



Differential use of trophic resources between an exotic and a coexisting native snail

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Abstract

Knowing the interactions between exotic and native species is essential to establish possible threats to the local fauna. In this study, we assessed the use of food resources and diet overlap between a recently introduced snail, *Sinotaia quadrata*, and a native species, *Pomacea canaliculata*. We analyzed the gut content and stable isotope of snails and resources in a lowland stream where both species coexist. Both Schoener's and isotope dietary overlap indexes supported dietary overlap. Conversely, gut content analysis showed differences in consumption: *S. quadrata* consumed more detritus and diatoms than *P. canaliculata*, whose diet was characterized by detritus and macrophyte remains. Macrophytes were the resource that most contributed to the diet of both species, as shown by stable isotope mixing models. The combination of both techniques, gut content and stable isotope analysis, indicated that *S. quadrata* consumed macrophyte detritus while *P. canaliculata* ate fresh macrophytes. This difference indicates differential use of food resources between the studied species coexisting in a lowland stream. Although no negative trophic interaction was found, we highlight the importance of continuing to monitor interactions for other resources and studying possible risks to the local fauna.

Keywords *Sinotaia quadrata* · *Pomacea canaliculata* · Non-native species · Gut contents · Stable isotopes

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Introduction

The introduction of exotic species has increased between continents as a consequence of human activities (Schreiber et al. 2003; Strayer 2010). As a result, native species of the same taxonomic groups and surrounding biotic communities can be impacted negatively via species replacement, food web reorganization, and community composition simplification (Sor et al. 2017). Knowing the ecological aspects of an exotic species allows one to establish the degree of functional similarity with local species and determine possible risks to them (Solomon et al. 2010). These risks could even lead to competitive exclusion scenarios (Hardin 1960).

Several aquatic and terrestrial gastropod species have become pests around the world, causing severe environmental and socioeconomic damage (Kesner and Kumschick 2018). Exotic snails, such as the New Zealand mud snail *Potamopyrgus antipodarum* in the USA, can compete directly with native gastropods for resources, including space and food (Lysne et al. 2008; Riley et al. 2008). When competition for food resources exists, the introduced snails could either induce dietary shifts in the native species

(Larson and Ross Black 2016) or promote the decline of native populations. An example of the latter is *Batillaria attramentaria*, which caused a decrease in native populations of *Cerithidea californica* in California (Byers 2000). However, the negative impacts of interspecific competition could be reduced if resource partitioning existed between species, allowing their coexistence (Schoener 1974; Fedosov et al. 2014).

Sinotaia quadrata (Benson 1842) is an Asiatic freshwater Viviparidae snail recently recorded for Argentina by Ovando and Cuzzo (2012) and Ferreira et al. (2017). This species has already gone through the introduction and establishment stages in its new area of distribution, two preconditions to be considered an invasive species (Ferreira et al. 2017). It has been warned that snails of this family can impact the benthic communities by altering algal biomass, algal species composition, and nutrient cycling (Johnson et al. 2009). However, like many other species introduced in this area, the impact of *S. quadrata* on native species remains poorly studied (Darrigran et al. 2020). Hence, the study of a potential threat of this species to the native fauna is relevant.

Pomacea canaliculata (Lamarck 1822) (Gastropoda: Ampullariidae), on the other hand, is a native species widely distributed in lowland streams of Argentina (Seuffert and Martín 2013), where it plays a key ecosystem role in trophic webs (López van Oosterom et al. 2013, 2016; Cadierno et al. 2017) and represents one of the most relevant macrophyte consumers (Manara et al. 2018; Maldonado and Martín 2019). Consequently, considering the similar densities and sizes of both species that can be found where they coexist (Ferreira et al. 2017), the presence of *S. quadrata* might represent a threat, not only for native *P. canaliculata* populations, but also for the whole ecosystem.

Studying the use of resources by exotic and native species is essential to establish a potential diet overlap (Zahn Seegert et al. 2014). Studies of feeding habits have traditionally used gut content analysis as a tool for reconstructing the resource use of a particular species (Nielsen et al. 2018). However, not all the incorporated food is assimilated, and its analysis may lead to overestimating the importance of some items and in other cases to underestimating it because the identification of the digested food is not always possible, especially for detritivores (McCutchan and Lewis 2002). Therefore, this method is frequently complemented with stable isotope analysis, which provides information only on the assimilated material (Cabana and Rasmussen 1994). Thus, the simultaneous use of both methods provides more complete and detailed information over time than if they were used separately (Nielsen et al. 2018). In this sense, we used gut content and stable isotope analyses to assess the use of food resources and diet overlap of the exotic snail *S. quadrata* and the native snail *P. canaliculata* in a stream where they coexist. This would be the first step in establishing a

possible risk for the local fauna by the introduced species and would provide relevant information about the ecology of this exotic snail.

Methods

Study area

The study was carried out in the Carnaval stream, belonging to the Rio de la Plata Basin, located in the Pampa Ecoregion, close to La Plata city (Buenos Aires province, Argentina). It is a peri-urban stream (Hurtado et al. 2006) and, like other lowland Pampean streams, it is characterized by a low slope (< 1%), slow flow, high turbidity, and high content of suspended solids. In addition, the lack of riparian forest vegetation, the development of a dense macrophyte assemblage, and elevated algal growth are also characteristics of all Pampean streams (Feijoó and Lombardo 2007). Thus, in these ecosystems, autochthonous detritus, algal and macrophyte assemblages provided the basal resources (Feijoó et al. 2014). For this study, a section of the stream (34°51'28.22" S, 58°4'5.17" W) was selected where both species, *P. canaliculata* and *S. quadrata*, were abundant (corresponding to S4 in Ferreira et al. 2017). This section showed a macrophyte coverage higher than 30% on all sampling dates and the typical characteristics of the lowland Pampean streams described above. The site's sediment was mainly composed of gravel followed by silt and sand and low percentages of clay. In addition, this reach passes through an urbanized area and receives untreated domestic wastewater, like most of the streams in the area.

Gut content analysis

Four samplings were carried out: April 2016, October 2016, April 2017, and October 2017. On each sampling date, 10 adult individuals of *S. quadrata* ($n=40$, shell length between 19.40 and 29.15 mm, Ferreira et al. 2017) and 10 late juvenile and adult individuals of *P. canaliculata* ($n=40$, shell length between 15.01 and 39.36 mm, Estebenet and Martín 2003) were collected for gut content analysis. Both species were present at the bottom of the stream and on top of the macrophytes. They were collected manually or with 500 μm sieves along a longitudinal transect of 100 m covering the two microhabitats where they were present (sediment and macrophytes) and fixed with 5% formaldehyde. In the laboratory, the snails were dissected under a stereoscopic microscope and the anterior part of the alimentary tract: the esophagus, of which the middle section is a crop, and the stomach (Andrews 1965) were separated and placed in vials with Bengal's rose colorant for 24 h to stain their contents. This colorant stains organic matter and helps to differentiate

organism tissue from other ingested material (Muñoz et al. 2009). Later, the content was homogenized in distilled water and mounted on microscope slides for observation under an optical microscope at a magnification of 400×. Photographs were taken by choosing 15 random fields (López van Oosterom et al. 2016) and analyzed with the Image J software.

For quantification, the area covered by each food item was considered relative to the total covered area of the digestive content (Jaarsma et al. 1998) and expressed as the relative frequency of each food item (Fi). Values of Fi were used as proxies of probabilities (pi) in the following formulas and in the Schoener's index (see below). Based on the results of gut content analysis, richness (S = number of total food items), Shannon diversity index ($H' = -\sum_{i=1}^S p_i \log_2 p_i$), Dominance ($D = 1 - \sum_{i=1}^S p_i^2$, 1 - Simpson diversity), and Pielou evenness ($J' = \frac{H'}{\log_2 S}$) of food items were calculated for each of the forty specimens of each species.

Stable isotope analyses

For stable isotope analysis, during the October-2017 sampling, 20 adult individuals of both species were collected in the studied section of the stream, using the same sampling technique as described above. The snails were taken to the laboratory alive, and placed in different containers with filtered stream water (filters with a pore size of 0.6 μm). Then, they were fasted for 24 h to ensure gut emptying and to include only assimilated substances in the analysis. The feces were siphoned out and individuals kept in a freezer at -20 °C until their processing. The shells were then mechanically discarded for the isotopic analyses (Bosley and Wainright 1999). Depending on the body mass of snails, two or three individuals were pooled to provide 3–4 mg dry weight samples, and three replicates were prepared per species. The potential food resources for both species were also sampled: macrophyte species present (*Stuckenia striata*, *Hydrocotyle bonariensis*, *Gymnocoronis spilanthoides*, *Hydrocleys nymphoides*, *Sagittaria montevidensis*, *Egeria densa*, *Schoenoplectus californicus*, *Nasturtium microphyllum*), fine particulate organic matter (FPOM < 65 μm), coarse particulate organic matter (CPOM > 65 μm), and epipellic biofilm (epipelon), the last three also taken in triplicate. For epipelon analysis, ten subsamples were collected by pipetting a superficial sediment layer (5–10 mm) in different places, following the recommendations of Gómez and Licursi (2001). In the laboratory, the coarse and fine fractions were separated with a 65-μm sieve. Macrophytes were sonicated for three 2-min cycles in an ultrasonic bath (Cleanson, 40-W power, 40-kHz frequency) to remove the attached algae from the plant surfaces (Romaní and Sabater 2001).

All the material was dried to constant weight for 48 h at 60 °C and then ground into powder to ensure homogeneity

and analyzed in continuous flow isotope ratio mass spectrometry (CF-IRMS Thermo Scientific, Flash 2000-Delta V) coupled to an elemental analyzer (Centro de Isótopos Estáveis, UNESP, São Paulo). Isotopic ratios ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) are typically expressed as the ratio between a heavier (higher atomic mass) and a lighter (lower atomic mass) isotope and converted into delta notation (δ values) through comparison of sample isotope ratios to ratios of internationally accepted standards. Standards for common systems include Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon ($\delta^{13}\text{C}$) and atmospheric N_2 for nitrogen ($\delta^{15}\text{N}$). The δ values are dimensionless ratios given in parts per thousand (‰) (Coplen 2011).

Data analysis

The differences in Fi, Shannon diversity, dominance, and evenness of Pielou of food items between species were analyzed with general linear mixed models (GLMMs). The Fi was first transformed by arcsin (\sqrt{X}) and Shannon diversity, dominance, and evenness of Pielou by $\log_{10}(X + 1)$ to fit with a Gaussian error distribution, because model residuals without transformation were not normally distributed (Shapiro test: $p < 0.01$). For richness analysis, we used generalized linear mixed models with a Poisson error distribution, which is typically used for counting data. In all the models, the predictor variable was the mollusk species (levels: *S. quadrata* and *P. canaliculata*), and it was fitted with a random effect “year” (intercept) because of the lack of independence of the data. The notation of the models was as follows: $y_i = \beta_0 + \beta_1 i + b_1 j + \epsilon_{ij}$, where y_i is the response variable (Fi, richness, Shannon diversity, dominance or evenness of Pielou), β_0 is the intercept, $\beta_1 i$ is the coefficient associated with the snail species, and $b_1 j$ is the coefficient of the random effect “year” (2016, 2017). The null model that included no explanatory variables and the random effect was established for each model for assessing the relative explanatory power of models containing the predictors of interest. All the analyses were carried out with ‘R’ version 3.4.4 (R Core Team 2018) with lme4 (Bates et al. 2015) and lsmeans (Lenth 2016) packages.

We performed a Student's t -test ($\alpha = 0.05$) to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between *S. quadrata* and *P. canaliculata*. Besides, the MixSiar Bayesian stable isotope mixing model (Semmens et al. 2013) was used to determine probability distributions for the proportional contribution of the food sources to the diet of each snail species. The trophic discrimination factor (TDF) used was 0.3 (± 0.14) ‰ for $\delta^{13}\text{C}$ and 2.2 (± 0.3) ‰ for $\delta^{15}\text{N}$ (McCutchan et al. 2003).

The diet overlap between species through gut content analysis was assessed using Schoener's index (SI, Schoener 1970), following Reynaga and Rueda Martín (2014): $I = 1 - 0.5 \sum_{i=1}^S |p_{ij} - p_{ik}|$, where p_{ij} and p_{ik} represent the

probability that item i is used by species j and k , respectively, being S the total number of food items used by the two species. On the other hand, the Isotopic dietary overlap index (IDO) was assessed following Miranda and Perissinotto (2012) with the same equation based also on Schoener's index: $IDO = 1 - 0.5 \sum_{i=1}^S |p_{ij} - p_{ik}|$, where p is the SIAR mean contribution of source i resulting from the final mixing models run for species j and k , respectively. Both indexes range from 0 to 1, as follows: 0 = no dietary overlap and 1 = complete overlap. A value equal to or greater than 0.6 is considered significant dietary overlap (Wallace 1981; Layman and Allgeier 2012).

Results

Gut content analysis

A total of nine food items were registered for *P. canaliculata*: detritus (unidentifiable organic matter), diatoms, macrophyte remains (fragments and seeds), invertebrate remains (legs, antennas, jaws, or chaetae), Chlorophyta, Charophyta, Cyanobacteria, Fungi, and Euglenophyta; and eight were found for *S. quadrata* (all the mentioned items except for Charophyta). The relative frequencies of food items are shown in Fig. 1. Although detritus was the dominant item for both species, its representation in the diet was significantly higher in the exotic species than in the native species (GLMM: $p < 0.001$, Table 1). In addition, the diet of *S. quadrata* was characterized by higher proportion of diatoms than that of *P. canaliculata* (GLMM: $p = 0.043$, Table 1), whereas *P. canaliculata*'s diet showed a higher frequency of macrophyte remains (GLMM: $p < 0.001$, Table 1). Macrophyte remains were present in the gut content of only one specimen of the exotic species. The diet of *P. canaliculata* contained

significantly more items, was significantly more diverse, and had lower dominance than the diet of *S. quadrata* (Table 1). The result of Schoener's Index was ecologically significant (SI = 0.73), indicating a diet overlap between *S. quadrata* and *P. canaliculata*.

Stable isotope analysis

Stable isotope signature value of $\delta^{15}\text{N}$ was significantly higher in *S. quadrata* (18.18 ± 1.36 ; $t = 5.171$, $df = 4$, $p = 0.007$) than in *P. canaliculata* (14.11 ± 0.04 , Fig. 2). The values of $\delta^{13}\text{C}$ (*S. quadrata* = -28.08 ± 0.76 , *P. canaliculata* = -27.46 ± 1.28 , $t = -1.014$, $df = 4$, $p = 0.368$), on the other hand, showed a similar use of resources, with high affinity for macrophytes, epipelton, and CPOM (Fig. 2).

The mean and standard deviations obtained from the Mix-Siar model analysis predicted the following contributions to the diet of *P. canaliculata* for each resource: macrophytes: 43.7% (± 16.9), epipelton: 20.6% (± 16.5), CPOM: 18.4% (± 14.6), FPOM: 17.2% (± 12.7); and for *S. quadrata*: macrophytes: 57.7% (± 21.4), epipelton: 14.8% (± 16.5); CPOM: 14.2% (± 15), FPOM: 13.3% (± 12.6). All the resources analyzed showed a considerable contribution (higher than 10%) to the diet of both species. Macrophytes were the resource with the highest contribution to the diet of both species. There was a significant overlap in the diet of *S. quadrata* and *P. canaliculata* (IDO = 0.86).

Discussion

Our study assessed the diet of an exotic species in its new distribution to estimate a possible diet overlap with a coexisting native species, by combining the gut content and stable isotopes analyses. The combination of these analyses allowed us to describe in detail the resource use by both

Fig. 1 Average relative frequency (Fi %) of food items in the gut contents of *P. canaliculata* and *S. quadrata* specimens

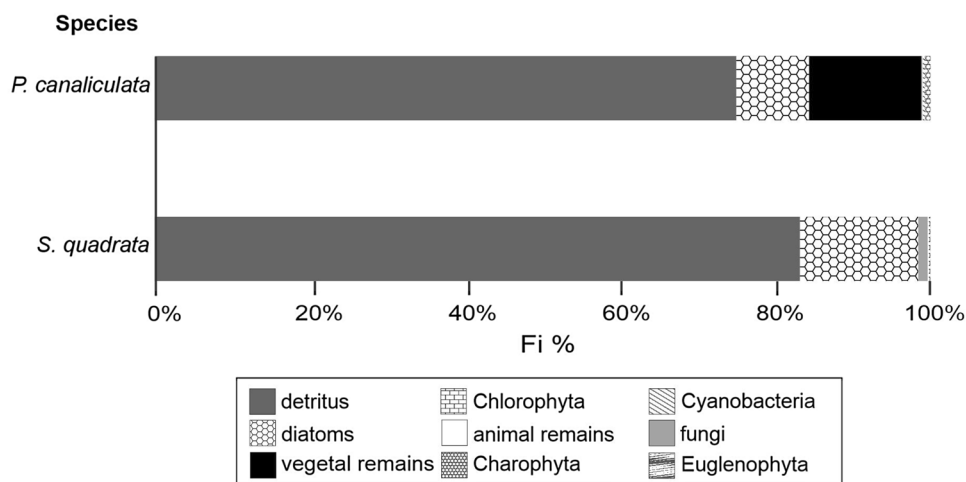


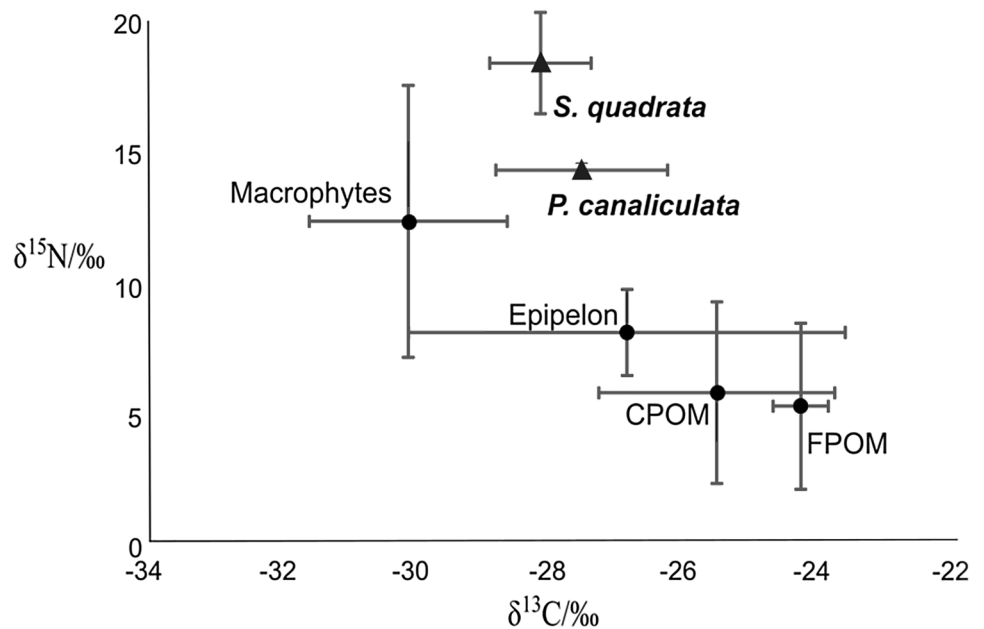
Table 1 Mean and standard deviation for each variable for both species

Response variable	<i>P. canaliculata</i>	<i>S. quadrata</i>	β	SE	<i>F</i>	<i>p</i> value
Food items relative frequencies						
Detritus	0.64 ± 0.24	0.83 ± 0.16	-0.246	0.060	16.760	<0.001*
Diatoms	0.09 ± 0.10	0.15 ± 0.14	-0.913	0.044	4.220	0.0433*
Macrophyte remains	0.25 ± 0.27	<0.01	0.427	0.061	49.280	<0.001*
Animal remains	0.00 ± 0.02	0.00 ± 0.01	0.013	0.012	1.110	0.295
Fungi	<0.01	0.01 ± 0.05	-0.017	0.018	0.910	0.343
Chlorophyta	<0.01	0.00 ± 0.01	0.001	0.008	0.030	0.870
Charophyta	0.01 ± 0.04	X	0.017	0.014	1.510	0.223
Cyanobacteria	0.00 ± 0.01	X	0.013	0.007	3.070	0.084
Euglenophyta	<0.01	<0.01	-3.47e-19	0.003	0.000	1.000
Food item indexes						
Shannon diversity	0.63 ± 0.28	0.38 ± 0.26	0.168	0.042	3.980	<0.001*
Dominance	0.62 ± 0.18	0.76 ± 0.18	-0.084	0.023	3.620	<0.001*
Pielou evenness	0.60 ± 0.17	0.63 ± 0.17	-0.017	0.022	0.790	0.433
Response variable	<i>P. canaliculata</i>	<i>S. quadrata</i>	β	SE	χ^2	<i>p</i> value
Richness	3.48 ± 1.15	2.52 ± 0.68	0.319	0.131	6.040	0.014*

Estimated (β), standard errors (SE), *F* and *p* values from the GLMM analysis with Gaussian (food items relative frequencies, Shannon diversity, dominance and Pielou evenness) and Poisson distribution (richness) between *S. quadrata* and *P. canaliculata* (df=77, n=80). X indicated the absence of that item in that species

*Significant differences between species ($p < 0.05$) are marked

Fig. 2 Stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) biplot of *S. quadrata*, *P. canaliculata* and basal resources. Dots and triangles represent average values and error bars indicate the standard errors



species since, while gut content analysis provided a snapshot of the individual's consumption, stable isotope analysis provided information about the assimilated materials (Nielsen et al. 2018). Therefore, although their separate interpretation indicated a diet overlap, a comprehensive examination of the results of both analyses allowed us to infer a differential use of resources by the species.

The stable isotope analysis evinced a high contribution of macrophytes to the diet of both species, suggesting diet overlap; however, we did not find vegetal remains in the gut content of *S. quadrata*. Conversely, we found a substantial amount of detritus. This could be explained by considering that the detritus consumed by this species probably originated from the decomposition of the macrophytes. This is in

agreement with Wolters et al. (2018), who stated that a possible route for the consumption of macrophyte-derived material might be the direct or incidental consumption of senescing macrophyte parts. As highlighted by other authors, the consumption of detritus and decaying macrophyte tissue is common in freshwater snails (Brönmark 1990; Madsen 1992; Qiu et al. 2011).

When aquatic ecosystems receive untreated wastewater discharges, like in the studied section of the stream, the environmental concentrations of $\delta^{15}\text{N}$ can increase, leading to a higher concentration of this isotope in the detritus (Hamilton et al. 2001; Morrissey et al. 2013; Smucker et al. 2018). Consequently, primary consumers that feed upon this resource tend to show higher values of $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen 1999), as recorded for *S. quadrata*. Therefore, the difference in $\delta^{15}\text{N}$ signal between both species supports the results of the gut content analysis, evidencing that detritus represents the most important food source for this exotic species. This is in accordance with Dudgeon and Yipp (1985), who classified *S. quadrata* as detritivore in its native range. Ovando and Cuzzo (2012), in contrast, mentioned this species as an herbivorous snail with a potential impact on the plant community in Argentina. However, their statement was not supported by a direct analysis of the diet of this species or a reference supporting that. On the other hand, the diet of *P. canaliculata* consisted mainly of detritus and macrophyte remains, in agreement with Kwong et al. (2010), Ocon et al. (2013), Hayes et al. (2015) and López van Oosterom et al. (2016). Kwong et al. (2010) found that this species was able to maintain a great proportion of macrophytes in its diet irrespective of seasonal changes in temperature, indicating that it forages on fresh macrophytes. Also, the higher food item richness and diversity show greater plasticity in the diet of *P. canaliculata* (López van Oosterom et al. 2016) than in that of *S. quadrata*.

The aforementioned differences between the diet of *S. quadrata* and *P. canaliculata* and the comprehensive examination of the results of both analyses allowed us to infer food partitioning between these sympatric species in a Pampean lowland stream. Such resource partitioning would allow both species to reduce interspecific competition and coexist. Several studies carried out in aquatic systems have demonstrated that species with similar ecological functions can coexist through the partitioning of food resources (Dubois et al. 2007; Novakowski et al. 2008; Borza et al. 2009). However, the possibility of overlapping with the native species due to other resources cannot be neglected. Miranda and Perissinotto (2012), for example, found a spatial overlap between *Tarebia granifera* and native gastropods. Other studies also reported that the increment in density of exotic snails, such as *P. antipodarum*, *Pomacea maculata*, and *P. canaliculata*, limited the growth of native species (Riley et al. 2008; Lysne and

Koetsier 2008; Kwong et al. 2010; Posch et al. 2013). Effects on the reproduction of native species have also been reported. Anto et al. (2005), for example, showed that the ampullaridae snail *Lanistes varicus*, limited populations of *Biomphalaria pfeifferi* by reducing the number of egg masses produced. In this context, and considering that bigger snail species can affect the smaller ones (Maldonado and Martin 2019), further studies are needed to assess overlap of other resources or other negative interactions that could affect, for example, growth or reproduction of native species.

In accordance with Miranda and Perissinotto (2012) and Nielsen et al. (2018), our findings demonstrate the importance of combining the gut content and the isotope analysis in this type of study. Both analyses are complementary, and their results allowed us to infer the origin of the detritus that *S. quadrata* was consuming. To conclude, the exotic species consumed macrophyte detritus while the native one ate fresh macrophytes. Because Pampean streams are autotrophic, macrophytes provide the main source of food as detritus upon death (Minshall 1978; Feijoó and Lombardo 2007). These resources are, in general, abundant in the streams of the region (López van Oosterom et al. 2013; Ocon et al. 2013) and may contribute to the successful establishment of *S. quadrata* in streams with similar characteristics. Additionally, as mentioned above, this exotic snail could affect local species in different ways. For this reason, we highlight the importance of continuing to study possible negative interactions between *S. quadrata* and other detritivore native species coexisting in its new areas of distribution.

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Data availability We affirm that the data support the results. In turn, laboratory and field standards were met.

Code availability Not applicable.

Declarations

Conflict of interest This research does not present conflict of interest and has not being considered for publication elsewhere.

Ethical approval Not applicable.

Consent to participate All the authors have fully participated in this manuscript and accept responsibility for it.

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