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Research Article

Dynamics of *Potamopyrgus antipodarum* infestations and seasonal water temperatures in a heavily used recreational watershed in intermountain North America

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Abstract

Following the discovery of New Zealand mudsnails, *Potamopyrgus antipodarum*, in the Silver Creek watershed in Idaho, we investigated the distribution and dynamics of the snail populations over two years in field surveys. Despite extensive fishing and recreational activities in the watershed, the infestations appeared limited in extent. As with other published studies, densities of *P. antipodarum* were highest during summer months, but the distribution in Silver Creek was patchy. We found that near-to-below freezing winter water temperatures in localized reaches of the watershed were related to reduced populations or lack of detection. Distributions observed in winter were associated with regions of groundwater releases, or downstream of impoundments that dampened the temperature extremes observed in locations elsewhere in the watershed. We speculate that the population has remained restricted because thermal conditions are not conducive to year-round survival and growth. However, these relationships could be altered with watershed alterations or global climate change.

Key words: New Zealand mudsnail; invasive species management; alien species; habitat requirements; thermal limits; Silver Creek

Introduction

The introduction of alien micro-organisms and invertebrates as "hitchhikers" associated with aquatic recreational activities, especially fishing and boating (e.g. Leung et al. 2006; Bothwell et al. 2009; Hulme 2009; Gates et al. 2009; Pyšek and Richardson 2010; Savini et al. 2010; Kilroy and Unwin 2011) poses risks to many aquatic systems. With the increasing frequency and global nature of commercial and recreational activities, understanding the habitat requirements of alien and potentially invasive species can assist prioritization of the management responses needed to contain or prevent infestations (Pyšek et al. 2010).

Recreational fishing and fish stocking has been associated as a common vector associated with the introduction of the small New Zealand mudsnail *Potamopyrgus antipodarum* (Gray, 1843), a hydrobioid snail native to New Zealand, into many continents of the world (Schrieber et al. 2003; Kerans et al. 2005; Loo et al. 2007; Cross et al. 2010). The snails were first observed in North America in 1987 as part of a mollusk survey in The Nature Conservancy's Thousand Springs Preserve near Hagerman, Idaho (Bowler 1991). Populations of closely related clones of *P. antipodarum* are now reported in all of the western United States and British Columbia, except New Mexico (Bersine et al. 2008; Davidson et al. 2008; Cross et al. 2010). Genetically different clones have become established in the Great Lakes, and streams and lakes of Wisconsin and Minnesota likely through ballast and transported through other human activities (Zaranko 1997; Grigorovich et al. 2003; Levri et al. 2008; Dybdahl and Drown 2011). The often successful colonization of *P. antipodarum* has been attributed to the snail's wide tolerance to physico-chemical factors and their ability to survive transport (Loo et al. 2007; Alonso and Castro-Díez 2008). However, the snails appear to be incapable of surviving for long periods when temperatures go below freezing (Hylleberg and Siegismund 1987; Cox and Rutherford 2000). Chen and LeClair (2011) estimated that only 1.8% of the population in an infested Washington lake survived after 4 days of freezing lakeshore temperatures.

The Nature Conservancy's Silver Creek Preserve attracts visitors from across North America and other continents. Silver Creek is known for its blue ribbon recreational trout fishing and water oriented recreation (Riehle and Griffith 1993; Young et al. 1997; Clark and Glasscock 1997). Within the Silver Creek watershed and upstream from the preserve, the Idaho Department of Fish and Game (IDFG) maintains a trout hatchery and family fishing area. Downstream of the preserve the IDFG owns another heavily used fishing access site. In 2009, the IDFG estimated that anglers spent nearly 30,000 hours fishing in the drainage (Scott Stanton, IDFG, personal communication).

Populations of *Potamopyrgus antipodarum* were first detected in the summer of 2001 in a routine sampling for invertebrates in the Silver Creek preserve. With the diversity of recreational activities (i.e. fishing, waterfowl hunting, and boating) in addition to fish and wildlife migration patterns, resource managers determined that this infestation of *P. antipodarum* was of potential high risk to the aquatic ecosystem and to the recreational economy. Several studies conducted in spring fed systems in the nearby greater Yellowstone ecosystem had documented food web alterations associated with high densities ($> 500{,}000/m^2$) of invasive *P. antipodarum* (Hall et al. 2003; Kerans et al. 2005; Hall et al. 2006). In addition to natural vectors of snail dispersal or vectors of waterfowl and fish in the watershed (Haynes et al. 1985; Siegismund and Hylleberg 1987; Levri and Lively 1996; Bruce et al. 2009), managers were concerned that human activities such as fish stocking and recreational traffic could provide additional dispersals, as shown in other investigations (Loo et al. 2007; Alonso and Castro-Díez 2008; Bruce and Moffitt 2010).

Following the initial discovery of *P. antipodarum* in the watershed, Richards and Lester (2003) conducted an additional survey of the benthos within and surrounding the Silver Creek Preserve and identified infested sites near IDFG's Hayspur Fish Hatchery, and on Silver Creek near the Silver Creek Preserve's Visitor Center.

To document the extent of infestations of *P. antipodarum* at sites within the drainage and assess the association of infestations with human recreational use, water temperature, and conductivity in the watershed, we sampled at three scales in the Silver Creek drainage. First, we conducted a broad scale investigation to document the extent of the infestation by sampling likely habitat at sites throughout the watershed in the summer. Secondly, we made fine scale observations of abundance in two infested reaches that were contained within the heavily used recreational areas of Silver Creek preserve to explore the spatial distribution of infestations in winter and summer conditions. Finally, we estimated the densities of *P. antipodarum* by quantitatively sampling substrates to estimate density within and downstream of known infested and uninfested reaches in summer and winter seasons.

Methods

Study site

Silver Creek watershed is a high-desert (elevation 1490 m) spring influenced stream system in central Idaho. The area is often referred to as the Big Wood River-Silver Creek watershed because of the interconnected nature of the nearby Big Wood River with the Silver Creek aquifers (Wetzstein et al. 2000). Annual discharge within Silver Creek averages 100 to 123 million m^3 per year (Brown 2000) with little intra-annual variability (Francis and Bjornn 1979). Silver Creek and its tributaries flow approximately 110 km to a confluence with the Little Wood River. A large portion of the watershed is open to public access through holdings or easements of The Nature Conservancy's Silver Creek Preserve, or through recreational access on Idaho Department of Fish and Game property (Clark and Glasscock 1997).

Broad scale distribution of Potamopyrgus antipodarum in the watershed

In the summer of 2004, we examined 56 sites to estimate the distribution of *P. antipodarum* in the Silver Creek watershed. When access to private property was available, we surveyed locations at approximately 1 km intervals within the drainage, and recorded UTM coordinates of each location surveyed (Figure 1, Appendix 2). To sample for snails, we selected the nearest gravel-pebble substrate in riffle habitat, and used a D-framed kick-net with a 500 μm mesh collection net to collect three separate 10-second kick-net collections, vigorously disturbing substrates to suspend the macroinvertebrates into the net. At each sampling site, we characterized the

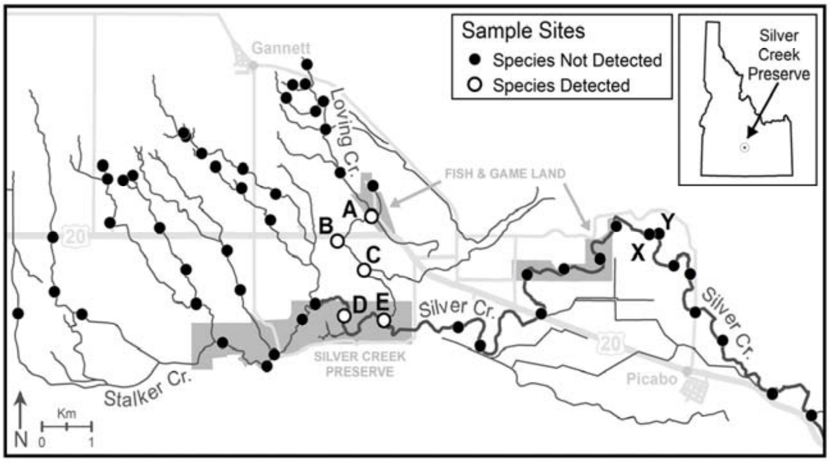

Figure 1. Location of study area in Silver Creek, Idaho. Circles indicate location of sites sampled in broad scale study in summer 2004. Open circles indicate locations with *Potamopyrgus antipodarum* detected. The borders of the Hayspur State Fish Hatchery (Loving Creek) and the fishing access (on Silver Creek) are shown as Idaho Fish and Game land. The boundaries of The Nature Conservancy's Silver Creek Preserve are indicated. Alpha characters (A, B, C, D, E) indicate sites summarized in Table 1. All positive sites corresponded to previous detections except sites X and Y in which no snails were detected in our study.

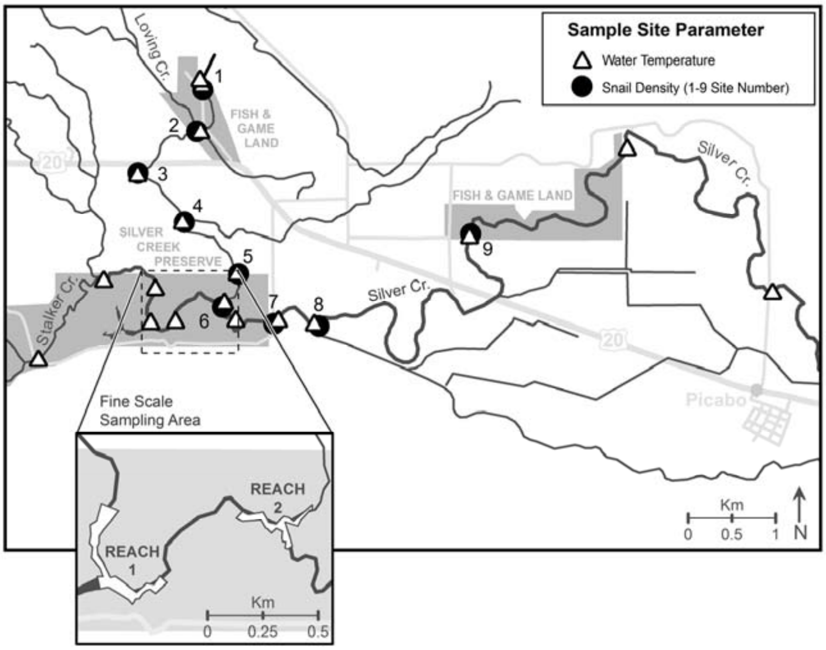

Figure 2. Locations of sampling areas evaluated in the fine scale study (Reach 1 and Reach 2) and the density sampling (solid dots 1-9). Triangles indicate locations of thermograph loggers recording temperatures at locations within the watershed during study.

dominant substrate using the Wentworth classification scale (McMahon et al. 1996) into one of five categories: small gravel = 2–4 mm; medium gravel = 4–8 mm; large gravel = 8–16 mm; small pebble = 16–32 mm; and large pebble = 32–64 mm.

Samples were processed in the field with sieves (4.75 mm, 2.36 mm and 1.70 mm) to separate juvenile or adult sized snails from large debris. The contents of each sieve were examined with the aid of 10× magnification, and *P. antipodarum* or other mollusks were retained in containers. At the end of each day, the samples were re-sorted to remove organic debris and the contents preserved with 10% formalin. After ~24 h, samples were rinsed and transferred to 70% ethanol for storage for further processing and quality assurance.

Fine scale distribution and relative abundance in two infested reaches

We selected two infested stream reaches identified in the broad scale survey within the nature preserve to assess the distribution and relative abundance of *P. antipodarum* in more detail in the summer and winter and examine patterns of infestation. These stream reaches were within areas of heavy recreational activity throughout the summer and fall. Study Reach 1, was located on Silver Creek near the outflow of Sullivan Lake, with segments of 250 m upstream and downstream from the lake (Figure 2). Study Reach 2 was located at the confluence of Loving Creek and Silver Creek and included 100 m segments on both creeks and a 100 m segment downstream from their confluence. Forty sampling points were randomly selected in each reach using a random sampling generator within GIS (http://www.dnr.state.mn.us). We constrained each sampling point to a 1-m diameter area, buffered by 5 m, to ensure that no two points were located closer than 6 m to provide greater extent of sampling effort. We sampled each site in the winter of 2004–2005, in the summer of 2005, and again in the winter of 2005–2006. Benthos was collected at each location with a 10-sec kick net procedure with the same equipment used in the watershed distribution survey, except that any vegetation and all substrates were collected to evaluate locations with and without gravel substrates. Each sample was sorted through sieves (2 mm, 1 mm, and 500 μm) to remove larger debris and fine sediments. The contents were placed preserved in 10% formalin solution overnight, and transferred to 70% ethanol for further processing and storage.

Density along a stream segment of infested and uninfested sites

To quantify the density of *P. antipodarum* infestations and explore the relationship along a gradient of water temperature and conductivity, we selected 9 locations (6 infested and 3 uninfested) along a ~ 9 km stream segment. At each site we sampled the substrate along a stream transect to estimate the density of *P. antipodarum* in winter and summer conditions (Figure 2). Two upstream sampling sites were located within the Hayspur State Fish Hatchery (IDFG) property where water temperatures were influenced by groundwater discharges from the hatchery. The lower sites were located downstream from the Silver Creek Preserve with the lowermost site at a location in the IDFG fishing access. All sampling was conducted in gravel substrate to reduce variation involved with sampling different substrates. At each site and sampling period (summer and winter) we collected three samples of the substrate along a transect using a modified Hess sampler with a 500-µm mesh net. The Hess sampler (sampling area of 0.086 m^2) was modified to allow for sampling in deeper water with a 91.4 cm long, 35.6 cm diameter tube of sheet metal, and additional 35.6 cm to 30.5 cm reducer inserted into the top of the sampler. A stable fork, with its width and tongs trimmed to approximately 20 cm, was used to manipulate gravel substrate confined inside of the sampler at each site.

Water temperature, conductivity, and sample analysis

We recorded water temperatures at selected locations throughout the watershed from June 2004 through February 2006 (Figure 2) with Hobo 8 data loggers (Onset Corporation, Pocasset, Massachusetts) at 2-h intervals. We placed temperature recorders in the upper, middle, and lower bounds of each of the two infested stream reaches studied at fine scale, and at each sampling location of the density study. At each sampling site in the reach and density studies we also measured conductivity (µS/cm) with a YSI Multi-probe 556 (Yellow Springs, Ohio).

To sort and quantify the snails in kick net collections from the two infested reaches examined at fine scale, and from Hess samples from the stream segment, we used a sub-sampling process in the laboratory. A large sorting tray was divided into 32 equally sized cells and enclosed with four plexiglass retaining walls ~10 cm. We selected four cells (1/8 of total sample) with a random number generator. The contents of these cells were removed using spatulas and a small pipette and the number of snails in each sample was adjusted for this sub-sampling. For the density studies, we divided our number by 0.086, the area of the Hess sampler, to express the estimated density of snails per m^2.

Data analysis

In the broad scale watershed survey, we estimated a mean count per kick-net by averaging the three 10 sec kick-net samples taken at each site. After verification of the normality of substrate measurements, we tested for differences in substrate size across infested and uninfested sites with two sample t-tests of the means from infested and uninfested sites. To explore for patterns in the fine scale studies of two infested reaches, all sampling locations were snapped to a line that followed the contour of the reach to achieve a measure of distance downstream. We then correlated the number of snails in the 10 second kick-net samples at each site with the distance downstream in Silver Creek by each stream reach and sampling time using Spearman correlations. We also compared the frequency of positive detections of snails within the 40 sampling sites between each reach across the three sampling times with adjusted chi squared analyses. To test for differences in density of *P. antipodarum* among the 6 infested sites between seasons (summer and winter samples) we used a nested split plot general linear model (GLM) to test for differences among sites and between season with the model: density = site+sample(site)+season+ site×season. Tests of significance for the site effect were conducted using the mean square of sample (site) as the error term. To achieve a normal distribution of residuals, we transformed data with a log (density +1) before analysis. In addition we performed Spearman correlations of density at all 9 sites and at sites that had summer detections with December mean temperatures. All analyses were conducted with SAS version 9.2 (SAS Institute, Cary, North Carolina). Factors with a $P \leq 0.05$ were considered significant.

Results

Broad scale distribution in watershed

We found *Potamopyrgus antipodarum* in five of 56 sites visited in the summer of 2004 (Figure 1). The mean abundance in the 10 sec kick-net sampling effort ranged from 0.7–740 snails (Table 1), with the highest relative abundance in Loving Creek, decreasing downstream to the confluence with Silver Creek. The lowest abundance was located at site D just upstream of the visitor center at The Nature Conservancy Preserve (Figure 2). We detected no *P. antipodarum* upstream of Hayspur State Fish Hatchery in Butte Creek or Loving Creek or in the old brood ponds that received hatchery effluent. We found no differences between the substrate particle size at uninfested compared with infested sites (P>0.25). The mean substrate size ± SD was 2.8 ± 1.34 mm, and 2.6 ± 1.30 mm at the uninfested and infested sites, respectively.

Fine scale seasonal distribution and relative abundance in two infested reaches

The frequency of infested sites in Reach 1 was higher than that observed in Reach 2 over all sampling times (adjusted chi square = 15.15; .P < 0.05). Sites infested with *P. antipodarum* were distributed throughout Reach 1 across all three sampling times, with 29 of 40 sites infested during the summer 2005 sampling. We found a correlation of snail numbers in Reach l with distance downstream in the summer samples (r = 0.432; P< 0.01; DF = 38). The winter samples 2005-2006, showed the same relationship but with weaker correlations (r = 0.284; P < 0.075; DF= 38). There were no correlations with distance apparent in Reach 2 or in sampling during the first winter in Reach 1 (0.280 > P<0.67; DF = 25). Water temperatures varied across all months and the lowest winter temperatures were recorded in the winter of 2005-2006 (Figure 4). Conductivity was higher in the summer sampling over the winter seasons, but values appeared consistent throughout the reach (Figure 4).

Density along a stream segment of infested and uninfested sites

Densities of *Potamopyrgus antipodarum* in the six infested sites sampled in the summer and the winter of 2005–2006 varied from a low of 62 snails/m^2 in winter samples at Site 6, to a high of 3751 snails/m^2 at Site 1, just below the Hayspur State Fish Hatchery (Figure 5). The patterns of distribution along Loving Creek were similar to those observed in the extensive sampling conducted in the summer of 2004. We did not detect snails in Silver Creek from Kilpatrick Bridge at the border of the preserve, or in the two reaches downstream (Sites 7–9). The density of snails declined from locations just downstream of Hayspur State Fish Hatchery, to the confluence with Silver Creek at Site 6 (Figure 5). The differences between sites were significant ($F_{5,12}$ = 8.83; P< 0.001), and density was significantly different between the two seasons ($F_{1,12}$ = 8.86; P < 0.02).

During the summer, conductivity was $\geq$ 300 µS/cm during sampling, and was comparable to values measured in infested Reach 2. During the winter, conductivity dropped below 200 µS/cm at

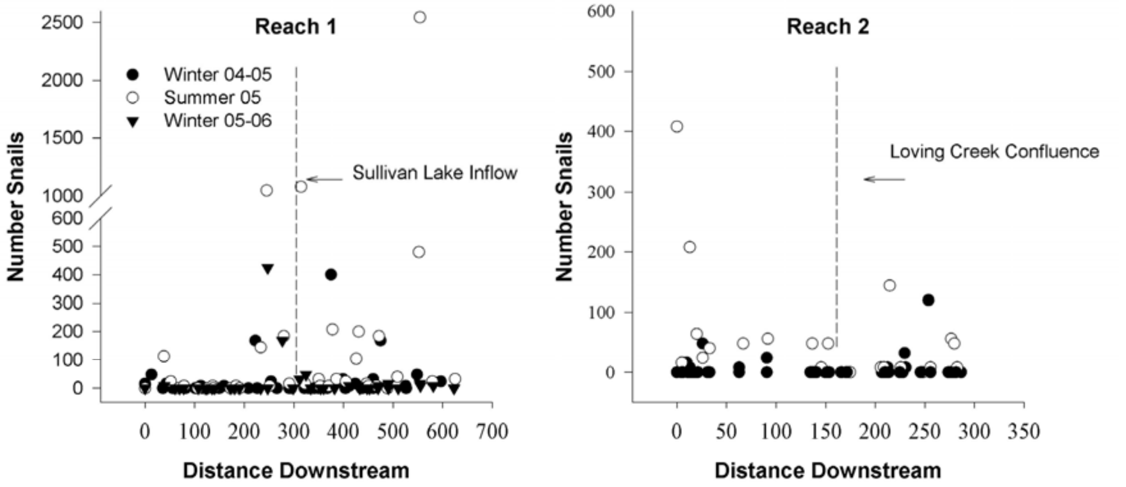

Figure 3. Number of snails collected in each of the 40 sites located in Reach 1 and Reach 2 versus distance downstream from the top of the reach over three sampling times (Winter 2004-2005; Summer 2005; and Winter 2005-2006).

sites 6, 8, and 9, and the drop in conductivity in winter was also observed in Reach 1 and 2 of The Nature Conservancy Preserve (Figures 4 and 5). Water temperatures in the Silver Creek watershed showed both diel and seasonal variation. Sites upstream and within The Nature Conservancy Preserve had summer daily maximum temperatures from 21.3 to 22.8°C and winter lows of –1.9 to 1.6°C (Figure 5). The least variation in water temperatures was measured in locations just downstream from Hayspur State Fish Hatchery, near sites with the highest densities of *P. antipodarum*. Minimum temperatures near the hatchery never were below 2.0°C, and maximum summer temperatures did not exceed 23°C (Appendix 1). Mean monthly temperatures in the downstream most portion of the watershed with no detectable infestations (sites 7–9), including sites in and below the Idaho Fish and Game fishing access area had the highest summer and lowest winter water temperatures. Correlations of mean density with mean December temperatures at all 9 sites were significant (r = 0.861; P < 0.01; DF = 7), whereas correlations of density with mean December temperature at sites that had detectable snails in the summer were less strong (r = 0.77; P = 0.07; DF – 4). At each of the three sites in and below the fishing access area (Appendix 1) we recorded 4–5 months in which minimum temperatures were <0°C, and summer maximum temperatures that exceeded > 25°C.

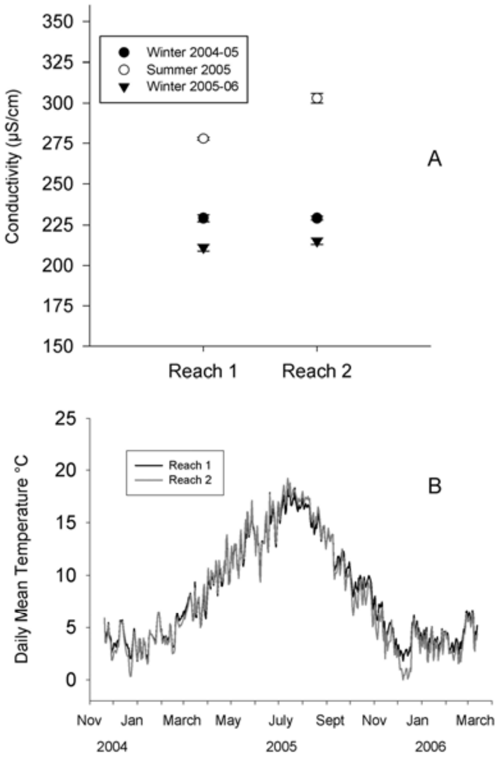

Figure 4. A). Mean and SE of conductivity in Reach 1 and Reach 2 at the time of snail sampling. Measurements were collected at each of the 40 sites with a reach. **B**). Water temperatures recorded in Reach 1 and Reach 2 from November 2004 to March 2006 over the length of the three sampling periods in winter, summer and winter. Daily mean temperatures were averaged from three recording thermometers deployed in each reach.

Table 1. Site code (location on Figure 1), sampling date, stream location, and relative abundance of *Potamopyrgus antipodarum* detected at infested sites in the broad scale survey of 56 sites located throughout the Silver Creek drainage in the summer of 2004. Three, 10-sec kick net collections were combined and mean number of snails per 10 second effort reported.

Site code	Date	Stream name	Number snails per 30 seconds
A	8 June	Loving Creek	740
B	2 July	Loving Creek	77
C	2 July	Loving Creek	2.7
D	4 June	Silver Creek	0.7
E	4 June	Silver Creek	3.3

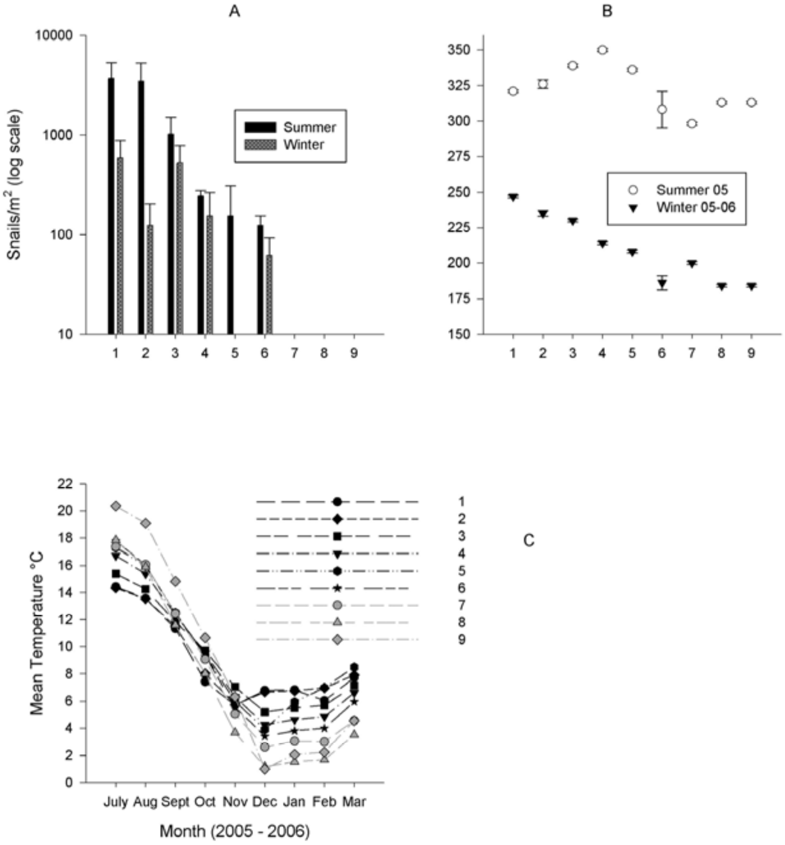

Figure 5. **A**. Mean density + SE of *Potamopyrgus antipodarum* (log scale) from three separate samples removed from gravel substrate at 6 infested sites across summer and winter sampling seasons, 2005-2006. **B**. Conductivity (µs/cm) and SE measured at each of the 9 sampling location at the time of substrate collections. **C**. Water temperatures recorded from July 2005 to March 2006 at the 9 locations established for quantitative estimates of snail density in summer and winter conditions shown on Figure 2.

Discussion

We found little to no evidence of expansive distribution or high densities of *Potamopyrgus antipodarum* in the Silver Creek watershed, despite heavy recreational use of portions of the watershed in the time since the first reported infestation. The invasion of *P. antipodarum* in the Silver Creek watershed appears to be limited to a patchy distribution in low densities. Small populations of *P. antipodarum* were observed in localized areas within The Nature Conservancy Silver Creek Preserve and in the Butte/Loving Creek tributary confluence downstream of Hayspur State Fish Hatchery. We found some correlation of numbers of snails with proximity to the outlet from Sullivan Lake in Reach 1. All infestations were located in areas consistent with distributions reported by Richards and Lester (2003). The highest summer density (Site 1; 3751/m^2) was more than 100 times lower than summer densities reported by Hall et al. (2006) for Polecat Creek, that has year-around temperatures near 15°C in the Greater

Yellowstone Ecosystem. In the Colorado ecosystem Cross et al. (2010) reported summer densities of 6,500/m^2 to 221,000/m^2 in gravel of similar size to substrates sampled in our studies. Richards et al. (2001) reported densities of *P. antipodarum* in a constant temperature fed spring environment ranged from 39,841 to 78/m^2, depending on the habitat sampled.

Cross et al. (2010) speculated that annual mean water temperatures were important factors correlated with total production and snail biomass of *P. antipodarum* populations. However, mean water temperatures may not be as important to snail population growth as are winter low temperatures. Cold water temperatures encountered by *P. antipodarum* in its native range are not severe, but populations outside of New Zealand occur in areas that winter temperatures can reach freezing. We found the lowest numbers of *P. antipodarum* in the Silver Creek drainage in winter samples and sites that were infested in the summer months had reduced or no detectable snails in the winter conditions. Previous studies reporting the effects of freezing temperatures on populations of *P. antipodarum* provide details of exposure to cold air temperatures. Hylleberg and Siegismund (1987) found that populations of *P. jenkinsi* (now *P. antipodarum*) in Denmark had a low tolerance to freezing atmospheric temperatures, and Richards et al. (2004) reported all size-classes of *P. antipodarum* died within 2 h at -3°C when snails were air exposed. Populations of *P. antipodarum* in Capitol Lake in Washington State appear to be limited by winter drawdown of the lake that exposes snails to air temperatures below freezing (Johannes 2010; Cheng and LeClair 2011).

In the Silver Creek watershed, source populations of *P. antipodarum* available for annual recolonization appear to be restricted to reaches of the watershed in which water temperatures did not drop below 0°C. We observed diel temperature fluctuations in summer and winter of considerable magnitude in the lower reaches of the watershed (Appendix 1) with multiple occurrences of below freezing temperatures in the winter. Diel fluctuations likely stress snails, and could increase the likelihood of mortality in winter conditions. Below freezing temperatures persisted for consecutive days in the IDFG fishing access site, and we observed heavy ice formations at that site and at locations several km downstream. Other studies of the Silver Creek watershed report freezing temperatures and extreme winter conditions occur regularly (Francis and Bjornn 1979; Riehle and Griffith 1993).

In addition to temperature, other physico-chemical factors such as light levels, calcium concentrations, alkalinity, conductivity, and nitrates have been correlated with productivity of snail populations (Hall et al. 2003; Tibbbets et al. 2010; Liess and Lange 2011; Kolosovich et al. 2012). Herbst et al. (2008) reported low specific conductivity limited the growth and survival of *P. antipodarum.* In their study, snails held in conductivity of 200 to 300 µS/cm had low mortality, compared with groups held in 10 µS/cm. In the Silver Creek watershed, we measured conductivity >200 µS/cm, even in winter conditions. Summer abundances measured in our study were positively correlated with increased conductivity. Conductivities of some ions are affected by water temperature (Kalff 2002), and we observed elevated levels in summer measures. Although we did not measure specific ions, total dissolved solids ranged from 238 to 243 mg/L in the sum-mer and 215–226 mg/L in the winter of 2005–2006. In heavily *P. antipodarum* infested springs at Hagerman National Fish Hatchery, Hagerman, Idaho, specific conductivity ranges from 280 to 370 µS/cm with a mean of 320 µS/cm (Hagerman Hatchery Evaluation Team 2010).

We were unable to sample several tributary reaches surrounded by private lands. In some of those un-sampled locations, habitat restorations are underway to deepen channels, and add small impoundments may stabilize stream temperature fluctuations and alter water chemistry in favor of more successful colonization. Managers of these restorations should consider the role of habitat features that could enhance the overwinter survival of *P. antipodarum* populations that could serve as source populations. An increase in the number of year-round source populations could increase the natural drift and downstream movement from infested sites in the summer (Haynes et al 1985; Holomuzki and Biggs 1999), and increase opportunities for dispersals from animal and human vectors (Schrieber et al. 2003; Alonso and Castro-Díez 2008; Bruce and Moffitt 2010). Our research suggests the need for further studies to define the lethal limits of *P. antipodarum* in fluctuating water temperatures, in ranges of specific conductivity, and within features of the aquatic habitat.

Despite the current limited distribution within the Silver Creek watershed, transport of snails through the numerous human recreational visits remains of high concern. Recent studies have shown that felt soled waders can provide refuges for invasive species (e.g. Bothwell et al. 2009; Gates 2009), resulting in New Zealand, and several US state agencies banning their use (Kilroy 2008; Collier 2009; Anonymous 2010). To reduce transport risks, resource managers should provide information and procedures that restrict the potential transfer of any alien organisms within and between watersheds through vigilant monitoring and disinfection protocols (Proctor et al. 1997; Segura 2011).

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Supplementary material (Appendix 1 and Appendix 2) is available as part of online article from:

http://www.aquaticinvasions.net/2012/Supplements/AI_2012_2_Moffitt_James_Supplement.pdf