

Research Article

Field surveys reveal physicochemical conditions promoting occurrence and high abundance of an invasive freshwater snail (*Potamopyrgus antipodarum*)

Michele D. Larson¹, Daniel Greenwood², Kara Flanigan², Amy C. Krist¹

¹ Department of Zoology & Physiology, Program in Ecology, University of Wyoming, Laramie, WY, USA

² Department of Zoology & Physiology, University of Wyoming, Laramie, WY, USA

Corresponding author: Amy C. Krist (krist@uwyo.edu)



Academic editor: Ian Duggan

Received: 15 September 2022

Accepted: 4 December 2022

Published: 18 April 2023

Citation: Larson MD, Greenwood D, Flanigan K, Krist AC (2023) Field surveys reveal physicochemical conditions promoting occurrence and high abundance of an invasive freshwater snail (*Potamopyrgus antipodarum*). *Aquatic Invasions* 18(1): 83–102, <https://doi.org/10.3391/ai.2023.18.1.103389>

Abstract

Environmental conditions promoting the occurrence and high abundance of non-native taxa are linked to critical stages of species invasions: establishment, whether a site can sustain a population of the non-native taxon, and impact, the extent to which the consequences of establishment negatively affect the invaded ecosystem. Using surveys across environmental gradients, we examined the physicochemical conditions associated with the occurrence and abundance of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) and co-occurring native mollusks. Abundance of *Potamopyrgus* very strongly increased with stream width and conductivity (specifically with chloride, sulfate, potassium, and sodium ions). Also, *Potamopyrgus* were most likely to occur at sites with relatively low pH and water velocity and relatively high calcium ion concentration and abundance also slightly increased in these conditions. The physicochemical conditions indicate the characteristics of sites that are suitable for establishment and secondary spread of *Potamopyrgus*. Native mollusks differed from *Potamopyrgus* in the physicochemical conditions associated with abundance suggesting that variation among habitats could permit native mollusks to persist at larger geographic scales even if they often co-occur with *Potamopyrgus*. Abundance of native *Physa* moderately decreased with abundance of *Potamopyrgus*. Because abundance of *Physa* and *Potamopyrgus* responded oppositely to stream width and conductivity, the negative relationship between the abundance of these two taxa may be caused by contrasting responses to physicochemical conditions, acting alone or in concert with biotic interactions.

Key words: establishment, impact, secondary spread, non-native, specific conductivity, stream width

Introduction

The environmental conditions critical to maintaining optimal evolutionary fitness differ widely among organisms and ecosystems. For non-native organisms, environmental conditions dictate whether they can establish, increase in population size, and expand their geographic range (Lockwood et al. 2007; Davis

Copyright: © Michele D. Larson et al.
This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

2009). Environmental conditions promoting the occurrence and high abundance of non-native taxa are linked to critical stages of species invasions: establishment, which addresses whether a site can sustain a population of the non-native taxon, and impact, the extent to which the consequences of establishment will negatively affect the invaded ecosystem (Vander Zanden and Olden 2008). Establishment is also critical to secondary spread, expansion of non-native taxa beyond the primary site of introduction, because suitable habitat is required for non-native taxa to persist. Because non-native taxa that are established at one or a few sites have the potential to greatly expand their geographic distribution in the non-native range, halting or slowing secondary spread of non-native taxa is a critical strategy for managing biological invasions (Vander Zanden and Olden 2008). Although ecological impact of non-native taxa is difficult to predict (Parker et al. 1999), abundance is widely recognized as a significant contributor to impact from both a theoretical (Parker et al. 1999; Ricciardi 2003) and empirical (Bradley et al. 2019; Strayer et al. 2019) standpoint. Thus, assessing the attributes that make sites suitable to establishment and high impact by particular non-native species are critical components to the successful management of non-native taxa.

In freshwater ecosystems, environmental conditions such as temperature, specific electrical conductivity, other aspects of water chemistry (e.g. specific ions, pH, nutrients), water velocity, light levels, substrate type, and surface area can affect organismal fitness. For example, water temperature affects both body size and size at maturity of ectotherms (Atkinson 1994, 1995; Angilletta et al. 2004), and ion concentrations differing substantially from organismal homeostatic levels demand organisms to expend energy to maintain osmotic balance (Willmer et al. 2004; Cain et al. 2011). In freshwater mollusks, slight increases in water temperature can increase basal resources (benthic algae, Lamberti and Resh 1983) and can have consequences on individual and population growth rates of aquatic mollusks (Van der Schalie and Berry 1973; El-Emam and Madsen 1982; Parashar and Rao 1988; Verhaegen et al. 2021) and ion concentrations (measured as specific electrical conductivity) have diverse and substantial effects on both native and non-native taxa (reviewed in Dillon 2000). Densities of freshwater mollusks increase with conductivity in field surveys (Camara et al. 2012; Tchakonte et al. 2014) and conductivity affects growth and survival of freshwater mollusks in laboratory studies (Herbst et al. 2008; Vazquez et al. 2016; Larson et al. 2020). Calcium ions, specifically, can alter fitness or distributions of freshwater mollusks because they are used to create calcium carbonate shells as well as for muscle contractions and nerve impulses (Thomas and Lough 1974; Madsen 1987; Dillon 2000; Zalizniak et al. 2009).

Relatively low conductivity can reduce abundance and restrict the range of the invasive snail, *Potamopyrgus antipodarum* (Gray, 1853) which has colonized five continents and 39 countries worldwide (Geist et al. 2022). Although this invader tolerates a wide range of environmental conditions, some physicochemical conditions including conductivity and temperature, can promote establishment and high densities. Outside the native range, densities of *Potamopyrgus* increase with conductivity (Kerans et al. 2005; Herbst et al. 2008; Moore et al. 2012; reviewed in Geist et al. 2022) and in the Greater Yellowstone ecosystem, *Potamopyrgus* only occurred in streams with geothermal activity and consequently high conductivity (Clements et al. 2011). Temperature affects life history traits, and thus evolutionary fitness, in invasive populations of *Potamopyrgus*. Cool water temperatures delay reproduction (Dybdahl and Kane 2005), lead to larger body sizes (Dybdahl and Kane 2005; Verhaegen et al. 2021), and alter fecundity (lower: Dybdahl and

Kane 2005; higher: Verhaegen et al. 2021) relative to optimal water temperatures. To predict sites where *Potamopyrgus* are most likely to invade and achieve high abundance, more information is needed about specific physicochemical conditions associated with establishment and high abundances of this invasive snail.

To understand how conductivity, temperature, and other physicochemical conditions affect the presence and abundance of *Potamopyrgus* and three sympatric native mollusks, we surveyed mollusks across a natural gradient in water chemistry and temperature created by geothermal springs (which release ions, minerals, and increase water temperature) in five rivers in the Greater Yellowstone Area (Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, and Yellowstone National Park). The three objectives of our study were: 1) to assess the physical and chemical conditions associated with the presence and abundance of the invasive snail, *Potamopyrgus*, 2) to determine the extent to which these environmental conditions favoring *Potamopyrgus* differed from co-occurring native mollusks. Also, because *Potamopyrgus* can compete with (Lysne and Koetsier 2008; Riley et al. 2008; Thon 2010; Larson and Black 2016) or facilitate (Cope and Winterbourn 2004) native mollusks, our third objective was 3) to assess whether the abundance of *Potamopyrgus* predicted the abundance or occurrence of any native mollusk taxa, suggesting possible effects (negative or positive) of the non-native snail on sympatric native mollusks.

Methods

Field survey

To assess the environmental factors associated with the presence and abundance of *Potamopyrgus* and sympatric native mollusks, in July 2014 and 2015 we surveyed biotic (abundances of co-occurring mollusks) and abiotic conditions (temperature, conductivity, ion concentrations, pH, stream velocity, and stream width) across an environmental gradient created by sampling sites above and below geothermal inputs (Table 1) in each of three (2015) to five (2014) rivers in the Greater Yellowstone Area (Suppl. material 1) where *Potamopyrgus* had occurred in the past. Although there are other approaches to assessing the environmental variables associated with the presence of *Potamopyrgus*, we focused on rivers where *Potamopyrgus* occurred and took advantage of variation in occurrence between sites above and below geothermal inputs to discern the environmental conditions associated with their occurrence and abundance.

At each site where we collected samples, we measured temperature, conductivity, pH, ion concentrations, stream width, and stream velocity using standard procedures for stream sampling. We measured temperature and conductivity at three locations (along each shoreline and in the middle of the stream) at each site using a sonde (Yellow Springs Instruments, model 85). We measured stream width at the greatest width at the water surface for each sampling site. We used the float method (Newbury and Bates 2017) three times/site to measure stream velocity. At each site, we collected two water samples (shoreline and mid-stream) to measure pH, cations, and anions. We filtered each sample using Whatman Grade GF/A glass microfiber 0.4 μm filters and cooled samples on ice. Within 12 hours of collection, we measured pH (Corning 430 pH meter) and acidified the sample for cation analysis with 0.5 M HCl until the pH dropped below 2. We refrigerated the cation samples and froze the anion samples until we analyzed them using ion chromatography (Thermo Fisher Scientific ICS 5000) at the Geochemical Analytical Laboratory (Geology and Geophysics Department, University of Wyoming).

Table 1. Abiotic factors differed widely among rivers and between sites above and below geothermal input. Sites were a minimum of 50 meters above or below geothermal inputs. All measurements are means except stream width, which is a single observation. Ion units are mg/L.

Abiotic Variable	Site	2014				2015		
		Marmot Springs	Polecat Creek	Crawfish Creek	Firehole River	Marmot Springs	Polecat Creek	Crawfish Creek
Temperature (°C)	Above	23.6	20.0	19.8	19.4	23.8	18.9	17.9
	Below	24.0	22.8	20.4	21.7	24.5	18.1	22.9
pH	Above	7.4	8.1	7.8	8.2	8.0	7.7	8.5
	Below	8.2	8.3	8.3	8.2	8.1	7.7	8.3
Conductivity (μS/cm)	Above	112.9	119.1	147.7	245.9	129.3	146.7	167.5
	Below	121.7	129.1	299.4	287.1	143.2	153.5	307.9
Sodium cations (Na ⁺)	Above	19.9	22.4	28.9	49.8	22.9	26.8	35.8
	Below	24.4	21.3	37.0	58.1	25.0	28.8	45.5
Potassium cations (K ⁺)	Above	3.6	3.8	2.9	5.1	4.0	3.3	3.4
	Below	4.0	3.5	2.9	5.4	4.1	3.6	3.7
Magnesium cations (Mg ⁺²)	Above	0.88	0.91	0.87	0.87	0.43	0.46	0.49
	Below	0.84	0.84	0.89	0.87	0.41	0.47	0.44
Calcium cations (Ca ⁺²)	Above	2.9	3.5	3.7	4.1	3.0	3.1	0.0
	Below	2.8	3.3	4.2	3.9	2.9	3.2	4.3
Chloride anions (Cl ⁻)	Above	8.5	11.1	12.5	35.7	10.7	13.0	15.0
	Below	14.0	11.1	15.4	42.5	14.9	15.4	20.0
Sulfide anions (SO ₄ ⁻)	Above	2.5	3.5	4.0	5.7	3.1	2.9	3.1
	Below	2.7	3.9	3.3	5.8	3.1	3.3	3.4
Stream Width (m)	Above	2.2	1.3	3.0	3.5	2.2	1.3	3.0
	Below	1.3	2.6	4.3	6.6	1.3	2.6	4.3
Stream Velocity (m/s)	Above	0.23	0.53	0.71	0.61	0.23	0.45	0.71
	Below	1.22	0.35	0.53	0.44	0.87	0.25	0.51

We used a stovepipe (0.032 m²) to sample abundance of mollusks at each site. We elutriated each stovepipe sample using 500-μm sieves to remove most cobbles, gravel, and other substrates and preserved each sample immediately in 95% ethanol. In July 2014, we collected 3–5 samples/site at 5 rivers along a single transect at a minimum of 50 meters from the geothermal hot spring. In July 2015, we sampled 10 replicates/site along 1 or 2 transects in 3 of the rivers sampled in 2014, increasing the replicate number to obtain a more robust estimate of sample variance (Suppl. material 1). In 2015, we also omitted two of the rivers that we sampled in 2014: the Firehole River because the frequency and intensity of geothermal activity precluded a gradient in conductivity and the Gibbon River because we found only one live snail and no *Potamopyrgus* and our study design required *Potamopyrgus* to occur. At sites dominated by bedrock or high stream velocities, we collected longitudinal rather than transverse transects (Suppl. material 1). In the laboratory, we sorted samples, identified mollusks to the genus level (Brown 1991), and counted snails to assess the abundance of each taxonomic group. The native mollusks that we found were *Pyrgulopsis* (Call & Pilsbry, 1886), *Physa* (Draparnaud, 1801), *Galba* (Schrank, 1803) and *Sphaerium* (Scopoli, 1777) clams. We did not analyze abundance of *Galba* because they occurred in samples from only three of fourteen sites (Table 2).

Table 2. Abundance of *Potamopyrgus* (individuals/sample) and native mollusks varied among rivers, between sites above or below geothermal input, and between years. Abundance are means of the number of individuals in 5 (2014) or 10 samples (2015). Samples were collected above and below geothermal springs. Although we found *Galba* (Family Lymnaeidae), we excluded them because they did not occur above geothermal springs and only below geothermal springs in two rivers.

River	Year	Sample	<i>Potamopyrgus</i>	<i>Pyrgulopsis</i>	<i>Physa</i>	<i>Sphaerium</i>
Marmot	2014	Above	2.0	11.0	5.3	0.3
		Below	5.4	12.0	7.8	0.0
	2015	Above	9.2	39.5	25.5	0.1
		Below	19.5	58.3	8.3	6.1
Polecat	2014	Above	76.4	0.2	2.6	11.2
		Below	33.6	35.2	0.0	11.0
	2015	Above	71.3	0.1	1.0	24.4
		Below	46.8	39.5	1.0	18.8
Crayfish	2014	Above	0.2	0.0	0.0	1.8
		Below	5.0	0.0	1.6	1.4
	2015	Above	1.3	0.0	0.0	0.3
		Below	5.1	0.0	0.0	0.3
Firehole	2014	Above	375.0	0.0	0.2	11.4
		Below	179.2	0.0	0.8	1.4

Statistical analyses

We used principal component analysis (PCA) to reduce the 11 abiotic independent variables (Table 1) to two uncorrelated principal components. Because we made multiple measurements for all variables except stream width, we analyzed mean values for each site (and year, for rivers with data from two years) such that each independent variable in the PCA resulted from 14 values (two sites at four rivers in 2014 [the Gibbon River was excluded from all analyses because of mollusk rarity] and two sites at three rivers in 2015). We used scaled and standardized independent variables in the PCA (resulting in all metrics having a mean of zero and a standard deviation of 1). Based on the limited number of sample sites in our study and the broken stick model (Legendre and Legendre 2012) we selected the principal components that explained more variance than random chance and the equilibrium circle of descriptors method (Legendre and Legendre 2012) to assess which principal component loadings were important for describing the principal components.

Because we had count data that was zero-inflated (all mollusk taxa were absent from > 27% of the samples) and overdispersed (Zuur et al. 2009), we used Zero-Inflated Negative Binomial (ZINB) regression models (using `zeroinfl` function with a log link for count models and a logit link for zero-inflated models in the `pscl` package in R; Zeileis et al. 2008) to address the extent that principal components predicted abundance (Count Model) and occurrence (presence or absence: Zero-Inflation Model) of each mollusk taxon. Zero-inflated models are mixture models which address both occurrence and abundance of organisms and are ideal for analyzing count data with many zeros (Zuur et al. 2009). Zero-inflated models combine logistic regression to analyze occurrence (zeros v. non-zeros; Zero-Inflation Model) and negative binomial GLM to analyze counts (zero and non-zeros; Count Model; Zuur et al. 2009). We included only first order terms in our analyses because evaluating interactions in principal component analyses is precluded (Aiken and West 1991). We combined data from two years for three of the rivers

(Marmot, Polecat, Crayfish) because the auto-correlation function (ACF; Zuur et al. 2009) revealed no significant auto-correlations for any of the native mollusks and very slight auto-correlation in 10% of the cases for *Potamopyrgus*. Following Zuur et al. (2009), and given the limited number of observations in our study, we did not include an auto-correlation structure in any of the models.

We assessed whether abundance of *Potamopyrgus* affected the abundance or occurrence of each native mollusk taxon using zero-inflated negative binomial (ZINB) regressions with abundance of *Potamopyrgus* as the independent variable and the abundance of each of the native mollusk taxa (tested individually) as the dependent variable. We conducted all analyses and made all plots using R statistical package (Version RStudio 4.1.2, 2021 R Foundation for Statistical Computing, Vienna).

Results

Abundance of *Potamopyrgus* very strongly ($p < 0.001$) increased with stream width and conductivity, and specifically with concentrations of chloride (Cl⁻), sulfate (SO₄⁻²), potassium (K⁺), and sodium (Na⁺) ions, (PC1, 45.4% of variance; Table 3, Table 4: Count Model, Figs 1, 2) and weakly ($p = 0.10$) increased with calcium, and relatively low water velocity and pH (PC2, 13.9% of variance; Table 3, Table 4: Count Model, Fig. 1). These same conditions also moderately promoted ($p = 0.04$) the occurrence of *Potamopyrgus* (PC2, Table 4: Zero-Inflation Model, Fig. 1).

Table 3. Loadings for principal components 1 (PC1 explains 45.4% of variance) and 2 (PC2, 13.9%). We excluded loadings less than +/- 0.30 following Legendre and Legendre (2012).

Variables	PC1	PC2
Temperature	–	–
pH	–	0.577
Conductivity	0.374	–
Chloride anions	0.424	–
Sulfate anions	0.396	–
Potassium cations	0.301	–
Sodium cations	0.426	–
Calcium cations	–	-0.437
Magnesium cations	–	–
Water Velocity	–	0.656
Stream Width	0.392	–

The abiotic predictors of abundance of native mollusks were distinct from *Potamopyrgus* (Table 4, Fig. 1). In contrast to *Potamopyrgus*, abundance of *Physa* was very strongly reduced ($p < 0.001$), and abundance of sphaeird clams was somewhat reduced ($p < 0.06$), by increasing stream width and conductivity, and specifically with increasing concentrations of sodium, chloride, sulfate, and potassium ions, (PC1, Table 3, Table 4: Count Model, Fig. 1). Abundance of *Pyrgulopsis* was not predicted by any of the abiotic characteristics included in PC1 and PC2. Occurrence of native mollusks were not predicted by any of the variables that we measured (Table 4: Zero-Inflation Model).

Abundance of *Potamopyrgus* weakly increased ($p < 0.07$) with the abundance of *Pyrgulopsis* (Fig. 3a) but was not associated with occurrence of this native snail or with native *Physa* (Table 5). Abundance of *Potamopyrgus* and *Physa* were moder-

Table 4. Zero-inflated negative binomial regression analyses reveal that the abiotic predictors of abundance (Count Model) differed between *Potamopyrgus* and the native mollusks. Abbreviations: SE = standard error, z = z-values, and p = p-values. P-values less than 0.05 are bolded.

Regression	Model	Coefficients	Estimate	SE	z	p
A. <i>Potamopyrgus</i>	Count Model	Intercept	3.75	0.19	19.71	<0.001
		PC1	0.32	0.08	4.09	<0.001
		PC2	-0.33	0.20	-1.65	0.10
		Log Theta	-0.87	0.23	-3.78	<0.001
	Zero-Inflation Model	Intercept	-2.67	1.36	-1.97	<0.001
		PC1	0.21	2.33	0.92	0.36
PC2		1.39	0.68	2.05	0.04	
B. <i>Pyrgulopsis</i>	Count Model	Intercept	4.96	1.15	4.33	< 0.001
		PC1	1.29	0.84	1.53	0.13
		PC2	0.18	0.26	0.70	0.49
		Log Theta	-1.67	0.21	-7.79	< 0.001
	Zero-Inflation Model	Intercept	49.03	133.20	0.37	0.71
		PC1	69.37	180.98	0.38	0.70
PC2		6.16	29.02	0.21	0.83	
C. <i>Physa</i>	Count Model	Intercept	1.20	0.25	4.73	<0.001
		PC1	-0.50	0.12	-4.21	<0.001
		PC2	0.29	0.29	1.02	0.31
		Log Theta	-1.43	0.22	-6.48	<0.001
	Zero-Inflation Model	Intercept	-33.45	99.19	-0.34	0.74
		PC1	5.51	21.18	0.26	0.80
PC2		18.45	55.59	0.33	0.74	
D. <i>Sphaerium</i>	Count Model	Intercept	2.01	0.27	7.55	< 0.001
		PC1	-0.20	0.11	-1.85	0.06
		PC2	-0.26	0.29	-0.90	0.37
		Log Theta	-1.26	0.29	-4.35	< 0.001
	Zero-Inflation Model	Intercept	-6.23	4.79	-1.30	0.19
		PC1	-3.47	2.81	-1.23	0.22
PC2		1.84	1.19	1.56	0.12	

ately negatively associated ($p < 0.02$; Table 5, Fig. 3b). In contrast, abundance of *Potamopyrgus* was not related to the abundance of *Sphaerium* clams but these clams were moderately more likely ($p = 0.05$) to occur at sites where *Potamopyrgus* were abundant (Table 5).

Discussion

We identified the physical attributes that promote high abundance of the invasive snail *Potamopyrgus* and three sympatric native mollusks. Abundance of *Potamopyrgus* strongly increased with stream width and conductivity, and specifically with chloride, sulfate, potassium, and sodium concentrations. Also, abundance of *Potamopyrgus* weakly increased with calcium and relatively low water velocity and pH and were more likely to occur at sites possessing these conditions. These physical conditions predict where the snail is most likely to achieve invasive densities and thus can reveal habitats most vulnerable to invasion. Because the

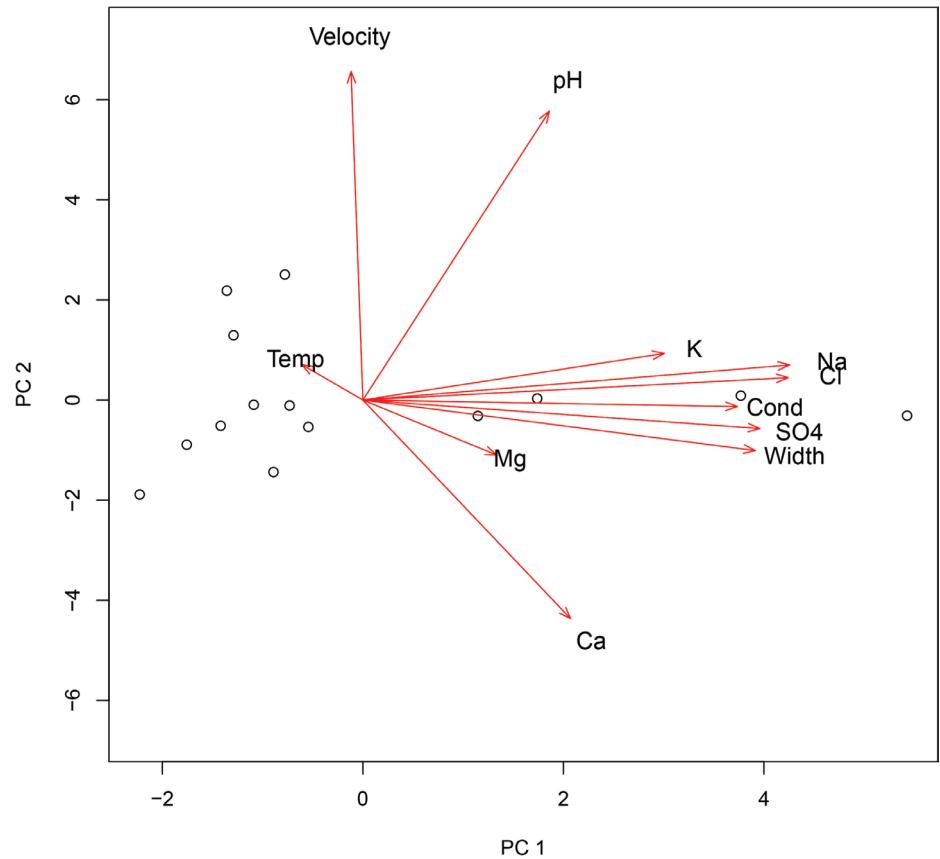


Figure 1. Relationships between Principal component 1 (x axis) and Principal component 2 show the chemical and physical attributes associated with mollusk abundance and occurrence. The points are means for each site. Abbreviations: Temp (temperature), Cond (conductivity), Na (sodium cations), K (potassium cations), Ca (calcium cations), Mg (magnesium cations), Cl (chloride anions), SO₄ (sulfate ions), Width (stream width), Velocity (stream velocity).

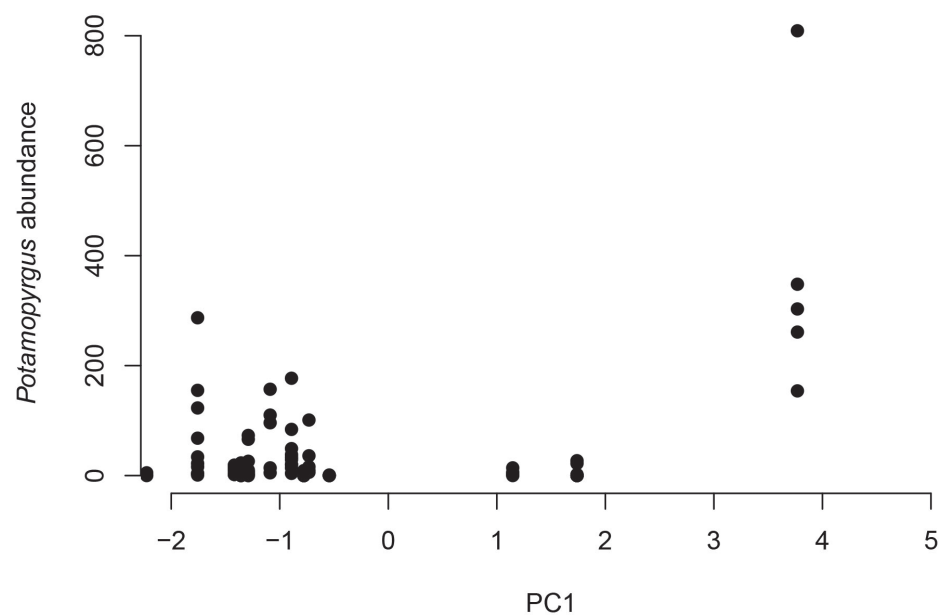


Figure 2. Principal Component 1 (stream width, conductivity, specifically chloride (Cl⁻), sulfate (SO₄⁻²), potassium (K⁺), and sodium (Na⁺) ions) very strongly predicted the abundance of the invasive snail, *Potamopyrgus* (Table 4). The abundances of *Potamopyrgus* per sample correspond with densities varying from 6–11,600 individuals/m².

Table 5. Zero-inflated negative binomial regression analyses show that abundance of *Potamopyrgus* weakly increased with the abundance of *Pyrgulopsis*, was moderately negatively associated with abundance of *Physa*, and was not related to abundance of *Sphaerium* clams (Count Models). Abundance of *Potamopyrgus* was not related to occurrence of either *Pyrgulopsis* or *Physa* but *Sphaerium* clams were more likely to occur at sites where *Potamopyrgus* were abundant (Zero-Inflation models). Abbreviations: SE for standard error, z for z -values, and p for p -values. P -values less than or equal to 0.05 are bolded.

Regression	Model	Coefficients	Estimate	SE	z	p
A. <i>Pyrgulopsis</i>	Count Model	Intercept	3.26	0.35	9.31	<0.001
		Invasive abundance	0.01	0.01	1.82	0.07
		Log Theta	-0.68	0.40	-1.70	0.09
	Zero-Inflation Model	Intercept	0.36	0.31	1.14	0.26
		Invasive abundance	0.00	0.00	1.07	0.29
B. <i>Physa</i>	Count Model	Intercept	2.24	0.31	7.13	<0.001
		Invasive abundance	-0.004	0.52	-2.31	0.02
		Log Theta	0.79	0.40	-1.53	0.13
	Zero-Inflation Model	Intercept	-0.05	0.51	-0.11	0.92
		Invasive abundance	-0.00	0.00	-0.84	0.40
C. <i>Sphaerium</i>	Count Model	Intercept	2.46	0.27	9.03	<0.001
		Invasive abundance	0.00	0.00	0.34	0.74
		Log Theta	-0.76	0.25	-3.04	<0.001
	Zero-Inflation Model	Intercept	1.41	0.46	3.07	<0.01
		Invasive abundance	-0.18	0.09	-1.96	0.05

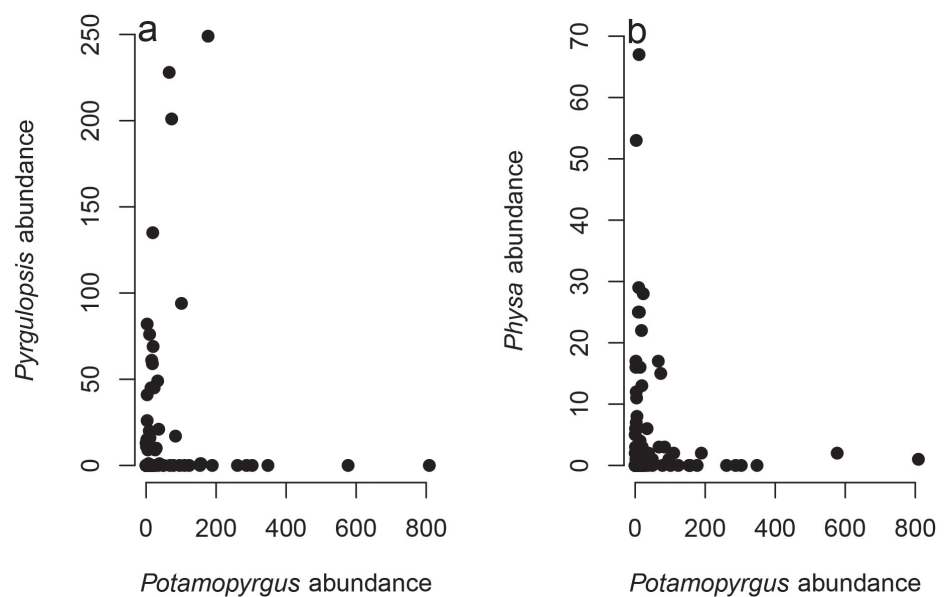


Figure 3. The abundance of the native snail *Pyrgulopsis* weakly increased ($p = 0.07$) with abundance of the invasive snail, *Potamopyrgus* (a) and the native snail *Physa* moderately decreased ($p = 0.02$) with abundance of *Potamopyrgus* (b). Although the relationship between the abundance of *Potamopyrgus* and *Physa* appears to be strongly influenced by the two sites where the abundance of *Potamopyrgus* was highest (>500 individuals/sample), the evidence for a negative relationship is much stronger when the two extreme values are omitted.

physical conditions associated with abundance and occurrence of *Potamopyrgus* were distinct from the native mollusks, our results also reveal probable physico-chemical conditions required for habitat refuges for natives that are negatively af-

ected by *Potamopyrgus* because they possess chemical and physical conditions that are not optimal for the invasive snail; *Potamopyrgus* may persist, but likely not in high abundance. Also, by revealing the abiotic conditions that promote high abundance of *Potamopyrgus*, we identify sites where impacts on natives, when present, are most likely to be greatest. Associations between abundance and occurrence of invasive and native mollusks reveal that either invasive snails reduced abundance of one of the native mollusks, *Physa*, or the two mollusk taxa possessed contrasting responses to the same physicochemical conditions.

Conditions favoring *Potamopyrgus*

Potamopyrgus increased in abundance with increasing stream width and conductivity and specifically with chloride, sulfate, sodium, and potassium ions. Also, *Potamopyrgus* were slightly more abundant and more likely to occur at sites with relatively more calcium and relatively lower water velocity and pH. By assessing the abundance of this invasive snail across a gradient of water and stream conditions, our survey reveals the ideal environmental conditions required for the clonal lineage US1 (Dybdahl and Drown 2011) of *Potamopyrgus* in the Western U.S.A. However, diverse genotypes in the native range in New Zealand (water velocity: Holomuzki and Biggs 1999) and other invasive genotypes (water velocity: Kefford and Lake 1999; conductivity: Levri et al. 2020; salinity: Jacobsen and Forbes 1997; Gerard et al. 2003) show similar responses to many of the same environmental conditions. By revealing the conditions required for the invasive snail to occur and thrive, our results can be used to predict sites that are suitable for secondary spread and invasion success of *Potamopyrgus*.

Positive associations between abundance of *Potamopyrgus* and conductivity and specifically with sodium, chloride, sulfate, and potassium ions (PC1; Fig. 2, Table 4) are consistent with many studies (Kerans et al. 2005; Herbst et al. 2008; Clements et al. 2011; Moffitt and James 2012; Spyra and Strzelec 2014; Spyra et al. 2015; Szocs et al. 2015; Halabowski et al. 2020; Levri et al. 2020, reviewed in Geist et al. 2022). For freshwater mollusks, ion concentrations must be high enough to permit locomotion, growth (Brodersen and Madsen 2003; Dalesman and Lukowiak 2010), and shell integrity (Brodersen and Madsen 2003). Consequently, laboratory experiments revealed stunted growth ($< 100 \mu\text{S}/\text{cm}$; Herbst et al. 2008; Larson et al. 2020) and high mortality ($< 50 \mu\text{S}/\text{cm}$; Herbst et al. 2008; Vazquez et al. 2016; Larson et al. 2020) of *Potamopyrgus* at relatively low conductivities. Although Murria and colleagues (2008) found a negative relationship between conductivity and *Potamopyrgus* abundance in streams in Spain, high pollutant levels (POM, DOC, and ammonium) probably contributed to this contrasting result.

In addition to adding to many studies showing that conductivity is important to the fitness of *Potamopyrgus* (Kerans et al. 2005; Herbst et al. 2008; Clements et al. 2011; Moffitt and James 2012; Spyra and Strzelec 2014; Spyra et al. 2015; Szocs et al. 2015; Halabowski et al. 2020; Levri et al. 2020, reviewed in Geist et al. 2022), our study also addresses six specific ions (magnesium, calcium, potassium, chloride, sodium and sulfate) contributing to conductivity. In a recent comprehensive review of the autecology of *Potamopyrgus*, Geist and authors (2022) stated the need for more knowledge and understanding of how water chemistry affects *Potamopyrgus*. Our study addresses this knowledge gap by measuring concentrations of specific ions and revealing four ions (sodium, chloride, sulfate, and potassium) that directly affected abundance of *Potamopyrgus*.

Abundance of *Potamopyrgus* also increased with stream width (PC1; Fig. 2, Table 4). Stream width may increase snail abundance because habitat diversity often

increases with habitat size. Densities of invasive zebra mussels (*Dreissena polymorpha*) increase with lake size possibly because larger lakes possess more habitat and available substrate (Naddafi et al. 2011). Stream width can also affect quantity of food for grazers. Relative to narrow streams with high canopy cover (and substantial allochthonous subsidies), primary production (Hill et al. 1995; Quinn et al. 1997; Kiffney et al. 2004; Stovall et al. 2009; Wootton 2012; Lesutiene et al. 2014; Warren et al. 2016) and consequently food quantity, is often higher with low canopy cover and high light penetration. Finally, stream width is often correlated with stable, less stressful environments for snails because water velocity is often inversely related to stream width (Dodds and Whiles 2010). Consistent with this relationship, we found that higher relative water velocities reduced the occurrence of *Potamopyrgus*.

The relationship between *Potamopyrgus* abundance and PC1 (stream width and conductivity and specifically with chloride, sulfate, sodium, and potassium ions), although statistically strong ($p < 0.001$), was uneven (Fig. 2). Relatively large variation in abundance of *Potamopyrgus* at low (negative) values of PC1 suggests that *Potamopyrgus* is tolerant of a large range of conductivity, especially chloride, sulfate, sodium, and potassium ions, and stream width. Wide environmental tolerance is consistent with our findings for pH (discussed below) and with a recent review of the autecology of *Potamopyrgus* (Geist et al. 2022). Future studies that include a wider range of environments, similar to intermediate values of PC1 (intermediate stream width, conductivity, and specific ions), will clarify the specific nature of this relationship.

Consistent with previous field studies and experiments (Jowett et al. 1991; Holomuzki and Biggs 1999; Kefford and Lake 1999; Shimada and Urabe 2003; Lysne and Koetsier 2006; Holomuzki and Biggs 2007; Murria et al. 2008; McKenzie et al. 2013; Schossow et al. 2016), *Potamopyrgus* were slightly more abundant and were more likely to occur in relatively low water velocities (PC2; Table 4). *Potamopyrgus* can dislodge from substrates at stream velocities > 0.12 m/s (Schossow et al. 2016) with most snails dislodging at > 0.70 m/s (Holomuzki and Biggs 1999; Kefford and Lake 1999). Additionally, *Potamopyrgus* locomotion decreases and rate of dislodgement increases with increasing water velocity (Sepulveda and Marczak 2012). Also, *Potamopyrgus* produce slightly fewer offspring in environments with high (lotic) versus low (lentic) water velocity (Verhaegen et al. 2021). Therefore, high water velocity conditions are stressful for *Potamopyrgus* by decreasing motility and fitness and increasing the likelihood of dislodgement.

Potamopyrgus were somewhat more abundant and more likely to occur at sites with relatively low pH. Multiple studies show effects of pH on mollusk presence or abundance (Lewin and Smolinski 2006; Spyra 2010; Sowa et al. 2019; Levri et al. 2020) and the direction of the relationship depends on the range of pH across the study sites and the taxa of mollusks. For example, most studies showing abundance or occurrence of mollusks increasing with pH included multiple mollusk taxa or sites with acidic (< 7 pH) water (Spyra 2010; Sowa et al. 2019; Levri et al. 2020, but Lewin and Smolinski 2006 is an exception). In contrast, the water at all of our survey sites was basic (pH 7.4–8.5, Table 1), which probably explains why we found that *Potamopyrgus* was more likely to occur where pH was relatively lower. However, *Potamopyrgus* can occur in acidic to alkaline waters (pH 5.6–6.0, Blakely and Harding 2005; pH 4.0–9.0, Spyra 2010; pH 5.7–9.0, Levri et al. 2020) suggesting that *Potamopyrgus* tolerates a large range of pH.

Potamopyrgus were slightly more abundant and were more likely to occur where calcium levels were relatively high (range in our study 0.0–4.3 mg/L). In freshwater mollusks, calcium is used to form shells (calcium carbonate) and, is required for muscle contractions and nerve impulses (Thomas and Lough 1974; Madsen 1987; Dillon 2000; Zalizniak et al. 2009). Consistent with our results, calcium concentrations al-

tered mollusk fitness in previous studies. Growth, reproduction, and locomotion of diverse snails increased with calcium concentrations in laboratory experiments (Thomas and Lough 1974; Madsen 1987; Dillon 2000; Zaluzniak et al. 2009) and low calcium concentrations can reduce growth and thin mollusk shells (Glass and Darby 2009).

Densities of the snails can increase with substrate complexity, perhaps by providing refuge from predation and stress from high stream velocity, or increasing access to forage (Stewart and Garcia 2002). Because we did not account for differences in substrate among samples, this omission probably increased the error of our estimates of abundance of all mollusks.

Differences between conditions favoring native and invasive snails

All native mollusks differed substantially from *Potamopyrgus* in the physicochemical conditions associated with abundance and occurrence. We found strong evidence that abundance of *Physa* and weak evidence that abundance of *Sphaerium* clams responded oppositely to PC1 (stream width, conductivity, specifically sodium, chloride, sulfate, and potassium ions) than *Potamopyrgus*. Abundance of both native mollusks decreased with increasing stream width and conductivity, specifically with sodium, chloride, sulfate, and potassium ions (PC1). We found no physicochemical attributes that predicted abundance of *Pyrgulopsis*. The limited sample size of *Pyrgulopsis* populations in our survey, only 34% of sites possessed *Pyrgulopsis* yet 74% of sites had *Potamopyrgus*, could explain or contribute to this result. Also, none of the physical or chemical attributes describing PC1 and PC2 predicted occurrence of any of the native mollusks. Possibly we were unable to identify the physicochemical attributes of water bodies that predict occurrence of these native taxa because the sites that we sampled do not represent the full range of physicochemical attributes where native mollusks occur and achieve high population abundance. We designed our field survey to target rivers with sites where *Potamopyrgus* were known to occur rather than sampling rivers based on the known distributions of any of the native mollusks. Thus, our findings about the physicochemical attributes associated with the occurrence and abundance of native mollusks are limited for the native mollusks.

Also, the Zero-Inflation models portion of ZINB, indicating no predictors of the occurrence of native mollusks should be interpreted with caution because our data were more likely to contain false negatives for the native taxa than for *Potamopyrgus*. This is because all native mollusks were much less common at our study sites than *Potamopyrgus* and less common taxa are more likely missed when the sampling area is too small (design error; Zuur et al. 2009). The sampling area may have been too small to detect some uncommon native taxa (area = 0.10–0.32 m² in combined samples/year). Consequently, the physicochemical conditions associated with the occurrence of *Potamopyrgus* are more likely to be robust than for the native mollusks simply because the natives were less common than the invasive snail. For this reason, and because we targeted our sampling at sites where *Potamopyrgus* were known to occur, rather than where specific native taxa occurred, we have less confidence in the habitat associations for native mollusks than for *Potamopyrgus*.

Even with the limitations of our data regarding the physicochemical attributes associated with presence and abundance of native mollusks, the different response of native mollusk taxa to physical attributes of their environments may inform management and conservation of native mollusks. For example, in habitats that are less hospitable to *Potamopyrgus* (e.g. above geothermal inputs), some native mollusks probably have higher fitness than the invasive snail. Consequently, variation among

habitats within and among rivers could permit native mollusks to persist at a larger geographic scale. Also, because *Potamopyrgus* populations can decline rapidly after reaching high population densities (Moore et al. 2012; Gerard et al. 2018; Greenwood et al. 2020), and *Potamopyrgus* can compete with native mollusks (Lysne and Koetsier 2008; Riley et al. 2008; Thon 2010; Larson and Black 2016), the ability to thrive in distinct environmental conditions could allow native mollusk taxa, and other native taxa, to persist and possibly rebound when *Potamopyrgus* populations decline (e.g. Moore et al. 2012; Gerard et al. 2018; Greenwood et al. 2020).

Relationship between abundance of *Potamopyrgus* and abundance and occurrence of native mollusks

Abundance of *Potamopyrgus* had variable effects on abundance and occurrence of native mollusks. Abundance of *Potamopyrgus* was moderately negatively associated with abundance of *Physa* but did not affect the likelihood of *Physa* presence (Table 5, Fig. 3b). A negative association between the abundance of the two taxa is consistent with our finding that stream width and conductivity (PC1) had opposing effects on abundance of the two mollusk taxa: abundance of *Potamopyrgus* strongly increased with stream width and conductivity whereas *Physa* abundance weakly decreased in these same conditions. Opposite relationships between the two mollusk taxa and the environmental attributes could be caused by differences between the two taxa in habitat use or by competition, the most likely interaction between non-native and native taxa occupying the same trophic level (Levine et al. 2003), or by an interaction between both the physical environment and competition (Shea and Chesson 2002). However, because our sampling design targeted rivers supporting populations of *Potamopyrgus* at some sites, rather than targeting habitats where *Physa* were known to occur, the physicochemical attributes associated with the abundance of *Physa* probably do not fully represent the range of sites where these native mollusks occur and achieve high population abundance. Although the negative relationship between *Potamopyrgus* and *Physa* may appear to be driven by two sampling sites where *Potamopyrgus* were very abundant and *Physa* were uncommon (Fig. 3b), omitting data from these two sites, increased the negative relationship between the abundance of the two taxa (increasing from strong evidence to very strong evidence, *sensu* Muff et al. 2021). Thus, abundance of *Physa* was depressed even at relatively low abundance and density of *Potamopyrgus*. In contrast, Cope and Winterbourn (2004) found reproduction and growth of *Physella acuta* (synonym *Physa acuta*) could be facilitated by the presence of *Potamopyrgus*. Although high densities of *Potamopyrgus* can reduce abundance of native mollusks by altering nutrient cycling (Hall et al. 2003), dominating secondary production (Hall et al. 2006), or attracting fish predators (Bowler 1991), to our knowledge, possible negative effects of *Potamopyrgus* on abundance of *Physa* have not been previously documented.

Similar to *Physa*, abundance of *Potamopyrgus* had no effect on the occurrence of *Pyrgulopsis* (Table 5). However, abundance of *Pyrgulopsis* weakly ($p = 0.07$) increased with *Potamopyrgus* (Table 5, Fig. 3a) but was completely driven by one sample (highest abundance for *Pyrgulopsis*; Fig. 3a) with the highest co-occurring abundance of *Pyrgulopsis* and *Potamopyrgus*. Thus, we suspect that the slight effect is not biologically relevant; both because of the outlier and because a positive relationship between the two taxa contrasts with experimental conditions where *Potamopyrgus* strongly limited growth of *Pyrgulopsis* (Riley et al. 2008).

Abundance of *Potamopyrgus* moderately increased the likelihood that *Sphaerium* clams occurred at a site (Table 5). Although we found no evidence that the abundance of *Potamopyrgus* affected the abundance of *Sphaerium* clams, our results contrast with

Gerard et al. (2018) who suggested that possible competition between *Potamopyrgus* and *Sphaerium* clams may have driven population declines of *Potamopyrgus*.

Conclusions

The results of our field survey revealed the physicochemical conditions associated with the presence and high abundance of the invasive snail, *Potamopyrgus*. Revealing the environmental conditions required for the occurrence of the invasive snail improves our ability to predict un-invaded sites that are acceptable for establishment and persistence of this snail. Management strategies focused on halting or slowing secondary spread of non-native taxa are critical for managing biological invasions (Vander Zanden and Olden 2008). Our results also revealed the combination of physicochemical conditions necessary to support populations of invasive snails with high ecological impact (Vander Zanden and Olden 2008). Predicting impact, the extent to which the consequences of establishment of non-native taxa will negatively affect an invaded ecosystem, is difficult (Parker et al. 1999) yet abundance of non-native taxa is theorized (Parker et al. 1999; Ricciardi 2003) and known (global meta-analysis, Bradley et al. 2019) to be a strong predictor of species impact. The physicochemical conditions that predict high abundance of the invasive snail, relatively high conductivity (especially chloride, sulfate, sodium, and potassium ions) and stream width, reveal sites where the snail is likely to achieve high impact. Invaded sites with these physicochemical conditions and where snails are present but do not occur at high abundances, should be monitored more frequently than invaded sites that do not match these criteria. Also, un-invaded sites matching the physicochemical attributes that we found to promote high abundance of *Potamopyrgus* should be granted higher levels of protection than sites without these attributes. Standardized methods for visual assessment and environmental DNA are effective methods for detecting *Potamopyrgus* (Geist et al. 2022). Actions focusing on preventing spread of *Potamopyrgus* and other aquatic invasive species should be prioritized because restoring ecosystems following introduction is often impossible (Havel et al. 2015).

Funding declaration

This work was supported by funding from Conchologist of America Grant, Western Society of Malacologists Student Research Grant, University of Wyoming Vern Bressler Fisheries Fund Scholarship, University of Wyoming Louis C. “Red” Rockett Memorial Scholarship to MDL and University of Wyoming EPSCoR undergraduate research grants to DG and KF. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Author contributions

Michele Larson devised the research questions. Michele Larson and Amy Krist designed the survey methods. Michele Larson, Amy Krist, Daniel Greenwood, and Kara Flanigan acquired funding for the research. All authors collected field samples. Amy Krist and Michele Larson analyzed the data and created the figures and tables. Amy Krist and Michele Larson wrote the manuscript.

Ethics and permits

No approval of ethics was required to complete this work. Four permits were required to conduct this work: “Evolutionary impacts of the New Zealand mudsnail on native macroinvertebrates in the Greater Yellowstone Ecosystem”, United States Department of the Interior, National Park Service, Grand Teton, GRTE-2014-SCI-0039 & GRTE-2014-SCI-0042 and “Evolutionary impacts of the New Zealand mudsnail on native macroinvertebrates in the Greater Yellowstone Ecosystem”, United States Department of the Interior, National Park Service, Yellowstone, YELL-2014-SCI-5618 & YELL-2015-SCI-5618.

Acknowledgements

We thank L. Kresl-Hotz, L. Looney, C. Harris, C. Barajas, J. Phelps, M. McCoy, J. Werner, L. Thelen-Wade, J. Cussins, M. Bochanski, and M. Collins for assistance with processing samples in the lab. We thank C. Tarwater for assistance with conducting principal component analysis in Program R and J. Dewey for ion chromatography analysis of water samples. We also thank Thematic Editor Ian Duggan and two anonymous reviewers for suggestions that improved our paper.

References

- Aiken LS, West SG (1991) Multiple Regression: Testing and Interpreting Interactions. Sage Publications, Newbury Park, USA, 224 pp.
- Angilletta Jr MJ, Steury TD, Sears MW (2004) Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* 44: 498–509. <https://doi.org/10.1093/icb/44.6.498>
- Atkinson D (1994) Temperature and organism size: A biological law for ectotherms? *Advances in Ecological Research* 25: 1–58. [https://doi.org/10.1016/S0065-2504\(08\)60212-3](https://doi.org/10.1016/S0065-2504(08)60212-3)
- Atkinson D (1995) Effects of temperature on the size of aquatic ectotherms: Exceptions to the general rule. *Journal of Thermal Biology* 20: 61–74. [https://doi.org/10.1016/0306-4565\(94\)00028-H](https://doi.org/10.1016/0306-4565(94)00028-H)
- Blakely TJ, Harding JS (2005) Longitudinal patterns in benthic communities in an urban stream under restoration. *New Zealand Journal of Marine and Freshwater Research* 39: 17–28. <https://doi.org/10.1080/00288330.2005.9517291>
- Bowler PA (1991) The rapid spread of the freshwater Hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the Middle Snake River, Southern Idaho. *Proceedings of the Desert Fishes Council* 21: 173–182.
- Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance-impact relationship for invasive species. *Proceeding of the National Academy of Sciences* 116: 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Brodersen J, Madsen H (2003) The effect of calcium concentrations on the crushing resistance, weight, and size of *Biomphalaria sudanica* (Gastropoda: Planorbidae). *Hydrobiologia* 490: 181–186. <https://doi.org/10.1023/A:1023495326473>
- Brown KM (1991) Mollusca: Gastropoda. In: Thorp JH, Covich AP (Eds) *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, Inc., San Diego, USA, 285–232.
- Cain ML, Bowman WD, Hacker SD (2011) *Ecology*. Second edition. Sinauer Associates, Inc., Sunderland, USA, 648 pp.
- Camara IA, Bony YK, Diomandé D, Edia OE, Konan FK, Kouassi CN, Gouréne G, Pointier JP (2012) Freshwater snail distribution related to environmental factors in Banco National Park, an urban reserve in the Ivory Coast (West Africa). *African Zoology* 47: 160–168. <https://doi.org/10.1080/15627020.2012.11407534>

- Clements WH, Arnold JL, Koel TM, Daley R, Jean C (2011) Responses of benthic macroinvertebrate communities to natural geothermal discharges in Yellowstone National Park, USA. *Aquatic Ecology* 45: 137–149. <https://doi.org/10.1007/s10452-010-9342-8>
- Cope NJ, Winterborne MJ (2004) Competitive interactions between two successful molluscan invaders of freshwaters: an experimental study. *Aquatic Ecology* 38: 83–91. <https://doi.org/10.1023/B:AECO.0000021018.20945.9d>
- Dalesman S, Lukowiak K (2010) Effect of acute exposure to low environmental calcium on respiration and locomotion in *Lymnaea stagnalis*. *Journal of Experimental Biology* 213: 1471–1476. <https://doi.org/10.1242/jeb.040493>
- Davis MA (2009) *Invasion Biology*, Oxford University Press, Oxford, 244 pp.
- Dillon Jr RT (2000) *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge, 509 pp. <https://doi.org/10.1017/CBO9780511542008>
- Dodds WK, Whiles MR (2010) *Freshwater Ecology: Concepts and environmental applications of limnology*, 2nd edn. Academic Press, Burlington, 829 pp. <https://doi.org/10.1016/B978-0-12-374724-2.00024-6>
- Dybdahl MF, Kane SL (2005) Adaptation vs. phenotypic plasticity in the success of a clonal invader. *Ecology* 86: 1592–1601. <https://doi.org/10.1890/04-0898>
- Dybdahl MF, Drown DM (2011) The absence of genotypic diversity in a successful parthenogenetic invader. *Biological Invasions* 13: 1663–1672. <https://doi.org/10.1007/s10530-010-9923-4>
- El-Emam MA, Madsen H (1982) The effect of temperature, darkness, starvation and various food types on growth, survival, and reproduction of *Helisoma duryi*, *Biomphalaria alexandrina* and *Bulinus truncates* (Gastropoda: Planorbidae). *Hydrobiologia* 88: 265–275. <https://doi.org/10.1007/BF00008506>
- Geist JA, Mancuso JL, Morin MM, Bommarito KP, Bovee EN, Wendell D, Burroughs B, Lutten-ton MR, Strayer DL, Tiegs SD (2022) The New Zealand mudsnail (*Potamopyrgus antipodarum*): autecology and management of a global invader. *Biological Invasions* 24: 905–938. <https://doi.org/10.1007/s10530-021-02681-7>
- Gerard C, Blanc A, Costil K (2003) *Potamopyrgus antipodarum* (Mollusca: Hydrobiidae) in continental gastropod communities: impact of salinity and trematode parasitism. *Hydrobiologia* 493: 167–172. <https://doi.org/10.1023/A:1025443910836>
- Gerard C, Herve M, Hechinger RF (2018) Long-term population fluctuations of the exotic New Zealand mudsnail *Potamopyrgus antipodarum* and its introduced aporocotylid trematode in north-western France. *Hydrobiologia* 817: 253–266. <https://doi.org/10.1007/s10750-017-3406-x>
- Glass NH, Darby PC (2009) The effect of calcium and pH on Florida apple snail, *Pomacea paludosa* (Gastropoda: Ampullariidae), shell growth and crush weight. *Aquatic Ecology* 43: 1085–1093. <https://doi.org/10.1007/s10452-008-9226-3>
- Greenwood DJ, Hall Jr RO, Tibbets TM, Krist AC (2020) A precipitous decline in an invasive snail population cannot be explained by a native predator. *Biological Invasions* 22: 363–378. <https://doi.org/10.1007/s10530-019-02093-8>
- Halabowski D, Lewin I, Buczyński P, Krodkiwska M, Płaska W, Sowa A, Buczyńska E (2020) Impact of the Discharge of salinised coal mine waters on the structure of the macroinvertebrate communities in an urban river (Central Europe). *Water Air and Soil Pollution* 231: 1–19. <https://doi.org/10.1007/s11270-019-4373-9>
- Hall RO, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1: 407–441. [https://doi.org/10.1890/1540-9295\(2003\)001\[0407:ESDNAC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0407:ESDNAC]2.0.CO;2)
- Hall RO, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. *Ecological Applications* 16(3):1121–1131. [https://doi.org/10.1890/1051-0761\(2006\)016\[1121:EHSP0I\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1121:EHSP0I]2.0.CO;2)
- Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB (2015) Aquatic invasive species: challenges for the future. *Hydrobiologia* 750: 147–170. <https://doi.org/10.1007/s10750-014-2166-0>

- Herbst DB, Bogan MT, Lusardi RA (2008) Low specific conductivity limits growth and survival of the New Zealand mud snail from the upper Owens River, California. *Western North American Naturalist* 68: 324–333. [https://doi.org/10.3398/1527-0904\(2008\)68\[324:LSCLGA\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2008)68[324:LSCLGA]2.0.CO;2)
- Hill WR, Ryon MG, Schilling EM (1995) Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* 76: 1297–1309. <https://doi.org/10.2307/1940936>
- Holomuzki JR, Biggs BJF (1999) Distributional responses to flow disturbance by a stream-dwelling snail. *Oikos* 87: 36–47. <https://doi.org/10.2307/3546994>
- Holomuzki JR, Biggs BJF (2007) Physical microhabitat effects on 3-dimensional spatial variability of the hydrobiid snail, *Potamopyrgus antipodarum*. *New Zealand Journal of Marine and Freshwater Research* 41: 357–367. <https://doi.org/10.1080/00288330709509925>
- Jacobsen R, Forbes VE (1997) Clonal variation in life history traits and feeding rates in the gastropod, *Potamopyrgus antipodarum*: performance across a salinity gradient. *Functional Ecology* 11: 260–267. <https://doi.org/10.1046/j.1365-2435.1997.00082.x>
- Jowett IG, Richardson J, Biggs BJF, Hickey CW, Quinn JM (1991) Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability surveys, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 25: 187–199. <https://doi.org/10.1080/00288330.1991.9516470>
- Kefford BJ, Lake PS (1999) Effects of spatial and temporal changes in water velocity on the density of the freshwater snail *Potamopyrgus antipodarum* (Gray). *Molluscan Research* 20: 11–16. <https://doi.org/10.1080/13235818.1999.10673721>
- Kerans BL, Dybdahl MF, Gangloff MM, Jannot JE (2005) *Potamopyrgus antipodarum*: Distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone ecosystem. *Journal of the North American Benthological Society* 24: 123–138. [https://doi.org/10.1899/0887-3593\(2005\)024%3C0123:PADDAE%3E2.0.CO;2](https://doi.org/10.1899/0887-3593(2005)024%3C0123:PADDAE%3E2.0.CO;2)
- Kiffney PM, Richardson JS, Bull JP (2004) Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. *Journal of the North American Benthological Society* 23: 542–555. [https://doi.org/10.1899/0887-3593\(2004\)023%3C0542:ELAACM%3E2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023%3C0542:ELAACM%3E2.0.CO;2)
- Lamberti GA, Resh VH (1983) Geothermal effects on stream benthos: separate influences of thermal and chemical components on periphyton and macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1995–2009. <https://doi.org/10.1139/f83-229>
- Larson MD, Black AR (2016) Assessing interactions among native snails and the invasive New Zealand mud snail, *Potamopyrgus antipodarum*, using grazing experiments and stable isotope analysis. *Hydrobiologia* 763: 147–159. <https://doi.org/10.1007/s10750-015-2369-z>
- Larson MD, Dewey JC, Krist AC (2020) Invasive *Potamopyrgus antipodarum* (New Zealand mud snails) and native snails differ in sensitivity to specific electrical conductivity and cations. *Aquatic Ecology* 54: 103–117. <https://doi.org/10.1007/s10452-019-09729-w>
- Legendre P, Legendre L (2012) *Numerical Ecology*. 3rd edn. Elsevier Science, Amsterdam, 1006 pp.
- Levine JM, Villa M, Antonio CMD, Duke JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B* 270: 775–781. <https://doi.org/10.1098/rspb.2003.2327>
- Lesutiene J, Gorokhova E, Stankeviciene D, Bergman E, Greenberg L (2014) Light increases energy transfer efficiency in a boreal stream. *PLoS ONE* 9(11): e113675. <https://doi.org/10.1371/journal.pone.0113675>
- Lewin I, Smolinski A (2006) Rare and vulnerable species in the mollusc communities in the mining subsidence reservoirs of an industrial area (the Katowicka Upland, Upper Silesia, Southern Poland). *Limnologia* 36: 181–191. <https://doi.org/10.1016/j.limno.2006.04.002>
- Levri EP, Macelko N, Brindle B, Levri JE, Dolney T, Li X (2020) The invasive New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) in central Pennsylvania. *BioInvasions Records* 1: 109–111. <https://doi.org/10.3391/bir.2020.9.1.15>
- Lockwood JL, Hoopes MF, Marchetti P (2007) *Invasion Ecology*. Blackwell, Malden, USA, 304 pp.

- Lysne S, Koetsier P (2006) Growth rate and thermal tolerance of two endangered Snake River snails. *Western North American Naturalist* 66: 230–238. [https://doi.org/10.3398/1527-0904\(2006\)66\[230:GRATTO\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2006)66[230:GRATTO]2.0.CO;2)
- Lysne S, Koetsier P (2008) Comparison of desert valvata snail growth at three densities of the invasive New Zealand mudsnail. *Western North American Naturalist* 68: 103–110. [https://doi.org/10.3398/1527-0904\(2008\)68\[103:CODVSG\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2008)68[103:CODVSG]2.0.CO;2)
- Madsen H (1987) Effect of calcium concentration on growth and egg laying of *Helisoma duryi*, *Biomphalaria alexandrina*, *B. camerunensis* and *Bulinus truncatus* (Gastropoda: Planorbidae). *Journal of Applied Ecology* 24: 823–836. <https://doi.org/10.2307/2403983>
- Mckenzie VJ, Hall WE, Guralnick RP (2013) New Zealand mudsnails (*Potamopyrgus antipodarum*) in Boulder Creek, Colorado: environmental factors associated with fecundity of a parthenogenic invader. *Canadian Journal of Zoology* 91: 30–36. <https://doi.org/10.1139/cjz-2012-0183>
- Moffitt CM, James CA (2012) Response of New Zealand mudsnails *Potamopyrgus antipodarum* to freezing and near-freezing fluctuating water temperatures. *Freshwater Science* 31: 1035–1041. <https://doi.org/10.1899/11-160.1>
- Moore JW, Herbst DB, Heady WN, Carlson SM (2012) Stream community and ecosystem responses to the boom and bust of an invading snail. *Biological Invasions* 14: 2435–2446. <https://doi.org/10.1007/s10530-012-0240-y>
- Muff S, Nilsen EB, O'Hara RB, Nater CR (2021) Rewriting results sections in the language of evidence. *TREE* 37: 203–210. <https://doi.org/10.1016/j.tree.2021.10.009>
- Murria C, Bonada N, Prat N (2008) Effects of the invasive species *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) on community structure in a small Mediterranean stream. *Archiv fur Hydrobiologie* 171: 131–143. <https://doi.org/10.1127/1863-9135/2008/0171-0131>
- Naddafi R, Blenckner T, Eklov P, Pettersson K (2011) Physical and chemical properties determine zebra mussel invasion success in lakes. *Hydrobiologia* 669: 227–236. <https://doi.org/10.1007/s10750-011-0689-1>
- Newbury RW, Bates DJ (2017) Dynamics of flowing water. In: Hauer FR, Lamberti GA (Eds) *Methods in Stream Ecology*, 3rd edn. Academic Press, San Diego, 71–88. <https://doi.org/10.1016/B978-0-12-416558-8.00004-4>
- Parashar BD, Rao KM (1988) Effect of temperature on growth, reproduction, and survival of the freshwater planorbid snail, *Gyraulus convexiusculus*, vector of echinostomiasis. *Hydrobiologia* 164: 185–191. <https://doi.org/10.1007/BF00008458>
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19. <https://doi.org/10.1023/A:1010034312781>
- Quinn JM, Cooper AB, Stroud MJ, Burrell GP (1997) Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. *New Zealand Journal of Marine and Freshwater Research* 31: 665–683. <https://doi.org/10.1080/00288330.1997.9516797>
- Ricciardi A (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussels. *Freshwater Biology* 48: 972–981. <https://doi.org/10.1046/j.1365-2427.2003.01071.x>
- Riley LA, Dybdahl MF, Hall Jr RO (2008) Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. *Journal of the North American Benthological Society* 27: 509–552. <https://doi.org/10.1899/07-119.1>
- Sepulveda AJ, Marczak LB (2012) Active dispersal of an aquatic invader determined by resource and flow conditions. *Biological Invasions* 14: 1201–1209. <https://doi.org/10.1007/s10530-011-0149-x>
- Schossow M, Arndt H, Becker G (2016) Response of gastropod grazers to food conditions, current velocity, and substratum roughness. *Limnologia* 58: 49–58. <https://doi.org/10.1016/j.limnologia.2016.02.003>
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *TREE* 17: 170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)

- Shimada K, Urabe M (2003) Comparative ecology of the alien freshwater snail *Potamopyrgus antipodarum* and the indigenous snail *Semisulcospira* spp. *Venus* 62: 39–53.
- Sowa A, Krodkiewska M, Halabowski D, Lewin I (2019) Response of the mollusc communities to environmental factors along an anthropogenic salinity gradient. *Science of Nature* 106: 1–17. <https://doi.org/10.1007/s00114-019-1655-4>
- Spyra A (2010) Environmental factors influencing the occurrence of freshwater snails in woodland water bodies. *Biologia* 65: 697–703. <https://doi.org/10.2478/s11756-010-0063-1>
- Spyra A, Strzelec M (2014) Identifying factors linked to the occurrence of alien gastropods in isolated woodland water bodies. *Naturwissenschaften* 101: 229–239. <https://doi.org/10.1007/s00114-014-1153-7>
- Spyra A, Kubicka J, Strzelec M (2015) The Influence of the Disturbed Continuity of the River and the Invasive Species—*Potamopyrgus antipodarum* (Gray, 1843), *Gammarus tigrinus* (Sexton, 1939) on Benthos Fauna: A Case Study on Urban Area in the River Ruda (Poland). *Environmental Management* 56: 233–244. <https://doi.org/10.1007/s00267-015-0483-3>
- Stewart TW, Garcia JE (2002) Environmental factors causing local variation density and biomass of the snail *Leptoxis carinata*, in Fishpond Creek, Virginia. *American Midland Naturalist* 148: 172–180. [https://doi.org/10.1674/0003-0031\(2002\)148\[0172:EFCLVD\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)148[0172:EFCLVD]2.0.CO;2)
- Strayer DL, Solomon CT, Stuart E, Findlay G, Rosi EJ (2019) Long-term research reveals multiple relationships between the abundance and impacts of non-native species. *Limnology and Oceanography* 64: S105–S117. <https://doi.org/10.1002/lno.11029>
- Stovall JP, Keeton WS, Kraft CE (2009) Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams. *Canadian Journal of Forest Research* 39: 2343–2354. <https://doi.org/10.1139/X09-137>
- Szocs E, Coring E, Bathe J, Schafer RB (2015) Effects of anthropogenic salinization on biological traits and community composition of stream macroinvertebrates. *Science of the Total Environment* 468–469: 943–949. <https://doi.org/10.1016/j.scitotenv.2013.08.058>
- Tchakonte S, Ajeegah GA, Diomande D, Camara AI, Ngassam P (2014) Diversity, dynamic and ecology of freshwater snails related to environmental factors in urban and suburban streams in Douala-Cameroon (Central Africa). *Aquatic Ecology* 48: 379–395. <https://doi.org/10.1007/s10452-014-9491-2>
- Thomas JD, Loughn A (1974) The effects of external calcium concentration on the rate of uptake of this ion by *Biomphalaria glabrata* (Say). *Journal of Animal Ecology* 43: 861–871. <https://doi.org/10.2307/3540>
- Thon HN (2010) Invasive and native species interactions: growth of a native snail is nearly halted by high levels of biomass produced by the invasive New Zealand mudsnail. M.S. Thesis. University of Wyoming, Laramie, USA, 39 pp.
- Van der Schalie H, Berry EG (1973) Effects of temperature on growth and reproduction of aquatic snails. Environmental Protection Agency, Technical report EPA-R3-73-021, 92 pp.
- Vazquez R, Ward DM, Sepulveda A (2016) Does water chemistry limit the distribution of New Zealand mud snails in Redwood National Park? *Biological Invasions* 18: 1523–1531. <https://doi.org/10.1007/s10530-016-1098-1>
- Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic* 65: 1512–1522. <https://doi.org/10.1139/F08-099>
- Verhaegen G, von Jungmeister K, Haase M (2021) Life history variation in space and time: environmental and seasonal responses of a parthenogenetic invasive freshwater snail in northern Germany. *Hydrobiologia* 848: 2153–2168. <https://doi.org/10.1007/s10750-020-04333-8>
- Warren DR, Keeton WS, Kiffney PM, Kaylor MJ, Bechtold HA, Magee J (2016) Changing forests – changing streams: riparian forest stand development and ecosystem function in temperate headwaters. *Ecosphere* 7: 1–19. <https://doi.org/10.1002/ecs2.1435>
- Willmer P, Stone G, Johnston I (2004) *Environmental Physiology of Animals* (2nd edn.). Blackwell Publishing, Malden MA, USA, 768 pp.

- Wootton JT (2012) River food web response to large-scale riparian zone manipulations. *PLoS ONE* 7(12): e51839. <https://doi.org/10.1371/journal.pone.0051839>
- Zalizniak L, Kefford BF, Nuggeoda D (2009) Effects of different ionic compositions on survival and growth of *Physa acuta*. *Aquatic Ecology* 43: 145–156. <https://doi.org/10.1007/s10452-007-9144-9>
- Zeileis A, Kleiber C, Jackman S (2008) Regression Models for Count Data in R. *Journal of Statistical Software* 27: 1–25. <https://doi.org/10.18637/jss.v027.i08>
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, 574 pp. <https://doi.org/10.1007/978-0-387-87458-6>

Supplementary material 1

Locations and sampling methods for the five rivers that we sampled above and below geothermal input

Authors: Michele D. Larson, Daniel Greenwood, Kara Flanigan, Amy C. Krist

Data type: table (docx. file)

Explanation note: We attempted to sample all sites with transverse transects (across the stream), but we had to sample longitudinal shoreline transects in a few sites because of extremely high flows or bedrock substrates. In 2014, we sampled along a single transect ($n = 3\text{--}5$ samples) and in 2015, along one or two adjacent transects because we collected twice as many samples ($n = 10$ samples).

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2023.18.1.103389.suppl1>