

Success of an exotic snail *Physella acuta* in anthropogenically impacted Patagonian streams

Establecimiento del caracol exótico *Physella acuta* en ambientes impactados por actividades antrópicas en arroyos patagónicos

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ABSTRACT. The expansion of exotic species is one of the greatest threats to biodiversity and is a significant component of global change that occurs at increasing rates due to the removal of natural barriers and the global transport of species. The snail *Physella acuta*, has expanded into numerous aquatic environments worldwide, given a set of traits that allows the species to thrive in new and harsh environments. This study documents changes in the composition and structure of the malacofauna and examines the presence of established and expanding populations of *P. acuta* in the Esquel-Percy basin (Patagonia, Argentina), which has been altered by wastewater treatment plants discharges (WWTPs). The population density of *P. acuta* in the studied area increased from less than 15 ind/m² in 2005 to 1800 ind/m² in 2016-2017. This species was the dominant mollusk at the two post-urban sites, under poor environmental conditions. Understanding the introduction pathways of exotic species to prevent and control their establishment and spread is essential since biological invasions constitute a major threat to freshwater ecosystems.

Keywords: stream pollution; benthic communities; exotic species; Patagonia.

RESUMEN. La expansión de especies exóticas es a la vez consecuencia y motor del cambio global y constituye una de las mayores amenazas a la biodiversidad, sucede principalmente por la desaparición de barreras naturales al transporte de especies a escala mundial. El gasterópodo *Physella acuta* ha expandido su distribución a un gran número de ambientes acuáticos en todo el mundo gracias a rasgos ecológicos que le permiten dispersarse eficientemente y reproducirse en condiciones desfavorables. Este estudio documenta cambios en la composición y estructura de la malacofauna, y examina la presencia de poblaciones establecidas y en expansión de *P. acuta* en la cuenca de los ríos Esquel y Percy (Patagonia, Argentina), caracterizada por la presencia de plantas de tratamiento de líquidos cloacales. La densidad poblacional de *P. acuta* ha aumentado de menos de 15 ind/m², en el año 2005, hasta 1800 ind/m² en el período 2016-2017. Esta especie es el molusco dominante en los dos sitios post-urbanos de la cuenca, que presentan las peores condiciones ambientales. La comprensión de las vías de introducción de especies exóticas es

esencial para prevenir y controlar su establecimiento y posterior expansión, dado el peligro que representan las especies exóticas para los ecosistemas acuáticos.

Palabras clave: contaminación; comunidades bentónicas; especies exóticas; Patagonia.

INTRODUCTION

Increasing human pressure on fluvial ecosystems and natural landscapes has influenced stream health for decades. Freshwater ecosystems are considered one of the reservoirs of biodiversity and thus deserve special attention for conservation policies (Dudgeon *et al.*, 2006; Thomaz *et al.*, 2015). During the last decades, population growth in Patagonia has increasingly impacted on its freshwater environments. Urbanization has significant consequences on macroinvertebrate communities and its effects are known to cause severe damage to the integrity of in-stream biota (Mor *et al.*, 2019; Richardson & Soloviev, 2021). Anthropization of natural landscapes promotes invasive processes in aquatic environments since human-induced disturbances can create space for the colonization of new species or modify the environmental conditions and resource availability, favoring tolerant species such as invasive ones (Lake, 2000; Schreiber *et al.*, 2003). The global movement of species to non-native ranges has provided important resources (i.e. food, fiber, and fuel) but has often resulted in widespread invasions that cause significant ecological and economic impacts (Pyšek *et al.*, 2012). This is a significant component of global change, causing biodiversity loss and decreasing water quality (Vitousek *et al.*, 1996; Pyšek *et al.*, 2012; Reid *et al.*, 2018; Gallardo *et al.*, 2024). Recent invasions in Patagonian rivers, including the diatom *Didymosphenia geminata*, and the mussel *Corbicula fluminea* have highlighted the region's vulnerability to aquatic invasions and underscored the lack of effective control measures (Lamaro *et al.*, 2019; Brand & Grech, 2020; Darrigran *et al.*, 2020; Labaut *et al.*, 2021). *Physella acuta* (Draparnaud, 1805) (in synonymy with *Physa acuta* Draparnaud, 1805) is a small

air-breathing snail of the family Physidae. This species is successfully invasive on four continents and is often considered one of the most effective invaders among freshwater snails (Dillon *et al.*, 2002; Appleton, 2003; Collado, 2017; Vinarski, 2017). *Physella acuta* differs from other physids in that it has a highly adaptable life cycle, being reported to be univoltine in their natural habitats, whereas bivoltine cycles have commonly been observed outside their native range, with a less massive second cohort produced in late summer (Duncan, 1959; Maqboul *et al.*, 2014). Other life history traits also account for the widespread success of this species around the world, such as hermaphroditism, high reproduction rates, passive dispersal capacity, coupled with high tolerance to diverse environmental conditions (Mouthon, 1996; Bernot *et al.*, 2005; Kefford & Nuggeoda, 2005; Albrecht *et al.*, 2008).

The worldwide spread of *P. acuta* is likely to be mediated by the aquarium and pet trade, as has happened with other common freshwater species such as *Pomacea canaliculata*, *Melanoides tuberculata* and *Ferrisia californica* (Appleton, 2003; Vinarski, 2017; Ng *et al.*, 2018), although other agents of dispersal, such as wild animals and other human activities, have been discussed in the literature (Van Leeuwen *et al.*, 2013). In Argentina, *P. acuta* was first recorded in the 1970s (Paraense, 2005), and nowadays it is widespread and abundant, particularly in environments related to the Del Plata river basin (Núñez, 2010). In Patagonia an expansion of this species was observed, with records in Chubut province since 2014 (Assef *et al.*, 2014 a), and recently its distribution has expanded to Santa Cruz province (Gutierrez Gregoric, *et al.*, 2024). The molecular identification of the *P. acuta* population in northwestern Chubut province was confirmed through PCR amplification and sequencing, in studies proposing this species as a biomarker for aquatic contamination (Assef

et al., 2014a; Horak & Assef, 2017; Horak, *et al.*, 2023).

The Esquel-Percy sub-basin is part of the Futaleufú-Yelcho watershed, which drains from Patagonia Argentina to the Pacific Ocean, through Chile. This emphasizes the importance of monitoring this rapidly expanding invasive species, threatening pristine, biodiversity-rich environments. The endemic species of Patagonian rivers and streams contribute to global biodiversity, and the native biota performs specific functions at different levels of freshwater environments. Therefore, the present paper aims to evaluate the development status of snail populations in different stream sections and their relationship with water quality and compare the dominance relationships of malacofauna between invaded and non-invaded sites.

MATERIAL AND METHODS

Study area and site selection

The study region is a transitional area located in the mountains and piedmont of north-western Chubut province, Argentina (between $42^{\circ} 37' - 43^{\circ} 10' S$ and $71^{\circ} 04' - 71^{\circ} 37' W$) (Fig. 1). The studied basins, Esquel and Percy, are part of the Futaleufú-Yelcho binational hydric system, and are located in the ecotone between two phytogeographical provinces, the Subantarctic Forest and the Patagonian Steppe. Both streams drain a densely populated area of the Andean Patagonia. The Esquel Stream is a third-order channel that originates southeast of the Esquel mountain range (1500 m a.s.l.). On its descent, it crosses the city of Esquel (37019 inhab.), flows through a valley area and finally joins the Percy River near Trevelin city (10729 inhab.) (430 m a.s.l.) (Miserendino *et al.*, 2021). Three sites were selected in each watercourse, one located upstream of each urban area (E1 and P1), one within urban influence (E2 and P2), and a third downstream of the urban areas and their wastewater treatment plants (E3 and P3) (Fig.1). Esquel and Percy confluence

is located between P1 and P2. The Esquel and Trevelin WWTPs were constructed in 2001 and 1999, respectively and include modules of *Phragmites australis* for phytoremediation. Although these facilities were successively expanded to accommodate the volume of domestic and rainwater effluents received, at present, the capacity of both plants appears to be inadequate (Assef *et al.*, 2014b; Manzo *et al.*, 2020; Williams-Subiza *et al.*, 2022). Sampling took place in May 2016 (autumn), September 2016 (winter), December 2016 (spring) and March 2017 (summer). High discharge events due to rainstorms or snowmelt were avoided.

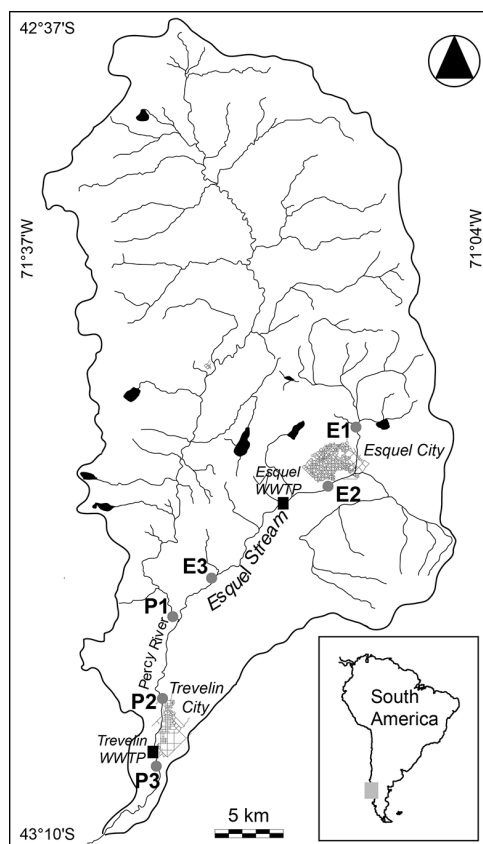


Figure 1. Map showing the Esquel-Percy basin, location of sampling sites in the Esquel and Percy streams (grey circles), the two largest urban areas (Esquel and Trevelin), and both wastewater treatment plants (black squares). Chubut Province, Patagonia, Argentina.

Limnological characterization of sampling sites

At each stream sampling station discharge was obtained by combining width, depth, and current velocity as in Gordon *et al.* (2004). Wet width was determined using a laser distance meter, channel depth was estimated from three to five equally spaced measurements with a calibrated stick along a transverse profile, and current velocity was measured by timing a float as it moved over a distance of 5–10 m (average of three measurements). Water temperature, pH, specific electrical conductivity (COND), total dissolved solids, dissolved oxygen (DO) and oxygen percentage saturation were measured with a Hach Senslon multiparameter probe. For nutrient analysis, water samples were collected below the surface, kept at 4 °C and transported to the laboratory. Nitrate plus nitrite nitrogen ($\text{NO}_3^- + \text{NO}_2^-$), ammonium (NH_4^+), and soluble reactive phosphate (SRP) were analyzed spectrophotometrically using standard methods (APHA, AWWA, WEF, 2012). Total suspended solids (TSS) were estimated gravimetrically as in Eloisegi Iruiria and Butturini (2009). At each sampling site, in-stream triplicate periphyton samples were randomly collected from riffles at each site and from independent substrate. Samples were transported in dark containers to the laboratory, where they were filtered through Whatman GF/F filters. Chlorophyll *a* was extracted from filters in 90% acetone and measured spectrophotometrically with phaeophytin correction according to standard methods (Hauer & Lamberti, 2007). For the molluscan community assessment, three samples from riffles and three from pools were taken at each site with a Surber sampler (0.09 m²; 250 µm pore size), fixed *in situ* with 4% formaldehyde and sorted in the laboratory under at least 5x magnification. Species were identified to the lowest possible taxonomic level using regional keys and counted (Fernández, 1981; Ituarte, 1996; Cuezco *et al.*, 2020).

Snail populations size distribution and age structure

The size and age of all individuals of *P. acuta* were allometrically assessed from maximum length of shells using stereoscope, following Maqboul *et al.* (2014). Three age classes for *P. acuta* were defined based on shell lengths, thickness of the outer lip and its degree outward flare:

- C1: tiny juveniles, size less than 2.5 mm;
- C2: juveniles, size between 2.5 and 5.5 mm;
- C3: adults size over 5.5 mm.

Historical data and *P. acuta* occurrence

A comprehensive revision of existing literature from the area was made to identify the dates and localities of this species' presence (Miserendino & Pizzolón, 2000; Miserendino, 2001; Miserendino, 2004; Miserendino *et al.*, 2008; Miserendino *et al.*, 2016; Brand & Assef, 2014), moreover specimens from Miserendino *et al.* (2008) were revised to avoid possible misidentification of *P. acuta*.

Statistical analysis

The relative importance of environmental factors in explaining the environmental variability of sampling sites on a seasonal basis was assessed using a Principal Component Analysis (PCA) (CANOCO program; ter Braak & Smilauer, 1998). All environmental variables (Table 1) (except pH) were transformed ($\log x + 1$) prior to analysis. Those variables that were strongly correlated with others (i.e. with an inflation factor >10) in the initial analysis were removed. Specifically, water temperature, total dissolved solids, salinity, oxygen saturation, pH, depth, width and discharge were removed due to their high correlation with other

Table 1. Environmental variables recorded at studied sites in Esquel-Percy basin (Patagonia, Argentina). Data are mean values (may 2016 – march 2017) $\pm$ SD (n=4).

	Esquel River			Percy River		
	E1	E2	E3	P1	P2	P3
Water temperature (°C)	8.0 $\pm$ 3.4	10.2 $\pm$ 5.3	10.8 $\pm$ 3.3	8.8 $\pm$ 3.7	9.5 $\pm$ 4.4	10.3 $\pm$ 4.9
Conductivity (μ S/cm)	79.6 $\pm$ 18.9	262.8 $\pm$ 33.7	328.8 $\pm$ 50.9	68.4 $\pm$ 15.3	95.1 $\pm$ 16.9	98.2 $\pm$ 16.1
TDS (mg/L)	54.7 $\pm$ 13.0	172.4 $\pm$ 23.2	210.1 $\pm$ 19.6	47.4 $\pm$ 9.3	66.2 $\pm$ 14.3	66.5 $\pm$ 14.5
Salinity (‰)	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.0	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1
Dissolved oxygen (mg/L)	11.5 $\pm$ 1.2	11.4 $\pm$ 1.3	8.4 $\pm$ 1.9	12.6 $\pm$ 1.6	13.4 $\pm$ 1.6	13.0 $\pm$ 1.8
Saturation (%)	98.2 $\pm$ 4.7	101.8 $\pm$ 4.4	76.6 $\pm$ 9.4	111.1 $\pm$ 4.5	119.4 $\pm$ 14.3	118.0 $\pm$ 8.5
pH	6.5 $\pm$ 0.7	6.8 $\pm$ 0.9	6.8 $\pm$ 0.6	6.2 $\pm$ 0.7	6.5 $\pm$ 0.8	6.6 $\pm$ 0.8
Depth (m)	0.3 $\pm$ 0.4	0.1 $\pm$ 0.0	0.2 $\pm$ 0.1	0.3 $\pm$ 0.0	0.3 $\pm$ 0.0	0.2 $\pm$ 0.1
Width (m)	2.6 $\pm$ 0.5	5.6 $\pm$ 0.8	3.6 $\pm$ 0.1	19.5 $\pm$ 1.5	12.5 $\pm$ 0.7	33.4 $\pm$ 16.9
Velocity (m/s)	0.4 $\pm$ 0.1	0.6 $\pm$ 0.2	1.1 $\pm$ 0.2	0.9 $\pm$ 0.3	1.2 $\pm$ 0.2	1.1 $\pm$ 0.2
Discharge (m ³ /s)	0.3 $\pm$ 0.2	0.5 $\pm$ 0.3	0.8 $\pm$ 0.4	5.3 $\pm$ 1.3	3.9 $\pm$ 1.2	7.0 $\pm$ 5.8
Chlorophyll <i>a</i> (μ g/cm ²)	0.5 $\pm$ 0.2	6.8 $\pm$ 5.2	21.1 $\pm$ 12.7	0.9 $\pm$ 0.7	9.7 $\pm$ 12.9	20.4 $\pm$ 21.9
NO ₃ ⁻ + NO ₂ ⁻ (μ g N/L)	6.8 $\pm$ 8.9	565.0 $\pm$ 319.1	182.7 $\pm$ 159.7	8.9 $\pm$ 11.3	760.7 $\pm$ 418.4	586.6 $\pm$ 397.1
NH ₄ ⁺ (μ g N/L)	5.2 $\pm$ 3.4	41.3 $\pm$ 37.3	9921.9 $\pm$ 2827.4	6.3 $\pm$ 2.2	45.7 $\pm$ 81.9	37.5 $\pm$ 62.3
PO ₄ ³⁻ (μ g P/L)	0.6 $\pm$ 0.5	24.6 $\pm$ 5.9	757.5 $\pm$ 340.0	2.1 $\pm$ 0.2	57.8 $\pm$ 20.5	34.2 $\pm$ 21.8
TSS (mg/L)	0.1 $\pm$ 0.0	5.4 $\pm$ 6.3	5.6 $\pm$ 2.1	1.2 $\pm$ 0.9	2.7 $\pm$ 1.2	4.3 $\pm$ 3.2

predictors and further analysis was carried out with the remaining environmental variables. To analyze habitat selection (i.e., preference for riffle vs. pool habitats), a Wilcoxon test was performed using the coin package (Hothorn *et al.*, 2008) in R software (version 3.5.1; R Core Team, 2018) via RStudio (version 1.0.136; RStudio Team, 2016). The response variable was *P. acuta* density, with habitat as a factor consisting of two levels: riffle and pool.

RESULTS

Sampling sites in the Percy stream had greater widths and discharges compared to those in the Esquel stream. Among the Esquel sites, E3 exhibited the highest current speed, whereas E1 and E2 were characterized by shallower depths, narrower widths, and lower velocities. Chemical variables, such as nutrient concentration, and chlorophyll *a* showed higher value at both urban (E2 and P2) and post-treatment plant streams (E3 and P3), than at pre-urban sites, regardless of the stream (Table 1). A total of 5613 individuals of *P. acuta* were

collected in this study, it was detected at site E3 in Esquel stream, and at sites P2 and P3 in Percy stream, and was the dominant species of malacofauna in the two post-wastewater treatment plant sites (E3 and P3). *Chilina* sp. or *Heleobia hatcheri*, followed by *Biomphalaria* sp. dominated the rest of the sampling sites, and *Pisidium inacayali* was less abundant (Fig. 2a). At the three sites where *P. acuta* was present, eggs and all three size classes of snails were found (Fig. 2b). At E3, the largest proportion of small juveniles (C1) was found in December samples, whereas at P2 and P3, the largest C1 proportion was found in May samples. Principal Component Analysis highlighted differences between sampling sites. PCA1 reveals a gradient of environmental pollution, with unpolluted sites grouped on the positive end of the axis (E1 and P1, all without *P. acuta* records), and polluted sites on the negative side of PCA1. Additionally, PCA2 segregates two groups: the site E3, related to high ammonium concentration and conductivity values and low dissolved oxygen concentrations (upper left quadrant); while E2, P2 and P3 sites were associated with high phosphate, nitrite-nitrate concentrations and total

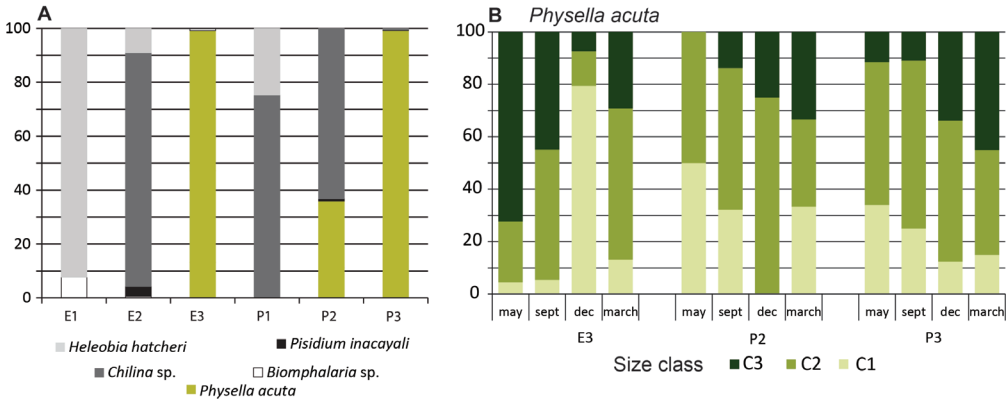


Figure 2. A. Mollusk species composition (relative abundance) at sampling sites (annual average). B. *Physella acuta* size class structure per date at each sampling site. Size classes are categorized as in Maqboul *et al.* (2014). Data represents the average of three riffles and three pools per site.

suspended solids, but high dissolved oxygen concentrations (lower left quadrant) (Fig. 3). Regarding habitat preference, although *P. acuta* was present at both sampling habitats (riffle and pool), it exhibited a spatial preference and had a significantly higher density at pool habitats at all sampling sites (Wilcoxon test; $p < 0.000$) (Fig. 4). Comparisons with earlier studies carried out at the same sites show that in the year 2005 the only record of *P. acuta* for both catchments was at site E3, and at this time its density was smaller than 20 ind/m². By 2014, E3's population was larger than 1800 ind/m², but still no presence of *P. acuta* had been detected at any of the sites of the Percy stream. The present study (2016-2017) indicates that site E3's snail population maintains its annual average density, while new populations have been established downstream at sites P2 (annual average: 44 ind/m²) and P3 (annual average: 760 ind/m²) of the Percy stream (Fig. 5).

DISCUSSION

The present study highlights the development of the recent invasion of *P. acuta* in Patagonia, from its initial arrival through the first 12 years. The current populations have active reproduction at the studied sites, and its size structure indicates

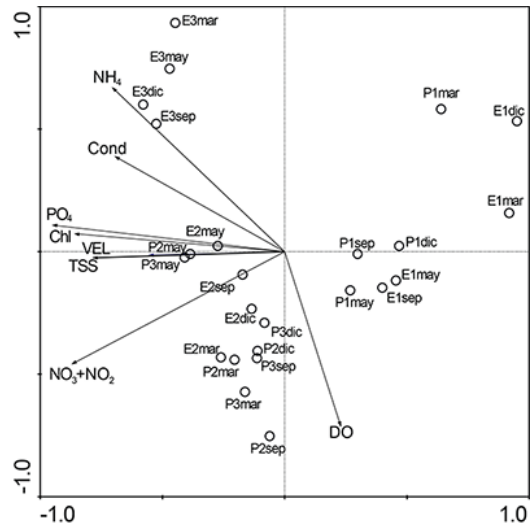


Figure 3. Biplot of the PCA ordination for the data set of all sampling sites and dates (2016-2017). Physicochemical variables are shown as arrows (NH₄⁺: ammonia; PO₄³⁻: phosphates; Chl: Chlorophyll *a*; VEL: velocity; TSS: total suspended solids; NO₃+NO₂: nitrate+nitrites; DO: dissolved oxygen; Cond: conductivity). The sampling dates are indicated in the labels (may: May 2016; sep: September 2016; dec: December 2016; mar: March 2017). The eigenvalues for the first 2 axes are indicated next to each label.

some synchronicity in its life cycle, at least at Percy stream, where recruitment occurs in May. There is also a strong indication of a preference for depositional habitats, characterized by low flow, a flat surface and a depth much

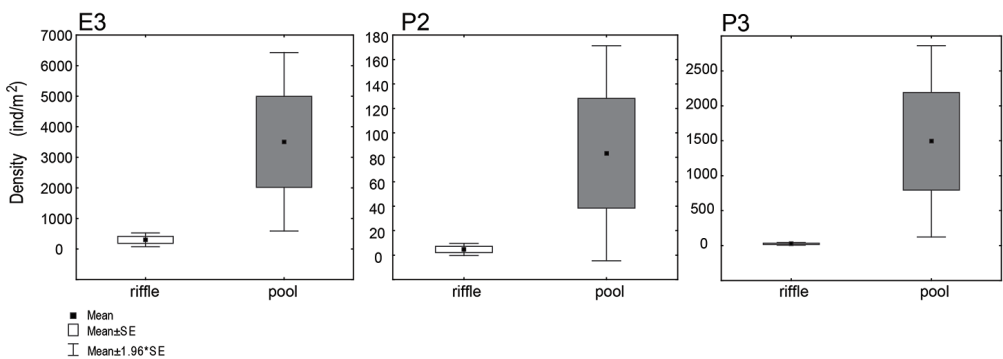


Figure 4. *Physella acuta* density (ind/m²) at riffle and pool habitats at each sampling site. Mean, mean $\pm$ SE and mean $\pm$ 1.96*SE, of 24 samples for each site.

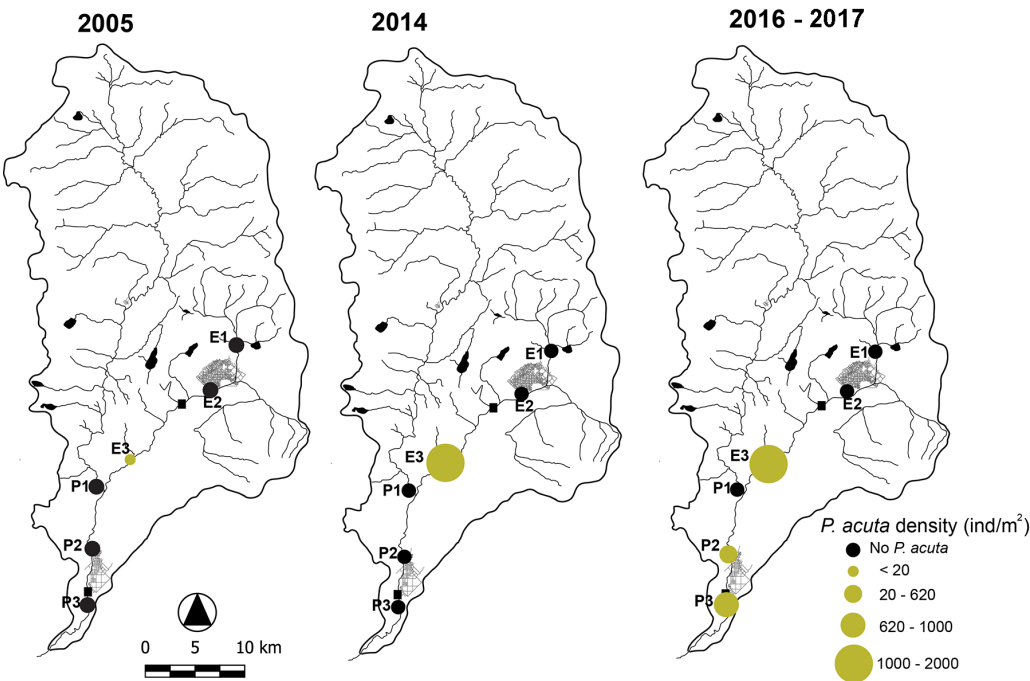


Figure 5. Mean densities of *P. acuta* recorded in 2005, 2014 and 2016-2017. Black squares indicate the location of the wastewater treatment plants. Sampling sites depicted with a black dot indicate no presence of *P. acuta*, coloured dots indicate the presence, and size is related to the density.

greater than the average depth of the stream. The first record of *P. acuta* in the Esquel-Percy drainage system occurred in 2005, with a low density. It can be assumed that the arrival of this species in the region would have occurred shortly before that time, coincidentally with the

construction of the wastewater treatment plant, suggesting that the origin of the invasion could be related to *Phragmites australis* specimens used in the phytoremediation process of such facilities. These specimens are relocated from other areas of the country and may

act as carriers of *P. acuta*, as well as other species. Another hypothesis is that it has been introduced to the region as an aquarium species trade, or as a hitchhiker attached to aquarium plants, as has been reported for other regions (Duggan, 2010), and then released accidentally into the watercourse. Nearly a decade after the first record, the species was still confined to a single site in the basin but showed a considerable increase in density (100-fold). It was only after 2014, with a two-year interval, that new populations spread downstream to two sites in the Percy stream. Although, given the lack of data for that period, it is not safe to infer the annual population growth rate. It can be assumed that local dispersion towards the Percy sites (P2 and P3) located downstream from the Esquel-Percy confluence, occurred only after the density reached 1000 ind/m². Probably, in addition to the time needed to reach a high population density (Simberloff, 2009), worsening of the environmental conditions of the streams could have contributed to rapid development. There is still no presence of *P. acuta* at upstream sites (P1, E1 and E2), however, since it is an actively dispersing snail, an upstream migration can also be expected (Appleton & Branch, 1989; Pointier *et al.*, 1998) and the establishment of new populations may occur in the future. Given that it is an animal with little long-distance dispersal capacity, and it is unlikely that its entry into the region was intentional, a single instance of entry could be assumed. This species possesses traits favorable to rapid reproduction and local dispersal, making it one of the dominant molluscan species in the places where it successfully establishes itself. Like other gastropod species, selective hermaphroditism, high reproduction rates and passive dispersal capacity are all life history traits that would explain the widespread distribution and success of this species worldwide (Mouthon, 1996; Bernot *et al.*, 2005; Kefford & Nuggeoda, 2005; Keller *et al.*, 2007; Albrecht *et al.*, 2008; Busset *et al.*, 2014). Moreover, *P. acuta* possesses a highly adaptable life cycle, having bivoltine cycles in favorable conditions, with a second generation of smaller animals appearing in late summer (Maqboul *et al.*, 2014). In addition,

Núñez (2011) has suggested that the success of the *P. acuta* in the native habitat of other species could be explained in part by the former's earlier sexual maturation, higher reproductive potential and greater longevity. Freshwater snails often share similar dietary requirements, such as biofilm or periphyton communities, which can lead to intense competition with other species (Chase *et al.*, 2001; Cross & Benke, 2002; Estebenet *et al.*, 2002). This competition may result in the displacement or elimination of native species with less efficient feeding strategies (Pointier & Augustin, 1999). The Enemy Release Hypothesis posits that the abundance or impact of some invasive species is related to the scarcity of their natural enemies in the introduced range compared with the native habitat and is highly supported as an explanation for the success of the invader outside its native range (Colautti *et al.*, 2004; Davies, 2006). In this sense, the absence of effective predators may be one of the causes of the successful establishment of this species in north-western Chubut. Many authors have reported that this species inhabits low-quality environments, has high reproductive capacity and exceptional tolerance to polluted waters (Mouthon, 1996; Dobson, 2004; Albrecht *et al.*, 2008; Tietze & de Francesco, 2010; Saha *et al.*, 2017). Urban treated wastewater is a harmful substance that has significant impacts on native benthic communities, and current evidence shows that native species do not perform well under this type of disturbance (Miserendino *et al.*, 2008). It is likely that under these conditions, most of the competitors and/or predators of *P. acuta* may be affected, thus favoring its development. Climate change and anthropic disturbances can alter the abiotic filters that determine the success of invasive species in aquatic environments. For example, facing changes in flow patterns due to climate change, invasive species will be favored by the episodic desiccation of streams. Such is the case of the New Zealand mud snail (*Potamopyrgus antipodarum*), a worldwide invader that tolerates desiccation and might have an advantage in streams that are affected by periodic droughts or pollution

(Rahel & Olden 2008; Sánchez-Morales *et al.*, 2018). Similarly, *P. acuta* has a great capacity to survive out of water and can endure periods buried in mud (Bousset *et al.*, 2004; Banha *et al.*, 2014). This trait provides an advantage in areas where climate change is altering hydroperiods and flow patterns, as projected for the Patagonian region (Pessacg *et al.*, 2020). The present study cannot clarify whether the success of *P. acuta* is due to its high plasticity and tolerance to poor conditions, to the fact that it outperforms its competitors, or to a lack of predators. It is probable that in the harsh conditions that occur in the urban sites of the Esquel-Percy basin, as in other urban environments, many of the native species lose their ability to compete. If this is indeed the case, then *P. acuta* would benefit from the situation. The question remains whether it is a highly effective competitor under any circumstance, or whether it performs well under conditions that other native species can't tolerate. Increased global connectivity through new trade routes and improved transportation technologies promote invasions to new and isolated regions worldwide. In addition, climate change and land-use changes contribute to facilitating the rapid spread of invasive species (Havel *et al.*, 2015). Aquatic non-indigenous species are difficult to detect, and even when detected, are extremely difficult to eradicate and control, posing a major threat to biodiversity and water resources. It is worth highlighting the need to study the introduction pathway of exotic species, to prevent and control their spread (Oscos *et al.*, 2010). Research on invasive species remains focused on developed countries (Núñez & Pauchard, 2010; Pysek *et al.*, 2012), while most natural ecosystems and biodiversity hotspots are in developing countries, where prevention and management strategies are lacking but urgently needed.

CONCLUSIONS

This paper documents the invasion dynamics of *P. acuta* in Patagonia over its first 12 years.

The initial arrival of this species may have been facilitated by human activities such as wastewater treatment plant discharge or aquarium trade, and the species has since effectively colonized various habitats. There is also evidence of active reproduction at studied sites, and preference for depositional habitats. Its biological traits such as high reproductive rates, tolerance to poor conditions, and selective hermaphroditism, and external factors like urban land use and climate change, are likely to be responsible for the species' success in a novel environment. Anthropogenic factors, such as urban wastewater and climate change, facilitate the spread of invasive species, posing a threat to native biodiversity in freshwater ecosystems. Therefore, the need for research and management strategies in developing countries is of utmost importance, which often lack resources to prevent and mitigate biological invasions.

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