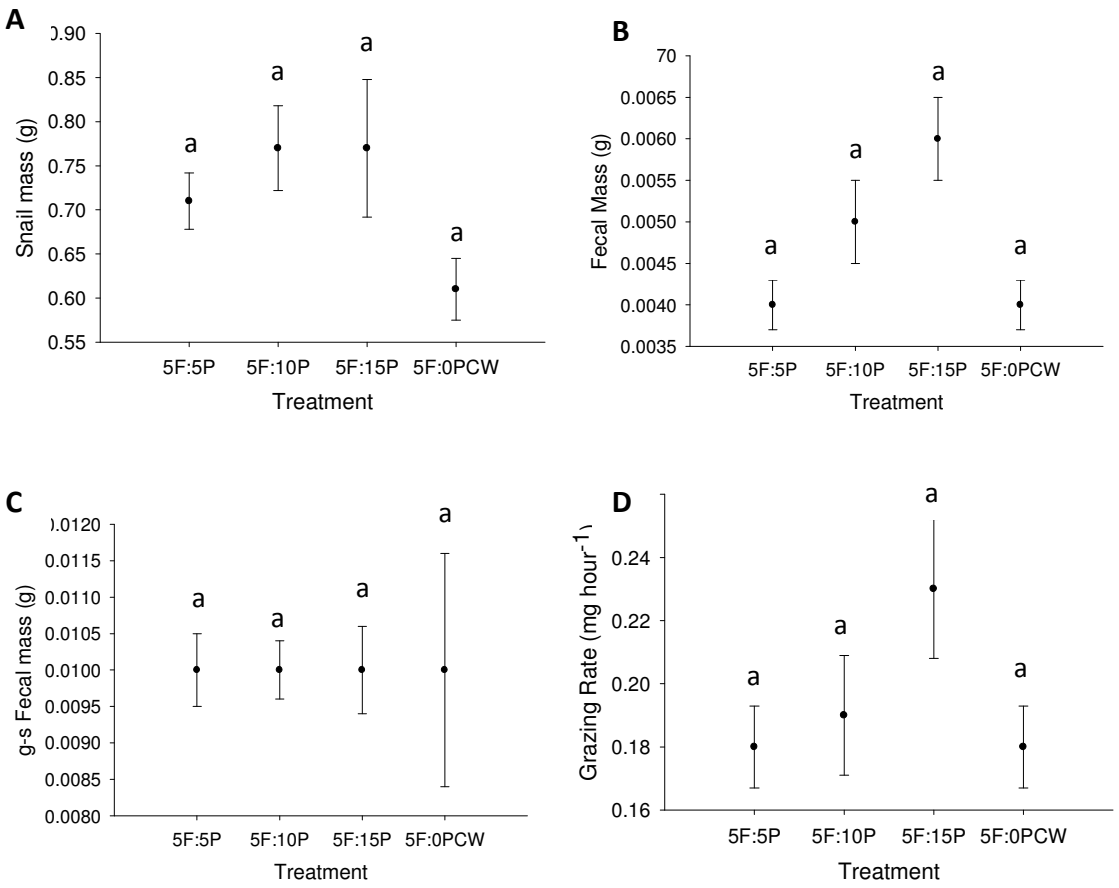
A
Snail mass (g)
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
a
a
a
a
5F:5P
5F:10P
5F:15P
5F:0PCW
Treatment
B
Fecal Mass (g)
70
0.0065
0.0060
0.0055
0.0050
0.0045
0.0040
0.0035
a
a
a
a
5F:5P
5F:10P
5F:15P
5F:0PCW
Treatment
C
g-s Fecal mass (g)
0.0120
0.0115
0.0110
0.0105
0.0100
0.0095
0.0090
0.0085
0.0080
a
a
a
a
5F:5P
5F:10P
5F:15P
5F:0PCW
Treatment
D
Grazing Rate (mg hour-1)
0.24
0.22
0.20
0.18
0.16
a
a
a
a
5F:5P
5F:10P
5F:15P
5F:0PCW
Treatment

Figure 2.

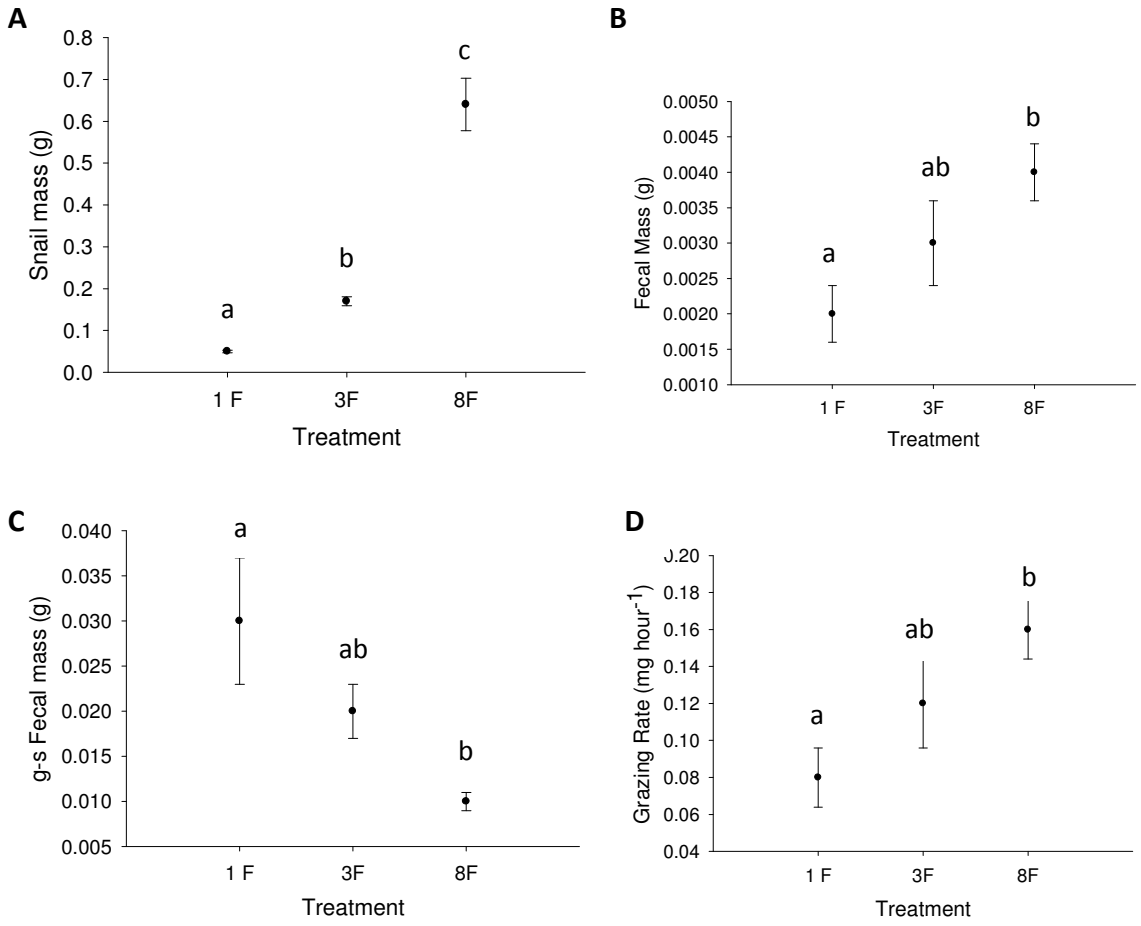
A
Snail mass (g)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
b
c
1 F
3F
8F
Treatment
B
Fecal Mass (g)
0.0050
0.0045
0.0040
0.0035
0.0030
0.0025
0.0020
0.0015
0.0010
a
ab
b
1 F
3F
8F
Treatment
C
g-s Fecal mass (g)
0.040
0.035
0.030
0.025
0.020
0.015
0.010
0.005
a
ab
b
1 F
3F
8F
Treatment
D
Grazing Rate (mg hour-1)
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
a
ab
b
1 F
3F
8F
Treatment

Figure 3.

Michele Larson

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Education

Ph. D in Science – Zoology and Physiology In Progress
University of Wyoming

Master's in Science - Biology June 2013
Eastern Washington University GPA 3.9
Master's Thesis: New Zealand Mud Snails (*Potamopyrgus antipodarum*): impacts of interspecific competition on native gastropod.

Certification and Master's in Education -- Biology Endorsement August 2006
Eastern Washington University GPA 3.9

Bachelors of Science Double Major: Biology and Zoology June 2001
University of Washington GPA 3.5

Experience

Laboratory Experience

- Eastern Washington University –Aquatic Ecology Lab Sept 2011- June 2013
  - Conducted snail grazing and competition trials
  - Dissected snails for gut content and stable isotope analysis
  - Conducted chlorophyll a and ash-free dry mass on algae samples
  - Used Hach water quality testing kits

- University of Washington – Neurobiology Lab March 2000- June 2001
  - Conducted immunostaining research
  - Prepared solutions, cleaned laboratory equipment, and maintained lab.
  - Provided daily care for a variety of laboratory animals.

Field Experience

- Snake River Gastropod Survey – Eastern Washington University Fall 2012
  - Sampled snails and limpets in lotic system using transect plots
  - Determined distribution, abundance, and diversity of native and invasive gastropods in Snake River and tributaries near Lewiston, ID
  - Over 150 hours supervising field assistant

- Turnbull Gastropod Survey – Eastern Washington University Spring 2012
  - Sampled snails in lentic system using dip netting
  - Determined distribution and relative abundance of native and invasive snails in ponds in Turnbull National Wildlife Refuge

- Beaver Project Field Internship – Lands Council Summer 2011
    - Conducted plant transects, green line transects, and shrub surveys as baseline data for areas of future beaver introductions

Teaching Experience

- Eastern Washington University Sept 2012- June 2013
    - Assisted professor and undergraduate students in laboratory courses
    - Set up laboratory specimens and experiments

- Upward Bound Program August 2012
    - Taught pond ecology to underrepresented high school students

- White River High School August 2006 - June 2011
    - Taught Algebra, Biology, Honor's Biology, and Advanced Placement Biology
    - Developed lesson plans, lectures, laboratory experiments and activities

Professional Presentations

- Western Society of Malacologists Annual Conference – June 2013
- EWU Graduate Symposium- May 2013 – "The density and genera richness of native gastropods in the Snake River and three tributaries near Lewiston, Idaho"
- Ecology Guest Lecture -Fall 2012- "Invasive Species"

Professional Memberships

*American Malacological Society 2012 *Ecological Society of America 2012

*EWU Biology Student Organization 2012-2013 – Vice President

Grants and Fellowships

- Eastern Washington University
    - Graduate Service Appointment Fellowship 2012-2013
- Eastern Washington University Mini-Grant Spring 2012
    - Snake River Gastropod Study
- National Wildlife Climate Change Mini-Grant 2008
    - High School Native Plant Garden

Publications

- "Feasibility of Reintroduction of Wolves into Washington State, Draft Report" Washington State Department of Fish and Wildlife, December 1999. (Co-author)
- "*Plethodon idahoensis* Egg Mass," *Herpetological Review,* September 1998