

Spatial distribution of two invasive freshwater snails and environmental correlates of the mollusc community abundance, a case study in Chile

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Abstract

Spatial distribution of two invasive freshwater snails and environmental correlates of the mollusc community abundance, a case study in Chile. Invasive species can produce negative effects on native species. We studied the densities of *Physa acuta* and *Potamopyrgus antipodarum*, two invasive freshwater snails in Chile, and analyzed the relationship between environmental parameters and the relative abundances of the mollusc community in several ecosystems. Densities of both species were studied in three habitat types (stones, smooth sediment, and vegetation) in the Consuelo Stream, Coquimbo Region. Densities of *Potamopyrgus antipodarum* were significantly higher on stones, while *Physa acuta* showed no significant differences between habitats. A canonical correspondence analysis (CCA) demonstrated that both *Physa acuta* and *Potamopyrgus antipodarum* were related to oxidation-reduction potential but not to salinity. The results also showed that native mollusc fauna is sparsely represented in the study area, possibly due to the presence of these invaders, although drought, water pollution, and other unstudied anthropogenic factors may also be involved.

Key words: Ecological interactions, Interspecific competition, Invasive species, Niche Segregation, *Physa acuta*, *Potamopyrgus antipodarum*

Resumen

Distribución espacial de dos caracoles de agua dulce invasores y parámetros ambientales de la abundancia de la comunidad de moluscos, un estudio de caso en Chile. Las especies invasoras pueden generar efectos adversos en las especies nativas. Estudiamos la densidad de *Physa acuta* y de *Potamopyrgus antipodarum*, dos caracoles de agua dulce invasores de Chile y analizamos la relación entre los parámetros ambientales y la abundancia relativa de la comunidad de moluscos en diferentes ecosistemas. La densidad de ambas especies fue estudiada en tres tipos de hábitats (piedras, sedimento blando y vegetación) en el estero Consuelo, en la región de Coquimbo. La densidad de *Potamopyrgus antipodarum* fue significativamente mayor sobre piedras, mientras que la de *Physa acuta* no mostró diferencias significativas entre hábitats. Mediante un análisis de correspondencia canónica (CCA) se demostró que tanto la densidad de *Physa acuta* como la de *Potamopyrgus antipodarum* estaban relacionadas con el potencial de oxidación-reducción, pero no con la salinidad. Los resultados también revelaron que la fauna nativa de moluscos está escasamente representada en la zona de estudio, posiblemente debido a la presencia de estos invasores, aunque la sequía, la contaminación del agua y otros factores antropogénicos aún no estudiados también pueden influir.

Palabras clave: Interacciones ecológicas, Competencia interespecífica, Especies invasoras, Segregación de nichos, *Physa acuta*, *Potamopyrgus antipodarum*

Introduction

Invasive species can lead to a range of alterations in invaded ecosystems, such as economic loss, health issues, and environmental disturbances (Wilcove et al 1998, Parker et al 1999, Mack et al 2000). The introduction of an invasive species to new habitats triggers ecological interactions that typically result in adverse effects on native species (Huxel 1999, Clavero and García-Berthou 2005, Sodhi et al 2009). Ecological studies involving competition among sympatric invasive species demonstrate that these interactions are often intense and enduring (Margarido et al 2007, Winkler et al 2007), particularly between ecologically similar species (Decottignies et al 2007, Gérard et al 2014, Sannolo et al 2018). To persist over time, competition theory predicts that niche partitioning would facilitate species coexistence (Levin 1970). Therefore, when two or more of these species coexist in the same area, mechanisms that promote their co-occurrence become relevant, as resource partitioning reduces niche overlap (Vieira and Port 2007, Sannolo et al 2018).

The New Zealand mudsnail (NZMS) *Potamopyrgus antipodarum* (Gray, 1843) (Tateidae Thiele, 1925), a gilled species, and the sewage snail (SWGS) *Physa acuta* Draparnaud, 1805 (Physidae Fitzinger, 1833), an air-breathing species, are two unrelated species. Nevertheless, these two snails share similar ecological requirements as they coexist in several ecosystems worldwide (Cope 1999, Gérard et al 2003, Cope and Winterbourn 2004, Collado 2014, 2017, Lewin and Smolinski 2006, Shield et al 2014, Spyra and Strzelec 2014, Odabaşı et al 2019), adapting to a wide range of habitats and environmental conditions (Dorgelo 1987, Alonso and Castro-Díez 2008, 2012). However, despite being generalists (Dillon et al 2002), they also exhibit certain differences regarding physicochemical water variables. For example, the NZMS tolerates waters with a substantial degree of salinity and a wide range of temperature and pH values (e.g., Winterbourn 1969, Hylleberg and Siegismund 1987, Hoy et al 2012, Cieplak and Spyra 2020, Larson et al 2023). Similarly, although the SWGS exhibits a wide range of temperature and ionic composition tolerance, it can withstand higher temperatures and lower salinity levels than the NZMS (Zalizniak et al 2009, Cieplak and Spyra 2020, Karmakar et al 2021).

The NZMS, native to New Zealand (Winterbourn 1970, 1972), has invaded a variety of aquatic ecosystems worldwide (Ponder 1988, Bowler 1991, Davidson et al 2008, Radea et al 2008, Butkus et al 2012, Levri et al 2012, Hamada et al 2013, Collado 2014, Collado et al 2019a, 2019b), in some cases reaching one of the highest recorded values of secondary productivity for a freshwater invertebrate (Hall et al 2006), with densities as high as 500,000 or 800,000 individuals/m² (Richard 2004, Dorgelo 1987), and potentially reaching six generations/year (Richards 2002). Something similar occurs with the SWGS, a species native to North America, which is now cosmopolitan (Dillon 2000, Dillon et al 2002, Cope and Winterbourn 2004, de Kock and Wolmarans 2007, Bousset et al 2014, Collado 2017, Vinarski 2017, Ebbs et al 2018, Collado et al

2020). This species has been called 'the sewage snail' because it can live in highly polluted water (Appleton 2003). An extreme example can be found in the Sakarya River, Turkey, where estimated densities have reached up to 18,703 individuals/m² (Çabuk et al 2004). The species can potentially reach three generations/year (McMahon 1975). The high reproductive potential and rapid population growth observed in these species (Dorgelo 1987, Bowler 1991, Appleton 2003, Wethington and Dillon 1993, Richards 2002, 2004, Núñez 2011, Maqboul et al 2014, Vinarski 2017, Spyra et al 2019) suggest the feasibility of competitive interactions in coexistence. The NZMS is an ovoviviparous and parthenogenetic species (Wallace 1992), with females potentially releasing up to 120 neonate juveniles, producing up to 230 offspring per year (Richards 2002, Cheng and LeClair 2011). Similarly, specimens of SWGS may lay more than 100 eggs per week, within gelatinous masses (Tsitrone et al 2003). Laboratory experiments have shown that interspecific competition between these snails is asymmetric, and that the NZMS primarily acts as the facilitating species (Cope and Winterbourn 2004). However, it remains unknown whether niche partitioning between these species also plays a role in reducing competition in nature. Larson et al (2023) reported negative effects of the NZMS on abundance of *Physa* sp. in Yellowstone (USA). Field observations conducted in Consuelo Stream, northern Chile, indicate that the NZMS and the SWGS coexist in various habitats where they feed on similar resources, suggesting a degree of ecological interaction. In fact, both species feed on similar resources. The New Zealand Mudsnail consumes macrophytes, detritus, and periphytic and epiphytic vegetation, whereas the SWGS feeds primarily on macrophytes and epiphytic vegetation (Haynes and Taylor 1984, Zaranko et al 1997, James et al 2000, Broekhuizen et al 2001, Radea et al 2008, Semenchenko et al 2008). Niche separation, a commonly observed phenomenon among ecologically similar sympatric species (Gregory and McIntosh 1980) is not entirely complete along the food dimension. Studies conducted on the NZMS and the crustacean *Gnorimosphaeroma insulare* (Van Name 1940) did not provide evidence of competition despite their common habitat use, possibly due to niche partitioning regarding food resources or habitats (Brenneis et al 2010). Similarly, Aberle et al (2005) found potential divergence in the food dimension of the NZMS and the crustacean *Asellus aquaticus* (Linnaeus, 1758) in syntopy.

Understanding the mechanisms that lead to the successful establishment of invasive species could provide predictive power against future invasions and help gather basic information for management of currently invaded ecosystems (Byers 2000). Several authors have emphasized the importance of a mechanistic interpretation of biological invasions by conducting experiments that reveal competitive interactions between ecologically similar species (Brenchley and Carlton 1983, Hylleberg and Siegismund 1987, Schreiber et al 2002, Cope and Winterbourn 2004, Richards 2004). Studies of niche overlap have also been associated with interspecific competition in a variety of taxa, including snails (Fenchel 1975, Brown

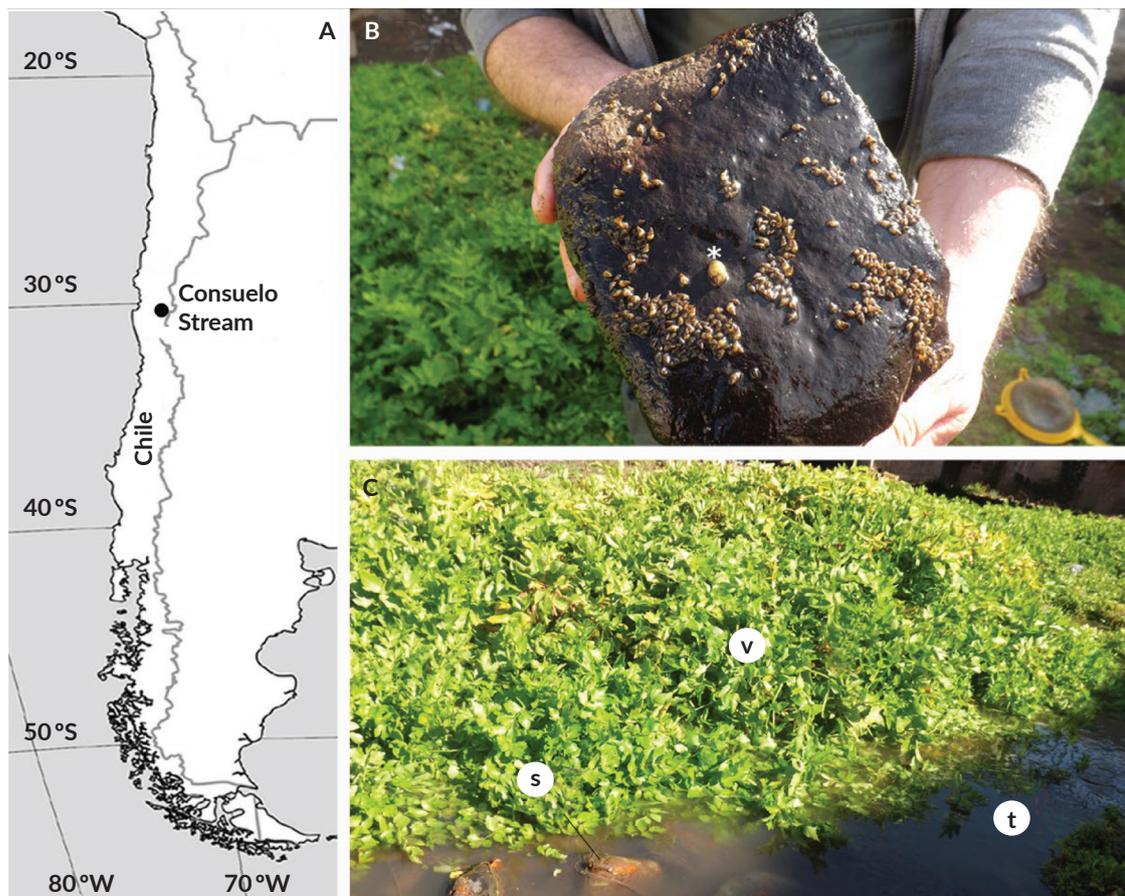


Fig. 1. Study site: A, the location of the Consuelo Stream in Chile; B, many individuals of *Potamopyrgus antipodarum* (NZMS), compared to a single individual of *Physa acuta* (SWGS) (asterisk), were photographed *in situ* under a stone; C, the three habitat types (s, stones; t, smooth sediment; v, vegetation).

Fig. 1. Sitio de estudio: A, ubicación del estero Consuelo en Chile; B, muchos individuos de *Potamopyrgus antipodarum* (NZMS), pero uno solo de *Physa acuta* (SWGS) (asterisco) fueron fotografiados *in situ* debajo de una piedra; C, los tres tipos de microhábitats (s, piedras; t, sedimento blando; v, vegetación).

1982, Byers 2000, Richards et al 2001, Cross and Benke 2002, Richards 2004, Krist 2006, Riley et al 2008, Thon and Krist 2011). Given that the NZMS and the SWGS have coexisted in Chile since at least 2011 (Collado et al 2011, Collado 2014, 2017), it is reasonable to assume that both species share resources such as food and space through niche partitioning.

Relative abundances have been used to investigate niche overlap in the habitat dimension in various freshwater snails (Brown 1982, Byers 2000), including the NZMS and SWGS (Richards et al 2001; Richards 2004, Núñez 2011). The objective of this study was to assess whether niche partitioning exists between NZMS and SWGS in an invaded ecosystem, using density as an indicator. We predicted that both snails would have reciprocal negative effects on each other's abundance. In addition, we analyzed the physicochemical water variables related to the occurrence and relative abundance of these invasive snails and the associated mollusc community.

Material and methods

The study was carried out in the north central zone of Chile, a geographical region comprising several freshwater ecosystems where both NZMS and SWGS sustain viable populations (Collado 2014, 2017). Spatial distribution of the two species was studied in Consuelo Stream (fig. 1A, 1B), a tributary of the Chalinga River, Choapa River basin, northern Chile, which runs from east to west in a semi-arid region. The water in Consuelo Stream is limited and intermittent since it disappears occasionally from the surface, but it sometimes increases slightly in the winter, during the short rainy season. Snails were sampled from three habitat types (stones, smooth sediment and vegetation) (fig. 1C) at six sites scattered irregularly along a transect of approximately 50 m in the stream, the only available water outcrop at the time of sampling. The distances between sampling sites were not uniform, as they depended on the presence of the three

Table 1. Presence-absence data of the freshwater molluscs in the north central zone of Chile: Poan, *Potamopyrgus antipodarum*; Phac, *Physa acuta*; Pi, *Pisidium*; Pot, *Potamolithus*; Pom, *Pomacea canaliculata*; Chil, *Chilina*; Lym, *Lymnaea*; Anc, *Ancylus*; Hel, *Heleobia*. (* native; ** non-native).

Tabla 1. Datos de presencia-ausencia de moluscos de agua dulce en la zona centroseptentrional de Chile: * nativo; ** no nativo. (Para las abreviaturas de las especies, véase arriba.)

Locality	Basin	Genera/species								
		Poan**	Phac**	Pi*	Pot*	Pom**	Chil*	Lym*	Anc*	Hel*
Huentelauquén (North)	Coastal	1	1	0	0	0	0	1	0	0
Huentelauquén (South)	Choapa River	0	0	0	0	0	0	0	0	1
Illapel River	Choapa River	1	1	0	0	0	0	1	0	0
Zapallar	Choapa River	1	1	0	0	0	0	0	0	0
Canal Zapallar	Choapa River	1	1	0	0	0	0	0	1	0
Cunlahua	Choapa River	1	1	0	0	0	0	0	0	0
La Brunina	Choapa River	1	1	1	0	0	0	0	0	0
Limahuida Stream	Choapa River	1	1	1	0	0	0	0	0	0
Camisas River	Choapa River	1	1	0	0	0	0	0	0	0
Consuelo Stream	Choapa River	1	1	0	0	0	0	1	0	0
Choapa River	Choapa River	1	1	0	0	0	0	1	0	0
Conchalí Lagoon	Conchalí	0	0	1	0	1	0	0	0	1
Sobrante River	Petorca	0	1	1	1	0	0	0	0	0
San Rafael Stream	Aconcagua	1	1	1	1	0	1	0	0	0
Fundo Los Tilos V2	Aconcagua	0	1	0	1	0	0	0	0	0
Romeral Stream	Aconcagua	1	1	0	0	0	0	0	0	0
Quebrada Escobares	Aconcagua	0	0	1	1	0	0	1	1	0
Parque O'Higgins	Maipo	1	1	0	0	0	0	0	0	0

habitat types in the small watercourse. Three quadrants (9 x 12 cm) were established at each site. All snails with a shell length (SL) of 1 mm or more were measured to the nearest of 0.05 mm using a Motic SMZ-168 stereomicroscope. Snail densities were standardized to number of individuals/m². Prior to statistical analysis, data were examined for the assumptions of normality and homogeneity of variance using Shapiro-Wilk and Levene tests, respectively, with $\alpha = 0.05$ (Rohlf and Sokal 1995). When these assumptions were made, we analysed significant differences in density between species and habitats using the parametric t-Student test. Alternatively, we used the Mann-Whitney (M-W) U test. Significant differences between treatments within the species were estimated using Kruskal-Wallis (K-W) ANOVA tests with a posteriori Dunn test. All statistical analyses were performed in PAST v. 4.03 (Hammer et al 2001). The relationship between species densities was examined using the Spearman correlation (r) (Rohlf and Sokal 1995). To assess whether habitat type influences species densities, we performed a χ^2 test. In this analysis, the null hypothesis of random species distribution was tested against the alternative hypothesis of distribution due to habitat preference (Chabwela et al 2017). Considering that Chi square test cannot be implemented for very high values, we simplified the densities by a factor of 100.

Canonical Correspondence Analysis (CCA) was performed using PAST to investigate the relationship between the relative abundance of molluscan com-

munity, water variables, and the various localities. Six electro-physical variables, including temperature (°C), pH, conductivity (mv), dissolved oxygen (DO) (ppm), salinity (psu) and oxidation reduction potential (ORP) (mV), were estimated *in situ* using a HI 9828 Hanna Instrument in 18 freshwater ecosystems (table 1). Eleven chemical water variables (total-Nitrogen (N) ($\mu\text{g/L}$), total-phosphate (P) ($\mu\text{g/L}$), sulfate (SO_4^{2-}) (mg/L), calcium (Ca^{+2}) (mg/L), magnesium (Mg^{+2}) (mg/L), sodium (Na) (mg/L), potassium (K) (mg/L), total alkalinity (mg/L), bicarbonate (HCO^{-3}) and chloride (Cl^{-}) (mg/L), were also obtained from 13 sites. A Shimadzu spectrophotometer was used to analyze water samples based on standard methods (APHA 1992). The significance of the contribution of each variable was assessed using 99 permutations in the Monte Carlo test conducted in PAST. Because native molluscs were frequently under-represented in the sample quadrats due to their low abundance -which could be attributed to the presence of invasive species- we sampled molluscs using a sieve for 15 minutes at each location for the CCA, or until their occurrences were confirmed. We then categorized species abundance into four levels: low, medium, high, and very high, each assigned a numerical value ranging from 1 to 4. Moreover, for species exhibiting high or very high abundances, these values were augmented by an order of magnitude. To identify ecosystems with similar species using a presence-absence matrix based on the Jaccard similarity index, we performed a cluster analysis in PAST.

Table 2. Mean densities (individuals/m²) and sizes (mm) of *Potamopyrgus antipodarum* (NZMS) and *Physa acuta* (SWGS) in the Consuelo Stream: max, density and maximum size of the snails; SD, standard deviation, SL, Shell length. (K-W test for NZMS densities: $H(2, N = 18) = 11.95, p = 0.0025$, significant; K-W test for SWGS densities: $H(2, N = 18) = 0.7476, p = 0.6881$, not significant; M-W U test for sizes between the species: $p = 0.4559$, not significant).

Tabla 2. Densidad media (individuos/m²) y tamaño (mm) de *Potamopyrgus antipodarum* (NZMS) y *Physa acuta* (SWGS) en el arroyo Consuelo: max, densidad y tamaño máximo de los caracoles; SD, desviación estándar; SL, longitud de la concha (prueba de K-W para densidades del NZMS: $H[2, N = 18] = 11,95, p = 0,0025$, significativo; prueba de K-W para el SWGS: $H[2, N = 18] = 0,7476, p = 0,6881$, no significativo; prueba U de M-W para tamaños entre especies: $p = 0,4559$, no significativo).

Habitat	<i>P. antipodarum</i>		<i>P. acuta</i>	
	Density ± SD	Size (SL)	Density ± SD	Size (SL)
Stone	24,535 ± 15,678 (max: 45,576)	4.2 ± 0.2 (max: 5.8)	265 ± 129 (max: 397)	5.4 ± 2.6 (max: 11.3)
Smooth Sediment	1,231 ± 1,491 (max: 3,732)	4.0 ± 0.4 (max: 5.3)	979 ± 1,053 (max: 2,461)	4.0 ± 1.4 (max: 12.3)
Vegetation	2,184 ± 2,062 (max: 6,034)	3.9 ± 0.3 (max: 5.9)	476 ± 341 (max: 873)	3.9 ± 1.0 (max: 12.9)

Results

The NZMS was the most abundant species observed across all three habitat types surveyed in the Consuelo Stream. The highest density of this species was observed on the stones, which, in turn, had the lowest abundance of SWGS (table 2). Conversely, the highest density of SWGS was found in the smooth sediment, which had the lowest abundance of the NZMS. Considering the stream as a whole, the NZMS exhibited a higher density than SWGS (M-W U-test: $p = 0.0015$) (table 2, fig. 2A). The NZMS mean densities were significantly greater than SWGS in the stone (M-W U-test: $p = 0.0049$) and vegetation microhabitats (t-test: $p = 0.0495$); differences were not significant in the smooth sediment (t-test: $p = 0.7428$). The NZMS mean densities were significantly greater in the stone than in the smooth sediment ($p = 0.0009$) and vegetation ($p = 0.0110$); densities in these last two microhabitats were not statistically significant ($p = 0.4488$) (fig. 2B). Mean densities of SWGS were similar among habitats (table 2, fig. 2C). On the other hand, mean size did not differ significantly between species (M-W U-test: $p = 0.3084$).

Abundance of the NZMS was not related to the abundance of SWGS in the Consuelo Stream (Spearmanr = -0.38; $N = 18, p = 0.1127$) (fig. 2D).

The NZMS and SWGS exhibited a high level of selectivity towards habitat types, particularly the NZMS. The SWGS showed a preference for smooth sediment (59.9%), followed by vegetation (27.7%) and stones (15.4%). Conversely, the NZMS predominantly inhabited stones (87.8%), with notably fewer individuals found in smooth sediment (4.4%) and vegetation (7.8%). The occurrence proportions for SWGS in stones, smooth sediment, and vegetation were 1.1%, 44.3%, and 17.9% respectively, whereas for NZMS, they were 98.9%, 55.7%, and 82.1% in the same respective habitats. The observed $\chi^2 = 77.1, p = 1.8e-17$

indicates that species distributions in the Consuelo Stream were not random [expected $\chi^2 = 0.05$ (α), 2 (df) = 5.991. Similarly, for species habitat preference, the observed $\chi^2 = 110.6, p = 9.7e-25$ showed that selectivity was not random [expected $\chi^2 = 0.05$ (α), 2 (df) = 5.991. Furthermore, the χ^2 test applied to the proportion of occurrence of species also confirmed that habitat preference was not random [expected $\chi^2 = 0.05$ (α), 2 (df) = 5.991; observed $\chi^2 = 57.8, p = 2.97e-13$.

Of the 18 sampled sites performed in the north central zone of Chile, NZMS occurred in 13 and SWGS in 15. Besides these invasive species, we identified seven other mollusc species, one of which was invasive, *Pomacea canaliculata* (Lamarck, 1828), and six were natives: *Pisidium* sp., *Potamolithus* sp., *Lymnaea* sp., *Chilina* sp., *Heleobia* sp. and *Ancylus* sp. In the plot depicting the electro-physical CCA matrix (fig. 3), the NZMS, SWGS, and *Ancylus* sp. were dispersed in the first quadrant, *Heleobia* sp. in the second, *Pomacea canaliculata* and *Pisidium* in the third, and *Potamolithus*, *Lymnaea*, and *Chilina* in the fourth. The correlation between the first axis and species axis was 0.7855, accounting for 49.7% of the variance, and it was statistically significant ($p = 0.005$). Conversely, for the second axis, the correlation was 0.3534, accounting for 22.3% of the variance. This was not statistically significant ($p = 0.061$). The first canonical root was strongly related to salinity, displaying a significant positive correlation of 0.9663. It also exhibited moderate associations with ORP and DO, with negative correlations of -0.5043 and -0.3598, respectively. Moreover, this axis showed a moderately positive correlation with pH (0.3342). In relation to the NZMS and SWGS, we observed a negative correlation with salinity and pH, and a positive correlation with ORP.

In the chemicals CCA matrix, the correlation between the first axis and the species axis was 0.8466, accounting for 49.9% of the variance, while on the second axis

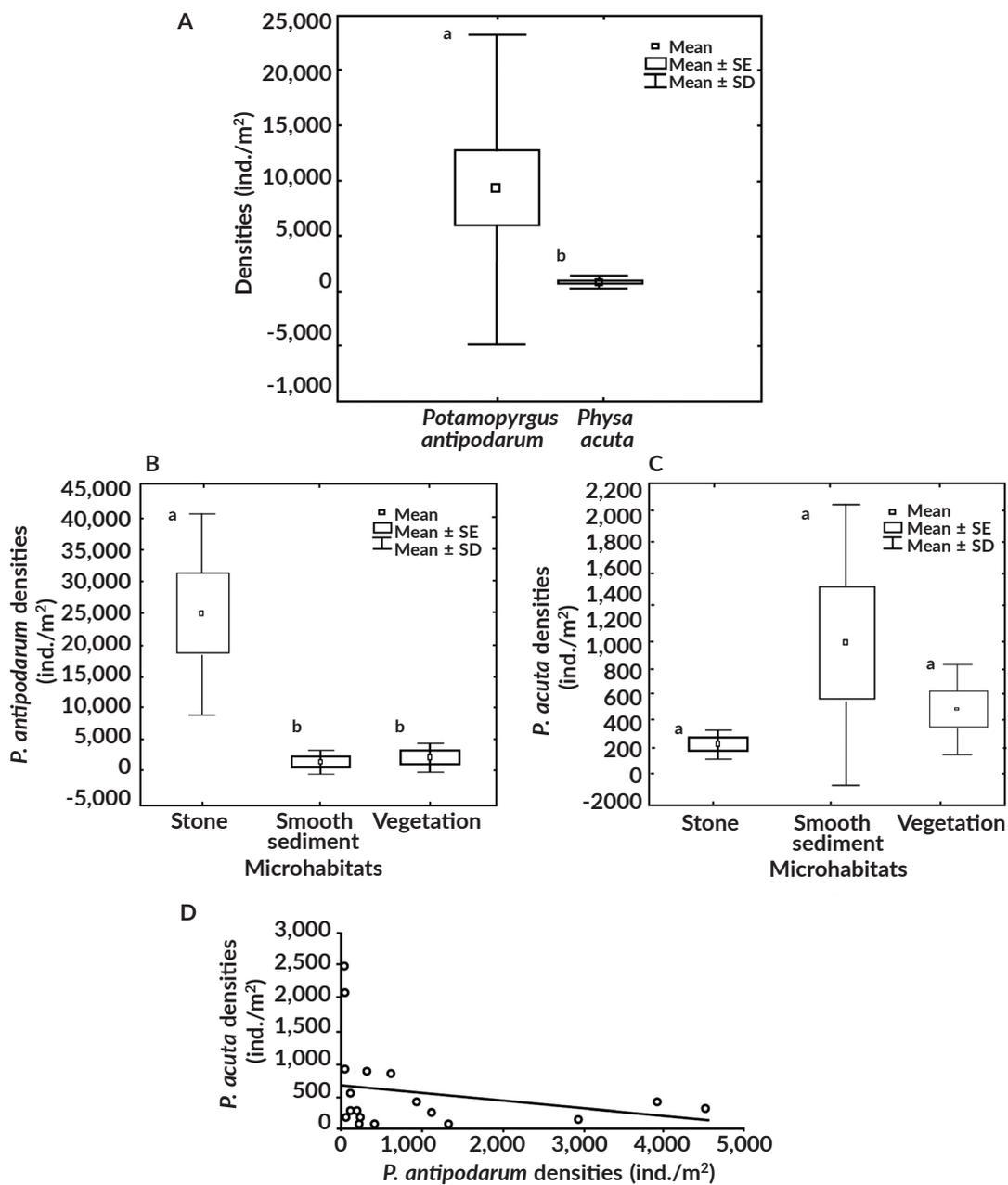


Fig. 2. Average densities of *Potamopyrgus antipodarum* (NZMS) and *Physa acuta* (SWGS) in the Consuelo Stream: A, mean density in each species; B-C, mean densities per species and microhabitat (different lowercase letters indicate significant differences); D, relation (Spearman's rank correlation) between the density of both species (not significant).

Fig. 2. Densidad media de *Potamopyrgus antipodarum* (NZMS) y *Physa acuta* (SWGS) en el estero Consuelo: A, densidad media en cada especie; B-C, densidad media por especie y microhábitat (diferentes letras minúsculas indican diferencias significativas); D, relación (correlación de rangos de Spearman) entre la densidad de ambas especies (no significativa).

it was 0.4646, accounting for 27.4% of the variance. However, neither correlation was statistically significant ($p = 0.128$ and $p = 0.370$, respectively). This dataset was therefore excluded from further consideration.

The dendrogram illustrates the similarities among localities in mollusk composition, and revealed three distinct clusters: one large cluster and two smaller clusters (fig. 4). The larger cluster encompassed nine

localities from the Choapa River basin, along with three others where NZMS and SWGS were present. A second cluster comprised two localities from the Aconcagua River basin and one from the Petorca River basin, two of them invaded by the SWGS. The third cluster comprised Huentelauquén Sur and Conchalí Lagoon, both being localities inhabited by *Heleobia* sp. Additionally, in the latter locality, *Pomacea canaliculate*, was also present.

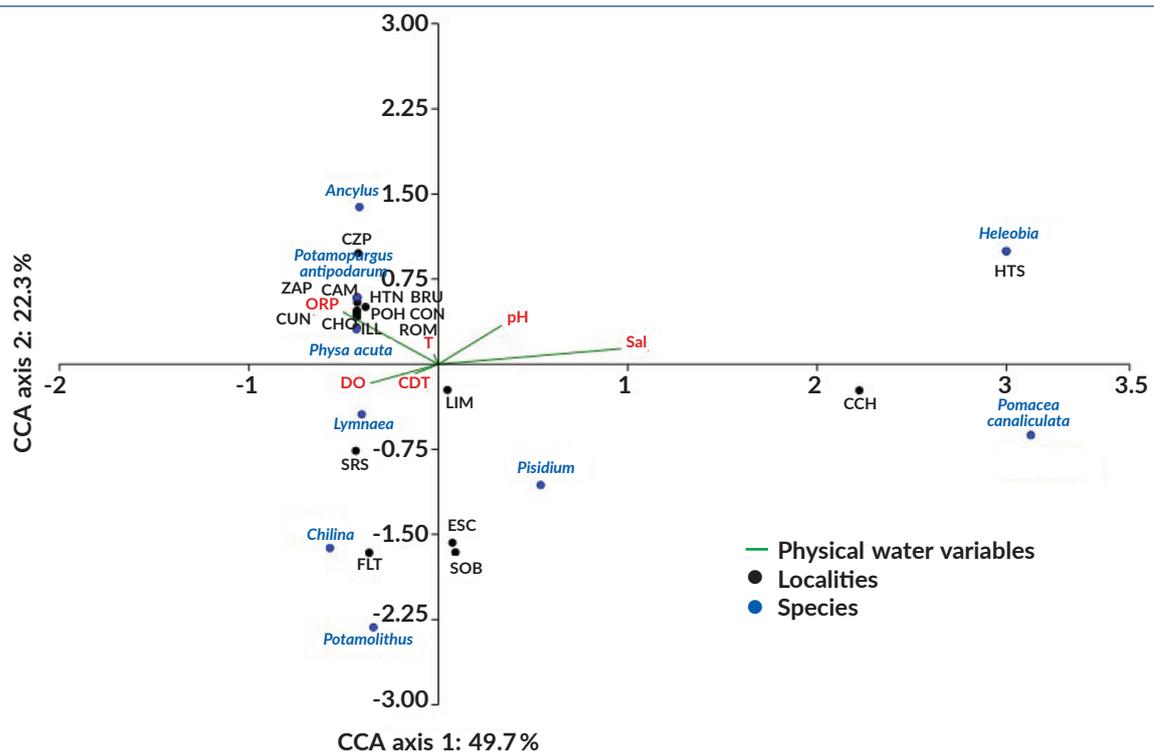


Fig. 3. Canonical Correspondence Analysis (CCA) plot depicting the relationship between the mollusc community and environmental factors in the north central zone of Chile: BRU, La Brunina; CAM, Camisas River; CCH, Conchalí Stream; CHO, Choapa River; CON; Consuelo Stream; CUN, Cunlahua; CZP, Canal Zapallar; ESC, Quebrada Escobares; FLT, Fundo Los Tilos V2; HTN, Huentelauquén North; HTS, Huentelauquén South; ILL, Illapel River; LIM, Limahuida; POH, Parque O'Higgins; ROM, Romeral Stream; SOB, Sobrante River; SRS, San Rafael Stream; ZAP, Zapallar.

Fig. 3. Gráfico de análisis de correspondencia canónica (CCA) que representa la relación entre la comunidad de moluscos y los factores ambientales en la zona centroseptentrional de Chile. (Para las abreviaturas de las localidades, véase arriba).

Discussion

The NZMS and SWGS coexist across all three habitats surveyed in the Consuelo Stream, suggesting these invasive species are generalists regarding the habitat they might choose. Further analysis revealed that the NZMS is the dominant species, with preference for stones, whereas the SWGS displayed a more uniform spatial distribution. Differences in density between the NZMS and SWGS in the studied habitats suggest species-specific habitat preferences at a fine-scale resolution by the NZMS. However, correlation analysis failed to establish a significant linear relationship between the abundance of the two species, in contrast with the findings of Larson et al (2023), who observed a moderate decrease in the abundance of the native *Physa* sp. and an increase in NZMS abundance in Yellowstone. Similar to our study, these authors did not observe a relationship between the abundances of *Physa* sp. and the native *Pyrgulopsis* sp. in the same location. Spyra and Strzelec (2014), on the other hand, reported that in invaded ecosystems in Poland, when the SWGS had a high density, the NZMS had a low density, and vice versa, depicting an alternate dominance. Overall, these findings support the notion that resource partitioning in habitat dimension plays

a role in reducing ecological interactions between species, allowing their coexistence. In this tug of war (ecological trade-off), the strength of biotic interactions would seem to be variable between species regarding habitat types. Jensen (1987) stated that under certain conditions, exploitative competition and interference competition models have identical equilibrium properties and very similar trajectories, so it would be difficult to distinguish between these two types of competition using only data of species densities. In agreement with this, the interactions between NZMS and other macroinvertebrates in Yellowstone have been determined as complex and may change from facilitation to competition as snail densities increase (Kerans et al 2005).

The presence and abundance of mollusc species in the study area appear to be influenced by environmental factors, particularly regarding the electro-physical matrix, albeit with varying degrees of impact on different taxa. Interestingly, the presence and abundance of the mollusc community were not predicted by the chemical water variables included in our study, aligning with previous research findings for specific data sets (Larson et al 2023). The first ordination axis of the electro-physical data set was statistically significant, further emphasized by a high eigenvalue of 0.7855.

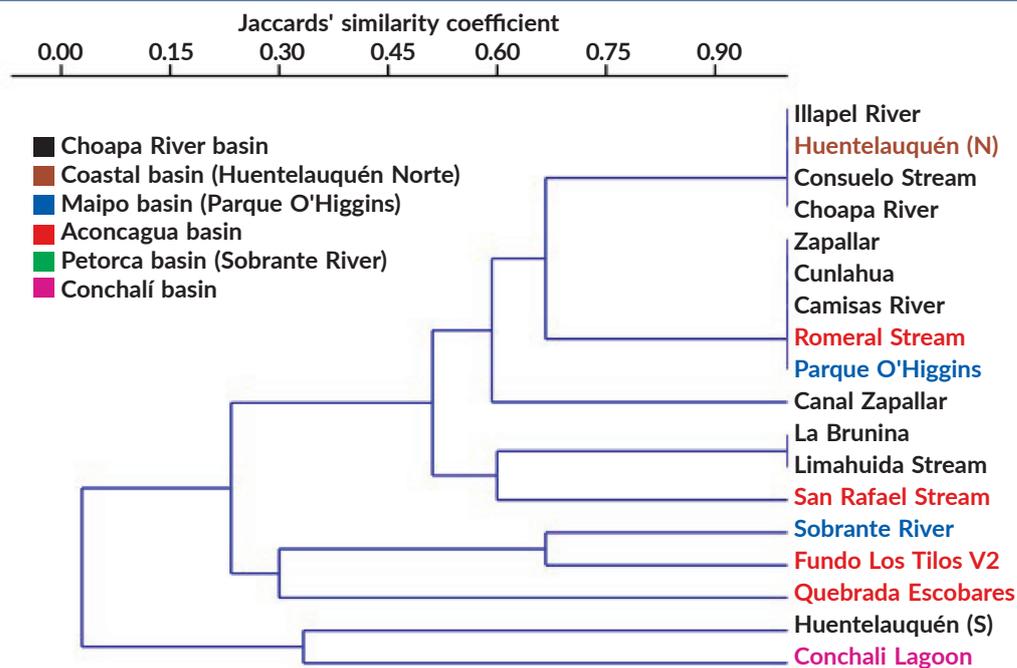


Fig. 4. Cluster dendrogram depicting similarities in mollusc taxonomic composition among localities using taxon presence/absence data.

Fig. 4. Dendrograma de conglomerados que representa las similitudes en la composición taxonómica de los moluscos entre localidades utilizando datos de presencia y ausencia de taxones.

For instance, the native *Heleobia* sp. exhibited a pronounced association with salinity, and to a lesser extent, with pH levels. Conversely, other native species like *Lymnaea* sp., *Chilina* sp., and *Potamolithus* sp. are primarily influenced by dissolved oxygen levels, displaying a negative association with salinity. The ordination of NZMS and SWGS in the second quadrant suggests they are primarily associated with ORP but negatively associated with salinity, suggesting that these variables influence the presence of both native and invasive species in the study area.

The NZMS is indeed commonly associated with freshwater habitats. Nevertheless, it has also been documented in brackish or estuarine environments, exhibiting a wide salinity tolerance both in its native range and in ecosystems where it has been introduced (Winterbourn 1970, Dybdahl and Lively 1995, Jacobsen and Forbes 1997, Gerard et al 2003, Bersine et al 2008, Hoy et al 2012, Szocs et al 2015). In Chile, this invasive species has been identified in 19 locations, all of which exemplify freshwater environments (Collado 2014, 2016, Collado et al 2019a, 2019b, Collado and Fuentealba 2020). The positive or negative association of NZMS with salinity worldwide could be attributed to the presence of various genotypes within the species, some of which may be better adapted to higher salinity environments (Jacobsen and Forbes 1997, Gerard et al 2003, Szocs et al 2015). To date, this particular genotype has not been identified in Chile.

Several studies have shown that the presence and abundance of NZMS are influenced by salinity, conductivity, temperature, pH and others chemical

variables (e.g., Hylleberg and Siegismund 1987, Kerans et al 2005, Herbst et al 2008, Hoy et al 2012, Spyra and Strzelec 2014, Spyra et al 2015, 2019, Halabowski et al 2020, Levri et al 2020, Spyra and Cieplok 2022). However, our results indicate that these variables do not play a major role in the presence of this species in the studied area. The discrepancies may be because the NZMS can tolerate a wide range of environmental conditions. For example, Murria et al (2008) discovered a negative correlation between conductivity and NZMS abundance in specific locations in Spain, while other studies found the opposite in invaded countries (Spyra et al 2015, Larson et al 2020, 2023, Spyra and Cieplok 2022). Something similar happens with pH, as the NZMS can also tolerate a wide range of values, sometimes being more abundant in sites with relatively low pH, while in other cases with basic pH (Blakely and Harding 2005, Levri et al 2020, Larson et al 2023). On the other hand, the temperature range for the NZMS spans from 0-28 °C, with lethal effects occurring at 28-29 °C (Winterbourn 1969, Hylleberg and Siegismund 1987). Nevertheless, this species has also been found inhabiting thermal springs with temperatures reaching 35.3 °C (Clements et al 2011). In addition, cool water temperatures affect the period of reproduction, fecundity, and body size (Dybdahl and Kane 2005, Krodkiwska et al 2021, Verhaegen et al 2021).

The abundance of the SWGS is known to decrease with salinity (Gerard et al 2003), although it supports medium salinities (Cieplok and Spyra 2020). This snail has been associated with high values of phosphates,

nitrites and pH and low levels of hardness, ammonia, conductivity, calcium content, and chlorides (Spyra and Strzelec 2014, Cieplik and Spyra 2020), although Spyra et al (2019) also reported an association of the species with high levels of ammonia. Similarly, Larson et al (2023) reported a slight decrease in the abundance of *Physa* sp. with increasing conductivity. On the other hand, the temperature range in this species spans from approximately 7 to 39.5°C in Texas, USA (McMahon 1975). In contrast with findings by Cieplik and Spyra (2020), we did not find the SWGS to be associated with salinity in the study area. Additionally, the species has recently been introduced to Lake Bullileo and Lake Llanquihue in southern Chile, two typical freshwater ecosystems (Collado and Aguayo, in press; Collado et al 2020). SWGS can resist relatively long periods of desiccation, being able to bury into the substrate and actively migrate horizontally over short distances, allowing survival in fluctuating environments and contributing to its invasive potential (Gulanicz et al 2018).

The introduction of the NZMS and SWGS can reduce abundance of native molluscs (Winterbourn 1980, Richards 2002, 2004, Manganelli et al 2000, Richards et al 2001, Dobson 2004, Lysne and Koetsier 2008, Riley et al 2008, Mouthon and Daufresne 2010, Nuñez 2011, Collado et al 2019a, 2019b, Karmakar et al 2021). In Banbury Springs, USA, the NZMS is considered a potential competitor for habitat with native snails *Valvata humeralis* Say, 1829, *Taylorconcha serpenticola* Hershler et al (1994) and *Fluminicola* sp. (Richards et al 2001, Gates 2012), while in Polecat Creek and Snake River it reduces the growth of the native snails *Pyrgulopsis robusta* Walker, 1908 and *Valvata utahensis* Call, 1884 (Lysne and Koetsier 2008, Riley et al 2008). The growth of *Fossaria* (*Bakerilymnaea*) *bulimoides* was also reduced by the NZMS in Yellowstone (Thon and Krist 2011). The NZMS has also established in various ecosystems in Europe, where it has become the dominant species (Spyra et al 2015). This has led to its classification as one of the 50 most detrimental invasive species on the continent (Nentwig et al 2018). Similarly, introduction of the SWGS to Italy and France has been associated with a decline in the abundance of the native *Physa fontinalis* (Linnaeus, 1758) (Manganelli et al 2000, Mouthon and Daufresne 2010), while in Mozambique it displaced the native snail *Bulinus forskalii* (Ehrenberg, 1831) (Dobson 2004). Under laboratory conditions, it has been shown that the native Australian *Glyptophysa gibbosa* (Gould, 1846) inhibited its growth and enhanced mortality in presence of the SWGS (Zukowski and Walker 2009). This snail had a similar effect on native populations of *Physa fontinalis* in experiments conducted in Germany (Fruh et al 2017), on *Stenophysa marmorata* Guilding, 1828 in Argentina (Nuñez 2011), and on *Racesina luteola* Lamarck, 1822 in India (Karmakar et al 2021, Paul and Aditya 2021).

Aside from the niche partitioning, the co-existence of NZMS and SWGS in the Consuelo Stream can also be explained by the abundance of food resources because vegetation is dense in this ecosystem (see fig. 1) and could therefore decrease competition. Larson et al (2023) found some opposing relationships between the

NZMS and *Physa* sp. regarding environmental factors that could be attributed to differences in habitat use or competition between the two species. It has also been suggested that niche partitioning in sympatric snails may occur through divergence in shell length (Brown 1982), enabling species to specialize in different particle sizes (Fenchel 1975). However, in the present study, we did not observe any significant differences in size between species. Competition may also be mitigated by divergence in reproductive size classes between species (Brown 1982), a parameter that has not been evaluated until now in Chile. Furthermore, NZMS and SWGS exhibit differences in their life history traits. NZMS, for instance, is ovoviviparous, giving birth to juveniles that closely resemble miniature adults, while SWGS adopts an egg-laying strategy, depositing eggs in gelatinous masses that adhere to stones or other hard substrates. Moreover, other factors, such as environmental variability, may also play a role in the coexistence of ecologically similar species, though further investigation is warranted.

The presence of NZMS and SWGS in the central-northern zone of Chile has been previously documented (Collado 2014, 2016, 2017, Collado et al. 2019a, 2019b), along with the potential for expansion throughout South America in the former case (Alexandre da Silva et al. 2019). Our study has confirmed that in La Brunina, the type locality of *Heleobia bruninensis* (Biese, 1944), both species were recorded, but the native species was not.

The same occurred in the Choapa River, type locality of *Heleobia choapaensis* (Biese, 1944), and in Zapallar, type locality of *Heleobia compacta* (Biese, 1944). In the Consuelo stream, where Biese (1944) reported a population of *H. choapaensis*, no individuals of the species were found, confirming findings from previous studies (Collado 2014, Collado et al 2019a). In the Illapel River, type locality of *Physa nodulosa* Biese, 1948, the presence of both invasive species has also been confirmed, but that of the native species has not, although it cannot be ruled out that perhaps it never existed here (Collado, 2017). In the Dehesa stream, in the Metropolitan Region, type locality of *Potamolithus santiagensis* (Biese, 1944), where NZMS and *Physa* sp. co-occur, no specimen of the native species has been found to date (Collado 2014, Collado et al 2019a, 2019b). This suggests the displacement or replacement of native species by invasive species. However, it is important to know that unexamined anthropogenic factors, such as, for example, drought, pollution, livestock farming, irrigation channels, and the construction of reservoirs, may also influence native populations. These potential effects require further evaluation and research.

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Author contributions

GA Collado conceived the idea for the study, conducted the sampling, and drafted the initial manuscript. GA Collado, MA Vidal, and C Torres-Díaz performed the analytical methods. All of these authors reviewed the final manuscript.

Conflicts of interest

No conflicts declared

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