

SPATIAL DISTRIBUTION OF THREE SNAIL SPECIES,
INCLUDING THE INVADER *POTAMOPYRGUS ANTIPODARUM*,
IN A FRESHWATER SPRING

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ABSTRACT.—The highly invasive New Zealand mudsnail, *Potamopyrgus antipodarum*, may compete with and displace native North American macroinvertebrates in freshwater systems wherever it becomes established. Densities and spatial distributions of 3 snail species including *P. antipodarum* and the threatened *Taylorconcha serpenticola* were compared among 3 adjacent habitat types (run, edge, and vegetation) in Banbury Springs, a tributary of the Snake River, near Hagerman, Idaho, USA. In all 3 habitats *P. antipodarum* was the most abundant snail species. All 3 species densities were highly variable within habitats, suggesting a nonrandom distribution pattern. Densities of *P. antipodarum* were significantly greatest in the vegetation habitat type, while densities of *T. serpenticola* were similar among habitats. Smaller-sized *P. antipodarum* were less abundant in the run habitat with its associated higher water velocities, and their densities were negatively correlated with velocity. Densities of *P. antipodarum* also were negatively correlated with distance from the highly infested, man-made Morgan Lake, while *T. serpenticola* densities were positively correlated with distance from Morgan Lake. *Potamopyrgus antipodarum* is a potential competitor with native aquatic species, although its colonization into some freshwater habitats may be limited.

Key words: threatened species, endangered species, biological invader, competition, spatial distribution.

By the mid-1980s, the exotic New Zealand mudsnail, *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae), had become established in the middle Snake River drainage and associated springs in southern Idaho, USA (Taylor 1987, Bowler 1991). It has subsequently become the dominant macroinvertebrate species in many of these waters and has spread into several river drainages in and near Yellowstone National Park, Wyoming and Montana, USA. *Potamopyrgus antipodarum* densities have been reported as high as $800,000 \cdot \text{m}^{-2}$ (Dorgelo 1987). We have recorded patches of *P. antipodarum* exceeding $500,000 \cdot \text{m}^{-2}$ at Banbury Springs, a tributary of the Snake River, near Hagerman, Idaho. These small patches (roughly 1 to 2 m^2) were in a spatially heterogeneous landscape and were often adjacent to patches with low densities of *P. antipodarum* (sometimes $<1000 \cdot \text{m}^{-2}$).

It is unknown what the effects of *P. antipodarum* will be on the native macroinvertebrate communities, but given its potential for rapid population growth and its present high densities in some waters, negative ecological and associated economical impacts could occur. *Potamopyrgus antipodarum* is native to New

Zealand and has become widely established throughout Europe, Australia, and now the USA. In Europe, *P. antipodarum* became established in the mid- to late 1800s and is now the dominant macroinvertebrate in many fresh to slightly saline aquatic communities (Anistratenko 1991, Coggerino et al. 1995). In the USA, *P. antipodarum* populations have been documented in (1) the Yellowstone, Madison, and Snake rivers in and near Yellowstone National Park, Wyoming and Montana; (2) the Snake River drainage, Idaho and Wyoming; (3) the Columbia River, Oregon; and (4) Lake Ontario, Canada and USA (Zaranko et al. 1997). *Potamopyrgus antipodarum* can reproduce sexually or asexually via parthenogenesis (Dybdahl and Lively 1995). Because of its ability to reproduce asexually, invading populations of *P. antipodarum* can quickly dominate an aquatic environment. Like all hydrobiid snails, *P. antipodarum* possesses an operculum, which can be used to seal itself tightly into its shell; thus, it is able to survive unfavorable conditions, including many fishes' digestive systems (Haynes et al. 1985).

The middle Snake River drainage is also home to several federally listed threatened

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and endangered snail species, including the threatened Bliss Rapids snail, *Taylorconcha serpenticola* (Rissoidea: Hydrobiidae), and the locally common pebble snail, *Fluminicola* sp. (Hydrobiidae; Bowler 1991). Very few data are available on habitat preferences and spatial distributions of any of these 3 species in the middle Snake River drainage.

For this study we collected and analyzed densities and spatial distribution data as related to 3 assumed habitat types (run, edge, and vegetation) for all 3 snail species, *P. antipodarum*, *T. serpenticola*, and *Fluminicola* sp., in Banbury Springs. We also related shell lengths of *P. antipodarum* with water velocity and habitat type in Banbury Springs.

STUDY SITE

Banbury Springs are located alongside the Snake River (river mile 589) at the southwestern end of the eastern Snake River Plain of Idaho, USA, and upriver of the Thousand Springs complex located at river mile 585 (Fig. 1). The Snake River runs through a steep-sided canyon within a larger trench-cut canyon through the Snake River Plain. Banbury Springs consist of 22 springs that convey water from basalt walls through an aquifer that underlies the plain. Average flow of the springs is approximately $3.5 \text{ m}^3 \cdot \text{s}^{-1}$. Surrounding acreage consists of forested wetlands, shrubland, and talus slopes. The springs form numerous braided channels that then flow into small, man-made Morgan Lake, which was created in 1965. The springs then empty into the Snake River through a culvert. Banbury Springs support several species of aquatic macrophytes, densities of which vary seasonally.

METHODS

We collected 54 small Surber samples from 3 delineated habitat types (run, edge, and vegetation) in a 30×30 -m section of the northernmost spring at Banbury Springs between 6 April and 11 May 1999. Our small Surber sampler was a 1-mm mesh, modified Surber sampler with a collection area of $15 \text{ cm} \times 15 \text{ cm}$ as compared to a 30×30 -cm collection area used in standard Surber sampler. We elected to use the smaller Surber sampler because of the very high numbers of *P. antipodarum* collected in our samples and because a full Surber sample would often overlap from

one delineated habitat type into the next. Of the 54 small Surber samples, 17 were in run habitats, 14 in edge habitats, and 23 in vegetation habitats. We delineated a run habitat as any riffle or flowing section that did not have emergent, aquatic vegetation growing and that was dominated by gravel size or larger substrates. Sample sites in runs remained free of vegetation, as of 5 November 1999. An edge habitat was that portion of the emergent aquatic vegetation habitat that was within 15 cm of a run. Vegetation habitat was defined as being more than 15 cm from a run habitat and composed of emergent, aquatic vegetation. Samples collected in the vegetation and edge habitats included both macrophytes and substrate.

To determine whether there was a relationship between size of *P. antipodarum* and habitat type, we measured 760 *P. antipodarum* shell lengths to nearest 0.05 mm: 235 from edge, 250 from vegetation, and 275 from run habitats. We measured an additional 889 *P. antipodarum* shell lengths from 12 samples in the study site from habitats with varying water velocities to determine whether there was a relationship between shell length and water velocity. Hourly water temperatures ($N = 4919$) were recorded at the upper and lower portions of the study site between 13 April and 5 November 1999 using HOBO temperature data loggers (Onset Computer Corp. 1998).

STATISTICAL ANALYSES

Descriptive statistics (including skewness and kurtosis), histograms, normal expected frequencies, Shapiro-Wilk W -tests, and normal probability plots of the 3 snail species densities were generated and analyzed for comparison. Densities that did not follow a normal distribution were log-normalized and reexamined. All log-normalized densities subsequently appeared to follow a normal distribution. A nonparametric Spearman rank order correlation was conducted between nontransformed *P. antipodarum* densities and water velocity. In addition, we related log-transformed *P. antipodarum* densities and water velocity using Pearson product-moment correlation. Both correlation methods were used to determine if there was a relationship between *P. antipodarum* densities and distance upstream from Morgan Lake. We also used Pearson product-moment correlation for examining the relationship

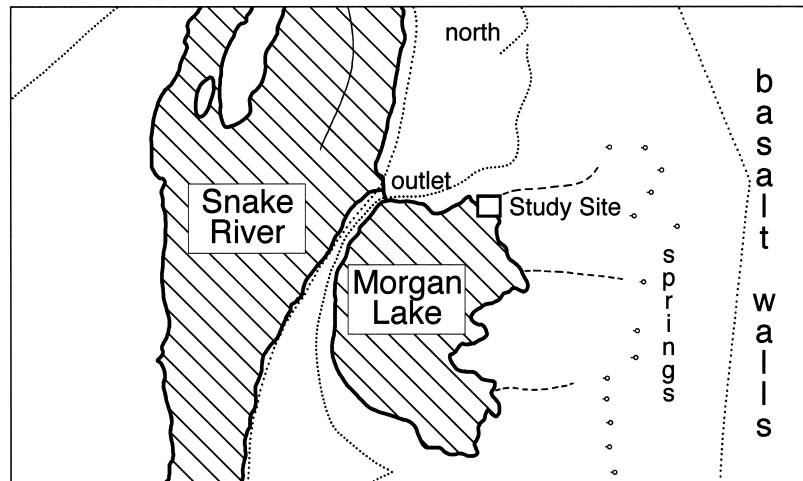


Fig. 1. Study area.

between *P. antipodarum* shell lengths and water velocity. One-way ANOVAs using Tukey HSD post hoc comparison were conducted on log-transformed densities of the 3 snail species for each species to determine if there were any differences in snail densities in the 3 habitats. *Potamopyrgus antipodarum* mean shell lengths were compared among the 3 habitats using 1-way ANOVA and Tukey post hoc comparison. We used STATISTICA for Windows (Statsoft, Inc. 1995) for all statistical analyses.

RESULTS

Potamopyrgus antipodarum had the highest densities of the 3 snail species in all 3 habitats but was more similar with *T. serpenticola* and *Fluminicola* sp. densities in the run habitat (Figs. 2, 3, 4). All 3 species densities showed a nonrandom distribution within all habitats (Shapiro-Wilk test $W < 0.01$, skewness and kurtosis > 0 , and by visualization of normal probability plots) with the exception of *Fluminicola* sp. in the vegetation and run habitats (Shapiro-Wilk test $W > 0.25$, skewness and kurtosis ~ 0 , and by visualization of normal probability plots), which showed a normal or random distribution.

Log-transformed mean densities of *P. antipodarum* were marginally different among habitats (1-way ANOVA, $F = 3.02$, $df = 2,26$, $P = 0.07$). Mean densities (log-transformed) of *P. antipodarum* were significantly higher in the vegetation than the run habitat (Tukey HSD

post hoc comparison, $P = 0.05$) but were not significantly greater in the edge than the run habitat ($P = 0.36$) or between the vegetation and edge habitats ($P = 0.53$). *Fluminicola* sp. mean densities (log transformed) were significantly different among the 3 habitats (1-way ANOVA, $F = 6.21$, $df = 2,26$, and $P = 0.00$). *Fluminicola* sp. mean densities were significantly greater in the vegetation and edge habitats than in the run habitat (Tukey HSD post hoc comparison, $P = 0.07$ and 0.01 , respectively) but were not significantly greater between the edge and vegetation habitats ($P = 0.48$). Mean densities (log-transformed) of the threatened Bliss Rapids snail, *T. serpenticola*, were not significantly different among any of the 3 habitats (1-way ANOVA, $F = 0.63$, $df = 2,26$, $P = 0.53$, and Tukey HSD post hoc comparison, $P > 0.60$ for all 3 habitats), but were most variable and had the lowest median density in the vegetation habitat (Fig 4).

Water temperature was constant throughout the study site and season. Mean hourly temperatures recorded between 13 April and 5 November 1999 were 14.19°C ($\pm 0.38^{\circ}\text{C}$ s ; $min = 12.93^{\circ}\text{C}$; $max = 14.85^{\circ}\text{C}$; $N = 4919$) at the upstream portion of the study site and 14.29°C ($\pm 0.57^{\circ}\text{C}$ s ; $min = 12.93^{\circ}\text{C}$; $max = 16.38^{\circ}\text{C}$; $N = 4919$) at the downstream portion. Therefore, we did not consider temperature to be a variable in our analysis within the study site, although temperature could have an effect on snail distribution in other areas, including Morgan Lake.

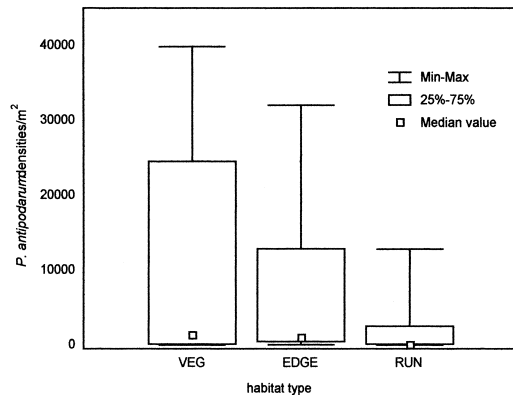


Fig. 2. Comparison of *P. antipodarum* densities $\cdot m^{-2}$ in 3 habitat types (vegetation, run, and edge) in the Banbury Springs study site, 1999. (Vegetation: median = 1328.04, mean = 10651.49, minimum = 0.00, maximum = 39841.20, lower quartile = 78.12, upper quartile = 24529.68, $N = 23$. Edge median = 996.03, mean = 7081.02, minimum = 39.06, maximum = 32029.20, lower quartile = 390.60, upper quartile = 12811.68, $N = 14$. Run median = 156.24 $\cdot m^{-2}$, mean = 2072.48, minimum = 0.00, maximum = 12811.68, lower quartile = 78.12, upper quartile = 2460.78, $N = 17$.)

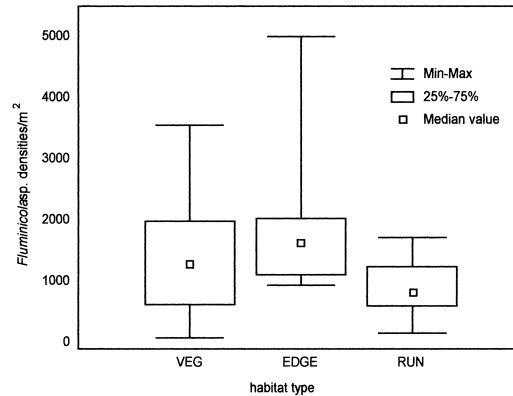


Fig. 3. Comparison of *Fluminicola* sp. densities $\cdot m^{-2}$ in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999. (Vegetation: median = 1288.98, mean = 1448.62, minimum = 78.12, maximum = 3554.46, lower quartile = 624.96, upper quartile = 1992.06, $N = 23$. Edge: median = 1640.52, mean = 1944.63, minimum = 937.44, maximum = 4999.68, lower quartile = 1093.68, upper quartile = 2031.12, $N = 14$. Run: median = 820.26, mean = 921.36, minimum = 156.24, maximum = 1718.64, lower quartile = 585.90, upper quartile = 1249.92, $N = 17$.)

Water velocities ranged from $0 m \cdot s^{-1}$ in thicker vegetation habitats to $0.52 m \cdot s^{-1}$ in runs. Mean water velocity was $0.04 m \cdot s^{-1}$ ($\pm 0.03 s$) for vegetation, $0.08 m \cdot s^{-1}$ ($\pm 0.12 s$) for edge, and $0.34 m \cdot s^{-1}$ ($\pm 0.15 s$) for run habitat. Velocities were significantly different ($P < 0.05$) between run and vegetation, and run and edge habitats, but not between vegetation and edge habitats.

Non-parametric Spearman rank order correlation on nontransformed data suggested that *P. antipodarum* densities were significantly negatively related to water velocity ($N = 54$; $r = -0.52$; $P = 0.00$). Log-transformed densities of *P. antipodarum* also showed significant negative correlation with velocity using Pearson correlation ($N = 47$; $r = -0.57$; $P = 0.00$). Densities of *T. serpenticola* and *Fluminicola* sp. were not significantly correlated with velocity using nonparametric or log-transformed data analysis.

Mean shell lengths of *P. antipodarum* were significantly correlated with water velocity using Pearson correlation ($N = 12$, $r = 0.68$, $P = 0.02$). Mean shell lengths of *P. antipodarum* were also significantly greater in the run habitat than in edge or vegetation habitats ($P < 0.00$ for both), but not significantly different

between edge and vegetation habitats ($P = 0.87$).

Log-transformed densities of *P. antipodarum* were negatively related with distance upstream from the pond section ($N = 60$, $r = -0.55$, $P < 0.05$), as were their nontransformed densities using nonparametric analysis ($N = 60$, $r = -0.70$, $P = 0.00$). Densities of *T. serpenticola* (log-transformed) were positively related with distance upstream from Morgan Lake ($r = 0.33$, $P = 0.03$). *Taylorconcha serpenticola* density (nontransformed) was positively related to distance from Morgan Lake ($N = 60$, $r = 0.30$, $P = 0.02$). Density of *Fluminicola* sp. was not related to distance from Morgan Lake.

Surface areas of macrophytes collected in the vegetation and edge samples were not measured in this study. Therefore, our results show only densities of snails in a 2-dimensional plane within the 3 habitats.

DISCUSSION

It appears that *P. antipodarum* may be establishing itself into the upper portion of the springs, mostly by spreading through vegetation and edges of the faster-flowing waters and

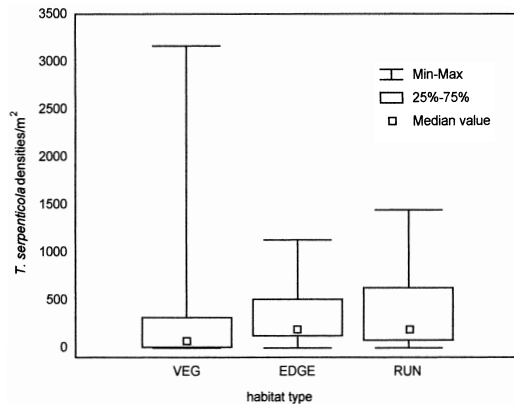


Fig. 4. Comparison of *T. serpenticola* densities $\cdot m^{-2}$ in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999. (Vegetation: median = 78.00, mean = 344.75, minimum = 0.00, maximum = 3163.86, lower quartile = 0.00, upper quartile = 312.48, $N = 23$. Edge: median = 195.00, mean = 351.54, minimum = 0.00, maximum = 1132.74, lower quartile = 117.18, upper quartile = 507.78, $N = 14$. Run: median = 195.00, mean = 353.84, minimum = 0.00, maximum = 1445.22, lower quartile = 78.12, upper quartile = 624.96, $N = 17$.)

then moving into new habitats, particularly unoccupied vegetation habitat. Faster water velocity possibly limits colonization of *P. antipodarum* into run habitats. The vegetation habitat with its associated slower water velocity seems to provide refuge for small-sized *P. antipodarum* and might also act as a nursery. Velocity could also affect smaller *P. antipodarum* more than larger ones due to a combination of physical, behavioral, physiological, or morphological factors. Current more easily dislodges *P. antipodarum* than *T. serpenticola* individuals. During this study, *T. serpenticola* remained attached to rock substrates when disturbed, whereas *P. antipodarum* immediately detached themselves from any substrate and readily entered the drift after disturbance. Interestingly, we found *P. antipodarum* to be the 2nd most abundant macroinvertebrate collected in 24-hour drift net samples at Banbury Springs, and we have often found them in floating vegetation mats in Morgan Lake. We have also timed their dispersal on flat substrates at up to $1 m \cdot h^{-1}$.

Continued invasions of *P. antipodarum* are likely, particularly in habitats with low water velocity and large amounts of vegetation (e.g., ponds, lakes, reservoirs, slower rivers, and backwaters), but may be limited in habitats with

higher water velocities. There was little water temperature gradient in our study area, but temperature may be important for snail distribution and abundance in other aquatic environments, including Morgan Lake.

Although densities of the threatened species, *T. serpenticola*, did not vary between habitats, we do not know whether this species would be more abundant in vegetation habitats if densities of *P. antipodarum* were lower. We are presently conducting field and laboratory competition experiments between *P. antipodarum* and *T. serpenticola* and are continuing to monitor temporal and spatial changes in snail densities on a bi-monthly basis from these same locations at Banbury Springs. We will also conduct population surveys of *T. serpenticola* throughout its range in the mid-Snake River drainage in the near future.

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