Limnologica 43 (2013) 91–99

Contents lists available at SciVerse ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Distribution of the apple snail *Pomacea canaliculata* in Pampean streams (Argentina) at different spatial scales

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ARTICLE INFO

Article history:
Received 5 January 2012
Received in revised form 1 June 2012
Accepted 1 June 2012
Available online 2 July 2012

Keywords:
Ampullariidae
Invasive
Encadenadas del Oeste basin
Habitat
Physic-chemical conditions
Extinction-colonization processes

ABSTRACT

Studies dealing with the distribution of freshwater mollusks in the Pampean plains are very scarce and have all focused on the determinants of their presence among different waterbodies. The aims of this study were to investigate the distribution of the apple snail *Pomacea canaliculata* among and within Pampean streams. The main sampling scheme included heterogeneous sections within different sites belonging to all the streams of the Encadenadas del Oeste basin (Buenos Aires Province), in which apple snails' presence and abundance as well as several environmental variables were recorded. *P. canaliculata* was present in long streams originating in the Piedmont area, with the exception of one that suffered extensive dredging works but it was absent in short streams originating in the plains. Lower altitudes and higher organic matter contents characterized the inhabited sites among the long streams. At a smaller scale, higher concentrations of Na^+ and lower levels of organic suspended matter characterized the inhabited sections. Within the short streams *P. canaliculata* was only found at sites located downstream from a connection to an inhabited long stream and hence constituted sink populations; short streams presented alkaline waters with high conductivity, very slow currents and no trees. The microhabitat of *P. canaliculata* was investigated at two sites from two different streams in which environmental variables were registered at individual snails' locations and at systematically distributed points. Apple snails were more frequently found in places located close to the shore, where current velocity was usually low, sediments fine and rich in organic matter, and macrophytes abundant. These variables were all correlated at this small scale thus making their individual interpretation difficult. All the streams in this basin appear to be habitable for *P. canaliculata*, but the populations would only persist autonomously in the medium and low reaches on the long streams. The distribution within long streams is probably governed by stochastic patterns of extinction-colonization as a consequence of the variability of the climatic and hydrological conditions in this region.

1. Introduction

Pomacea canaliculata (Lamarck, 1822) is an invasive freshwater snail (commonly known as golden apple snail) belonging to the Ampullariidae family whose natural range extends from de la Plata river basin southwards to the Encadenadas del Oeste basin (37°S, Buenos Aires province, Argentina), making it the southernmost apple snail in the world (Martín et al. 2001). During the '80s, this and three other species of the genus were introduced from multiple sites in Argentina into several Asian countries where it became a major pest of rice and other aquatic crops (Cowie 2002; Hayes et al. 2008). In addition, it has been shown that *P. canaliculata* can promote ecosystemic changes in natural wetlands resulting from the depletion of macrophytes and filamentous algae and an increase in phytoplankton biomass with an associated change in composition (Carlsson et al. 2004; Fang et al. 2010). This species is considered as one of the world's 100 worst invasive alien species on account of all these attributes (Lowe et al. 2000). *P. canaliculata* and *Pomacea insularum* have also been detected in southern United States, where they could compete with native congeners and many areas are still susceptible to invasion (Rawlings et al. 2007; Karatayev et al. 2009). Recently, *P. canaliculata* and *P. insularum* were reported in Chile (Letelier and Soto-Acuña 2008; Jackson and Jackson 2009) and Europe (López et al. 2010), respectively, for the first time, suggesting that apple snails are still expanding worldwide. Rawlings et al. (2007) highlighted the need of niche models for aiding the prediction of *Pomacea* distribution in invaded areas but a mechanistic niche model had only been developed for *P. canaliculata* at a microhabitat scale (Seuffert and Martín 2010).

Typically, studies about the distribution of freshwater invertebrates are designed at three different spatial scales: among streams, within each stream and at the microhabitat (Crowl and Schnell

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http://dx.doi.org/10.1016/j.limno.2012.06.002

1990). Studies dealing with the distribution of freshwater mollusks in Pampean streams are very scarce (Martín et al. 2001; Tietze and De Francesco 2010; Hassan et al. 2011) and were all focused on the presence or the absence among different waterbodies. Aquatic vegetation is one of the main forces spatially structuring the biological communities within Pampean streams and the big-sized apple snails of the genus *Pomacea* are probably one of the main consumers of submersed macrophytes (Giorgi et al. 2005).

Factors determining the presence of *P. canaliculata* in both lotic and lentic waterbodies have been studied in the center and south of Buenos Aires province, where it generally inhabits shallow, quiet and turbid sites with low $Na^+/(K^+ + Mg^{++})$ ratios (Martín et al. 2001). The distribution of this species among different waterbodies was also investigated in Hong Kong two decades after its introduction, where the inhabited sites were characterized by their high levels of phosphate and alkalinity (Kwong et al. 2008). However, the determinants of the distribution of freshwater gastropods usually differ according to the spatial scale being considered (Lodge et al. 1987; Crowl and Schnell 1990). Studies on *P. canaliculata* at the microhabitat level are even scarcer than those at higher levels and have been conducted in artificial or heavily modified environments in invaded areas (Ichinose et al. 2000; Ito 2002; Teo 2004). Knowledge of the factors limiting the distribution of invasive species is essential for determining their potential ranges in invaded areas and for the development of efficient management strategies (Guo 2006).

P. canaliculata has been considered a lentic dweller but it is also capable of inhabiting lotic systems and channels (Martín et al. 2001; Ito 2002; Kwong et al. 2008), environments which are favorable for the active and passive dispersal of this and other apple snails in invaded regions. Downstream dispersal is probably a result of individual drift and would be enhanced by water velocity (Seuffert and Martín 2012); open flume experiments showed that these snails are able to withstand fast currents during short periods although at the expense of a behavioral limitation (siphon extension for lung ventilation, crawling direction and velocity, etc.). Knowledge of the factors affecting the distribution of *P. canaliculata* in lotic waterbodies would be helpful for understanding and controlling its dispersal.

The habitat of *P. canaliculata* in its native range has only been described qualitatively (Martín et al. 2001) and quantitative information of the prevailing environmental conditions in inhabited sites is very limited. The streams of the Encadenadas del Oeste basin show a marked gradient of some environmental variables in relatively short sections, making them suitable for studying the use of different microhabitats. Three variables have been recognized as "universal" for lotic freshwater snails: current velocity, depth and substratum type (Utzinger et al. 1997a). *P. canaliculata* presents singular features such as cleidoic aerial egg masses (Pizani et al. 2005), obligatory aerial respiration (at least under certain conditions, Seuffert and Martín 2009, 2010) and a macrophytophagous habit (Estebenet 1995) which suggest that other environmental variables might also be important for microhabitat use in this species. Hitherto, only the influence on microdistribution of the dependence on aerial respiration has been demonstrated (Seuffert and Martín 2010).

The aims of this study were to investigate the determinants of the distribution of *P. canaliculata* at different spatial scales in order to describe its habitats and microhabitats among and within the streams of the Encadenadas del Oeste basin. Based on the results found in previous studies (Martín et al. 2001; Seuffert and Martín 2010, 2012) we hypothesized that physicochemical characteristics of water and current velocity are among the variables influencing the distribution at a higher scale and that distance to a substratum suitable to ventilate the lung and current determine the microhabitat of this species.

2. Materials and methods

2.1. Study area

The sampling area extended from 36°56′S to 37°41′S and from 61°43′W to 62°39′W in the southwest of Buenos Aires province, Argentina (Fig. 1). The climate is semi-arid with an average annual rainfall of 733 mm, mainly concentrated in autumn and spring. The average annual temperature is 13.8 °C with a mean range of 15.1 °C. The Encadenadas del Oeste basin comprises a series of lakes in which the conductivity increases from east to west (IATASA 1994); all of them are very salty and are not inhabited by *P. canaliculata* (Martín et al. 2001; Martín and Estebenet 2002) except for the most eastern one (Alsina lake). It is an endorheic basin with a pluvial hydrological regime that is supplied by a group of streams that run in a south-north direction from the Ventania mountains; after rainy years this basin becomes connected to the Vallimanca stream, an affluent of the Salado river basin which flows into the mouth of de la Plata river.

The streams of the Encadenadas del Oeste basin are characterized by scant and highly variable water discharge. From a geomorphological viewpoint two different groups can be distinguished among these streams: long streams that originate near the Ventania mountains (Pigüé, Guaminí, Curamalal Grande and Sauce Corto) and short streams originating from the water table within the plains, between the mountains and the lakes (Venado, Malleo Leufú, Cochicó Chico and Pescado). Most of the short streams are figured as intermittent on official topographical maps, although the interruption of the flow is not seasonal but sporadic (after several years of drought). None of these streams was found to be totally dry during several surveys performed between 1998 (Martín et al. 2001) and the present study.

Sampling was conducted during February 2007 since the highest levels of copulas and ovipositions have been recorded during this month (Burela et al. 2004; Pizani et al. 2005). During the breeding season (October–April), the pink aerial egg masses of this species are clear evidence of the presence of apple snails, even at low densities (Martín et al. 2001).

2.2. Distribution among and within streams

The sampling scheme included all the lotic waterbodies belonging to the Encadenadas del Oeste basin, composed entirely of first order streams (according to the Strahler Number); as follows (from west to east): Pigüé (PI), Venado (VE), Guaminí (GU), Malleo Leufú (ML, an affluent of Guaminí stream), Cochicó Chico (CC), Curamalal Grande (CG), Pescado (PE) and Sauce Corto (SC); and also an artificial channel connects the Pigüé and Venado streams (Fig. 1).

We sampled 1–5 evenly distributed sites along the course of each stream, depending on its length and accessibility; the sites considered as inhabited by *P. canaliculata* were those where eggs masses or live snails were found after a preliminary inspection from the shores. At sites with *P. canaliculata* populations we sampled 2–3 sections of ca. 25 m located within less than 500 m, which were selected to represent the diversity of habitats (pools, riffles, etc.); at sites without *P. canaliculata* only one section was sampled. Sampling comprised a total of 39 sections from 26 sites distributed within the eight streams.

At each section, two people carefully inspected both shores while wading upstream in search for egg masses on the emergent aquatic vegetation and other substrata; apple snails were searched for among the submerged vegetation, under stones or buried in the substratum. The relative abundance of apple snails was estimated by reference to standardized search effort (number of snails caught per hour per operator and number of egg masses per meter of shore; Martín et al. 2001).

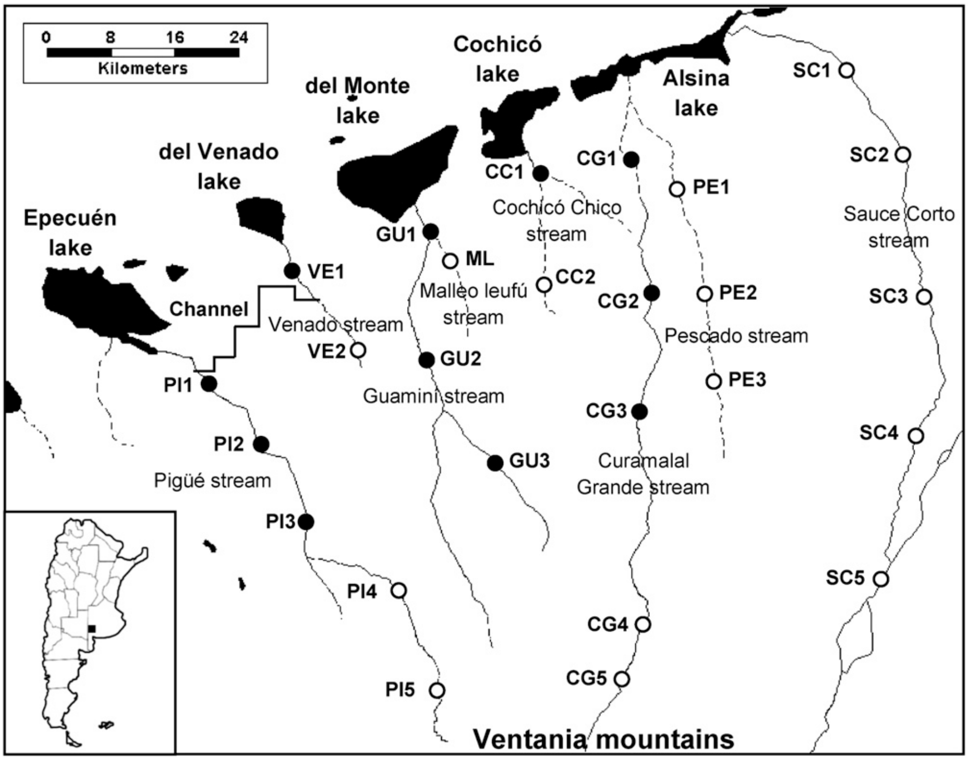

Fig. 1. Map of the Encadenadas del Oeste basin showing the location of sampling sites ($n = 26$); full and empty circles indicate sites inhabited and uninhabited by *P. canaliculata*, respectively. The streams surveyed were (from west to east): Pigüé (PI), Venado (VE), Guaminí (GU), Malleo Leufú (ML), Cochicó Chico (CC), Curamalal Grande (CG), Pescado (PE) and Sauce Corto (SC).

We recorded the presence of other species of freshwater snails and the richness and cover (%) of submerged, floating and emergent macrophytes and visually estimated the tree cover (%) above the water. We also recorded the following environmental variables: mean section width (m), depth (m) and current velocity ($\mathrm{m\,s^{-1}}$; with a digital flowmeter FP101 Global Water®) in the middle of the section; pH, conductivity ($\mathrm{mS\,cm^{-1}}$), turbidity (NTU) and temperature (°C) were determined in situ with a multimeter (Horiba® U-10). A subsurface water sample was collected and fixed with formaldehyde for posterior chemical analyses. The concentrations ($\mathrm{mequiv\,l^{-1}}$) of Na^+, K^+, Ca^{++}, Mg^{++} and $SO_4{}^=$ were measured with an inducted plasma emission spectrometer (Shimadzu ICPS 1000-III) and the concentrations of Cl^-, $NO_3{}^-$ and $PO_4{}^{\equiv}$ were measured by titration. Suspended organic matter ($\mathrm{g\,l^{-1}}$) was determined by filtering a one liter water sample through 1.2 μm pore glass microfiber filter and calculating the difference between the organic dry weight (obtained after 24 h in an oven at 70 °C) and the dry weight of ashes (obtained after incineration in a muffle furnace at 500 °C during 30 min). In addition, a substratum sample was collected to determine its organic matter content (% of total weight) as the difference between the total dry weight (obtained after 72 h at 75 °C) and the dry weight of ashes (obtained after incineration at 500 °C during 3 h).

The dominant substratum was characterized on an arbitrary scale according to the size of particles: 1 (sapropel, mud), 2 (sand), 3 (gravel), 4 (pebbles, boulders) and 5 (limestone). The trophic resource availability was coded as 0 (nil), 1 (low), 2 (medium), 3 (high) and 4 (very high) by visual estimation of the abundance of macrophytes, algae, riparian vegetation and debris. The altitude (m) and slope (%) of each site were obtained using Google Earth©.

The association of environmental variables with the presence of *P. canaliculata* was evaluated by stepwise discriminant analysis (Martín et al. 2001, 2005) that produces a linear combination of variables maximizing distances between groups of inhabited and uninhabited sites. The variables were included one by one according to their individual discriminant power and they were kept or removed after assessing whether they improved the total discriminatory power or not. For the analysis among streams and at the site level the average of the values recorded at the section level was used for all variables except substratum, which was only considered in the analysis at section level. For the inhabited sites, the relationship between environmental variables and the density of apple snails and egg masses was explored using a multiple linear regression analysis.

2.3. Microhabitat characterization

Sampling was conducted during February 2008 in a section of the Pigüé stream (within site PI1 of the previous sampling) and a section of the Guaminí stream (within site GU2), which were selected on the basis of the high density of apple snails and diversity of microhabitats. The sections were around 50 m in length (i.e. they comprise more than one of the sections of the previous sampling), with a maximum width between 7.8 and 8.9 m, a maximum depth of 1.0–1.5 m and a current velocity varying between 0 and $1.61\,\mathrm{m\,s^{-1}}$.

In each section, *P. canaliculata* snails were searched for visually (with a diving mask) or by touch covering the entire reach in an upstream direction; all snails found were measured in situ with a Vernier caliper. We recorded depth (m), distance to the shore and to the nearest emergent substratum (boulder, log, snag, macrophyte or the shore, m) and mean current velocity ($\mathrm{m\,s^{-1}}$) at the point where each snail was found; the threshold measurement of the flowmeter is $0.1\,\mathrm{m\,s^{-1}}$ so any current velocities below that value were considered as zero. The dominant substratum types were also recorded; inorganic substrata were categorized using an ordinal scale according to particle size: 1 (sapropel and silt), 2 (sand and gravel), 3 (pebbles and boulders) and 4 (limestone). Organic

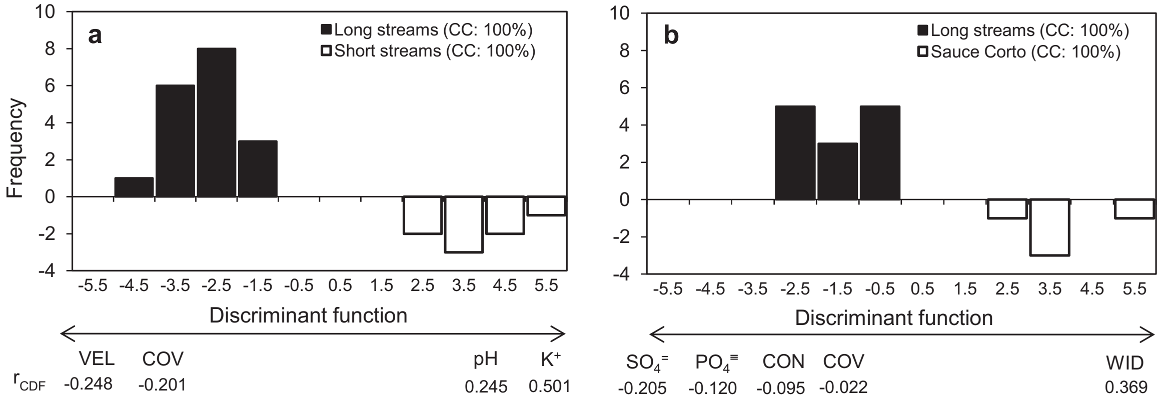

Fig. 2. Frequency histograms of discriminant scores for: (a) sites on the long streams (Pigüé, Guaminí, Curamalal Grande and Sauce Corto; $n = 18$) and short streams (Venado, Malleo Leufú, Cochicó Chico and Pescado; $n = 8$) and (b) sites on Sauce Corto stream ($n = 5$) and sites on the remaining long streams ($n = 13$) (CC: percentage of correctly classified cases; r_{CDF}: correlation between discriminating variables and canonical discriminant function; VEL: current velocity; COV: tree cover; CON: conductivity; WID: width).

substrata were categorized with an arbitrary scale: 1 (no organic substratum), 2 (submerged macrophytes (*Potamogeton* sp.), algae, moss), 3 (emergent macrophytes (*Hydrocotyle bonariensis*)) and 4 (roots and debris). The day after sampling the apple snails, the same environmental variables were recorded at systematic points spaced 1–1.5 m apart and located on 22 transects evenly distributed along the reach in order to estimate the availability of points with different characteristics (Utzinger and Tanner 2000).

Kolmogorov–Smirnov tests and χ^2 independence tests were performed for continuous and discrete variables, respectively (Utzinger and Tanner 2000) to test for differences between the frequency distribution of environmental variables recorded at points with apple snails and at systematic points. The differential use of microhabitat types was estimated using an adaptation of Jacobs' Index (Utzinger et al. 1997a):

$$D = \frac{r - p}{(r + p) - 2rp}$$

where r is the proportion of snails found in a certain microhabitat category and p is the proportion of available points with that microhabitat category; the continuous variables were divided in classes. D varies between 1 and -1, where the positive and negative values indicate that the microhabitat type is used in a greater or lesser proportion, respectively, relative to its availability and the values close to zero when it is used according to its availability.

3. Results

3.1. Distribution among and within streams

We recorded five other species of snails at the sampling sites ($n = 26$), the most common being *Chilina parchappii* (Chilinidae), *Biomphalaria peregrina* (Planorbidae) and *Gundlachia concentrica* (Ancylidae), while *Heleobia parchappii* (Hydrobiidae) and *Physa* sp. (Physidae; probably an introduced species) were occasional. The presence of *P. canaliculata* at the site level was independent of the presence of the three most common species (χ^2 independence tests, $p > 0.192$ in all cases); the lower expected frequencies obtained for the two rarer species precluded the execution of the independence test in both cases.

A differential pattern of *P. canaliculata* distribution among the long and short streams was quite evident when the map of the Encadenadas del Oeste basin (Fig. 1) was observed. Three out of the four long streams were inhabited by *P. canaliculata* at different sites along their courses. In contrast, *P. canaliculata* was only recorded at two sites among the short streams: VE1 and CO1, both being connected to inhabited sites on the long streams (Pigüé-Venado channel and Curamalal Grande stream, respectively; see section 'Discussion'). A discriminant analysis (considering the information recorded at site level) revealed that higher concentrations of K^+ and a more alkaline pH as opposed to a higher current velocity and tree cover characterize short and long streams, respectively (Wilks' $\lambda = 0.122$, $\chi^2 = 46.331$, $p < 0.0001$, canonical correlation = 0.937; Fig. 2a). The same variables discriminated among short and long streams when the information obtained at section level was considered (Wilks' $\lambda = 0.178$, $\chi^2 = 60.468$, $p < 0.0001$, canonical correlation = 0.907).

P. canaliculata snails were not recorded at any of the five sites sampled along the Sauce Corto stream, the only uninhabited long stream in the study area. These sites were discriminated from the sites on the other long streams by the section width in opposition to the concentrations of $SO_4^=$ and $PO_4^{\equiv}$, conductivity and tree cover (Wilks' $\lambda = 0.150$, $\chi^2 = 25.622$, $p < 0.0001$, canonical correlation = 0.922; Fig. 2b). When considering the information recorded at section level, the variables included in the discriminant analysis reduced to section width as opposed to concentration of $SO_4^=$ (Wilks' $\lambda = 0.511$, $\chi^2 = 16.786$, $p < 0.0001$, canonical correlation = 0.699). Sauce Corto stream showed a clearly higher mean section width relative to the other long streams (10.82 m and 5.73 m, respectively); the sites of this long stream without *P. canaliculata* were excluded from further analyses since its absence was apparently related to anthropogenic activities (see section 'Discussion').

Therefore, for the characterization of the sites and sections with and without *P. canaliculata* within streams, we only considered information recorded in the three long streams inhabited by this species. *P. canaliculata* was recorded in highly variable densities (from 1.58 to 153 snails h^{-1} operator^{-1}); at four sites (PI4, PI5, CG4 and CG5) we did not find any snails or eggs of *P. canaliculata*, whereas we found eggs (0.4 egg masses m^{-1}) at one site (CG2) but were unable to find any live snails (this site was considered as inhabited). The substratum organic matter content as opposed to altitude characterized the sites with and without *P. canaliculata*, respectively (Wilks' $\lambda = 0.183$, $\chi^2 = 17.005$, $p < 0.0001$, canonical correlation = 0.904; Fig. 3a). The mean altitude of the inhabited and uninhabited sites was 171 and 310 m, respectively, while the levels of substratum organic matter were 7.60 and 5.73%, respectively.

In order to characterize the places with and without *P. canaliculata* at a smaller scale, the sections we considered as inhabited were those in which we found living specimens and not only egg masses. Higher concentrations of Na^+ as opposed to higher levels

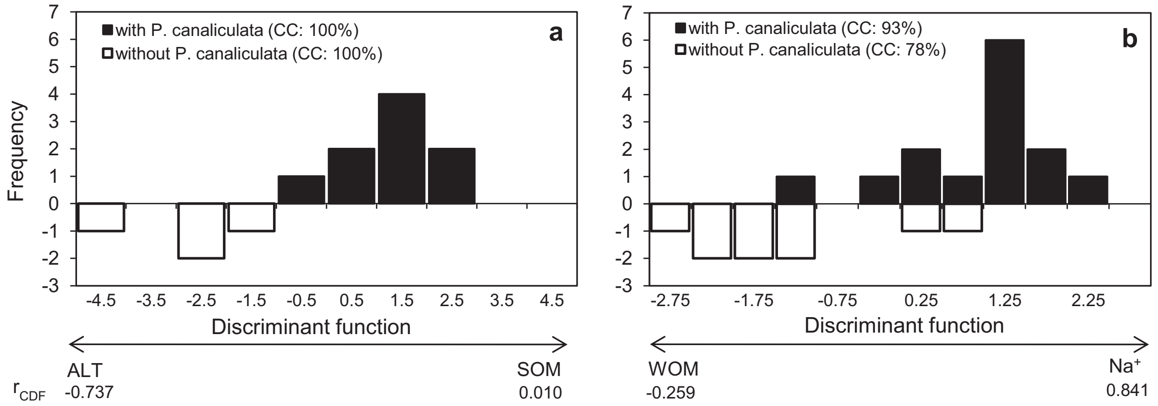

Fig. 3. Frequency histograms of discriminant scores for: (a) sites inhabited ($n = 9$) and uninhabited ($n = 4$) by *P. canaliculata* and (b) sections inhabited ($n = 14$) and uninhabited ($n = 9$) by *P. canaliculata* (CC: percentage of correctly classified cases; r_{CDF}: correlation between discriminating variables and canonical discriminant function; ALT: altitude; SOM: substratum organic matter content; WOM: water suspended organic matter).

of volatile suspended matter characterized the sections with and without *P. canaliculata*, respectively (Wilks' $\lambda = 0.441$, $\chi^2 = 16.384$, $p < 0.0001$, canonical correlation = 0.748; Fig. 3b). The mean concentrations of Na^+ for the inhabited and uninhabited sites were 5.95 and 2.78 mequiv l^{-1}, respectively, while the values of volatile suspended matter were 0.0066 and 0.0081 g l^{-1}, on average.

Despite the large variation in snail density recorded at the different sites (mean: 48.3 snails h^{-1} operator^{-1}, range: 1.6–153 snails h^{-1} operator^{-1}), this variable was not affected by any of the environmental variables recorded. In contrast, the density of eggs (mean: 2.2 egg masses m^{-1}, range: 0.7–9.84 egg masses m^{-1}) was positively correlated with the concentration of $PO_4^{\equiv}$ ($F_{1,18} = 12.330$, $p = 0.0025$, $R^2 = 0.407$). However, a graphical analysis revealed the existence of four possible influential points; indeed, after eliminating those points the regression was not significant ($F_{1,16} = 1.217$, $p = 0.2886$). On the other hand, the density of egg masses did not correlate with the density of snails (Spearman nonparametric correlation: $\rho = 0.326$, $p = 0.2013$) nor with the density of females ($\rho = 0.541$, $p = 0.1063$).

3.2. *Microhabitat characterization*

A total of 60 snails (shell length: 21–47 mm) were found in the section within site PI1 and 81 snails (shell length: 22.5–53 mm) in the section within GU2. The water temperature fluctuated between 19.4 and 22.9 °C during sampling and the aquatic vegetation present in the sections consisted mainly of *Potamogeton* sp., *H. bonariensis*, an unidentified Brassicaceae, the rodophyte *Batrachospermum* sp. and green filamentous algae.

We found no differences between the depths recorded at the points with snails and the systematic points in any of the two sections sampled ($p > 0.06$; Fig. 4a and b). The mean depth was 0.47 m and reached a maximum of 1.5 m in the Pigüé stream.

In both sections, mean current velocity was significantly lower ($p < 0.001$) at the points occupied by snails than at those located systematically (0.029 and 0.401 m s^{-1}, respectively, $Z = 3.756$ for PI1; 0.068 and 0.312 m s^{-1}, respectively, $Z = 2.508$ for GU2). In PI1, all snails were found at points where current velocity was below 0.3 m s^{-1} and in 81.7% of the points velocity was zero (Fig. 4c), while in GU2 most snails (96.3%) were also located below 0.3 m s^{-1} and the points with higher velocities were used in a clearly smaller proportion than was available (Fig. 4d). At the systematic points, current velocity reached a maximum of 1.61 m s^{-1}, with velocities greater than 0.63 m s^{-1} only being recorded in shallow places with coarse substratum (pebbles and boulders) and *Potamogeton* sp.

In PI1 section, snails were recorded at a greater frequency than expected when associated with sapropel (73% of the cases) and lower than expected at points with sand, gravel and limestone ($\chi^2 = 56.46$, $p < 0.001$); no pebbles or boulders were present in this section (Fig. 4e). In GU2 the snails also showed a positive association with the points with sapropel, while the points with pebbles and boulders were less used in relation to their availability ($\chi^2 = 42.37$, $p < 0.001$; Fig. 4f); the points with sand or gravel and limestone were used according to their availability.

In PI1, snails were more frequently associated with submerged macrophytes and algae, while at points without organic material they were scarcer ($\chi^2 = 31.51$, $p < 0.001$; Fig. 4g); no emergent macrophytes were recorded in this section. In GU2, snails were recorded at a higher frequency at points with emergent macrophytes, roots and organic debris; at points with submerged macrophytes they were less frequent than expected ($\chi^2 = 28.11$, $p < 0.001$; Fig. 4h). In most cases (95.2%), submerged macrophytes were found at shallow points with pebbles and boulders, characterized by the highest current velocities.

The distances to the shore and to the nearest emergent substratum recorded for the snails were significantly lower than those recorded for the systematic points ($Z = 2.978$ and $Z = 1.697$, respectively, for PI1, $Z = 1.368$ and $Z = 3.511$, respectively, for GU2; $p < 0.05$ in all cases; Fig. 4i and j). In both sections, most snails were found at less than 1 m from the shore and at less than 0.5 m from the nearest emergent substratum; 61.7% of the snails were located upon some emergent substratum (i.e. the distance was zero), mostly macrophytes.

4. Discussion

A fact that may hamper the understanding of the factors that determine the distribution of organisms is a non-equilibrium state due to continued expansion, as may occur in recently invaded areas for *P. canaliculata* (Kwong et al. 2008). No paleontological record of mollusks are available for the Encadenadas del Oeste basin, but its past hydrological connection to the *P. canaliculata* realm (de la Plata river basin; Malagnino 1989; Martín and Estebenet 2002; Martín and De Francesco 2006) and the widespread occurrence of *P. canaliculata* (Martín et al. 2001; this study) both suggest an ancient presence in this basin.

At the site level, *P. canaliculata* was not associated with any of the three widespread species of pulmonate snails that inhabit this basin. This may be the result of the wide tolerance ranges of these snails (Tietze and De Francesco 2010) and the peculiar

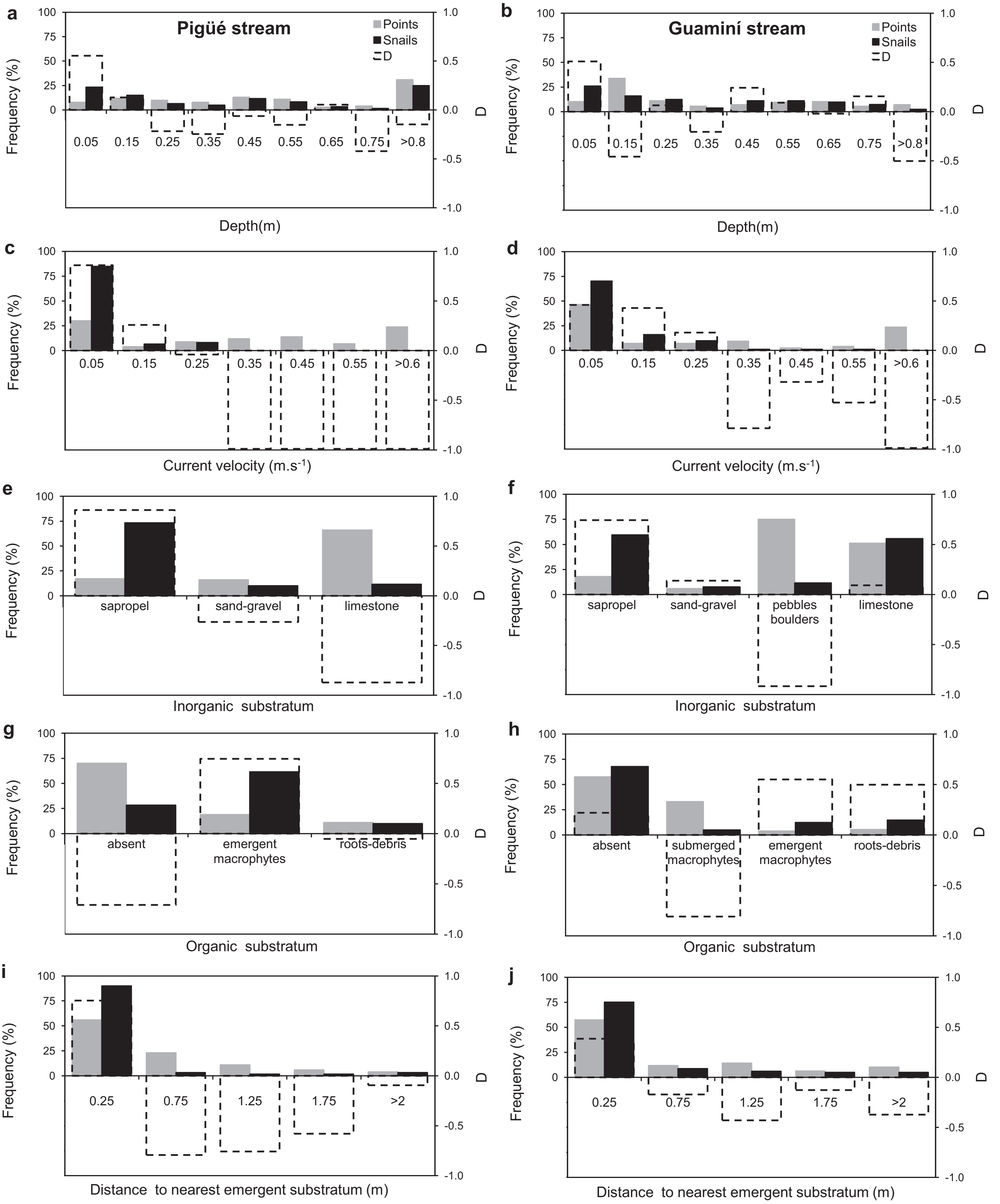

Fig. 4. Microhabitat variables recorded in the Pigüé (left) and Guaminí (right) streams. Gray bars show the frequencies recorded for the systematic points and black bars the frequencies for the snails; the dotted bars correspond to Jacobs' index (*D*).

ecophysiological features of *P. canaliculata*, such as aerial egg masses and a macrophytophagous habit.

P. canaliculata was generally found in the long streams of the Encadenadas del Oeste basin while the short streams were rarely inhabited by this species. Short streams were characterized by higher concentrations of K^+, more alkaline pH, very low or nil current velocities and the absence of trees on the margins. The waterbodies of this basin receive important underground discharges through salty halomorphic soils (Montesarchio 1989; IATASA 1994; González Uriarte and Orioli 1998), being of relatively greater importance for the short streams, which present less rocky and less steep catchment areas. These streams rarely dry out but the flow can become very scarce, especially after severe droughts. The levels of K^+ per se are probably not one of the main detrimental chemical conditions of the short streams but perhaps its high concentration reflects the higher values of conductivity prevailing in these streams as compared to the long ones (2.36 vs. 0.90 mS cm^{-1}, on average). The complete absence of trees on the margins also suggests that the soil or groundwater close to these streams is of very poor quality. The lack of shade would explain the higher water temperatures that the short streams may attain in summer as compared to long streams; the extreme temperatures were high enough to inactivate the snails in the Cochicó Chico stream but not in the Curamalal Grande (36.2 and 31.1 °C, respectively; Seuffert et al. 2010).

In contrast to the situation reported here, sites inhabited by *P. canaliculata* in Hong Kong have been characterized by high alkalinity (Kwong et al. 2008). However, the mean pH recorded in the streams of the semiarid temperate Encadenadas del Oeste basin was 9.2 while the mean pH in the waterbodies of the humid subtropical Hong Kong territory was only 6.7. This marked difference reflects the contrasting chemical conditions found in the surface water in both places and highlights the importance of understanding the local conditions that influence the snails' distribution since they may differ greatly in different inhabited regions worldwide.

Only two sites among the short streams were inhabited by *P. canaliculata* and both were located downstream from a connection to inhabited sites (Curamalal Grande stream, and the Pigüé-Venado channel). The short streams Pescado and Malleo Leufú were uninhabited even though both streams drain into waterbodies where *P. canaliculata* is present; the same situation occurs in the upper sections of Venado and Cochicó Chico streams. This lack of colonization is probably related to the combined effects of unfavorable conditions found in these short streams and the lack of positive rheotaxis in this species (Seuffert and Martín 2012).

The most extreme values of conductivity and concentration of ions were recorded at site CC1 on the Cochicó Chico stream that, nonetheless, showed a relatively high density of *P. canaliculata* (27 snails h^{-1} $operator^{-1}$). The conductivity at this site during sampling (4.27 mS cm^{-1}) was significantly higher than the maximum conductivity reported for inhabited sites in this area (2.89 mS cm^{-1}, Martín et al. 2001), indicating that this species is even more tolerant, at least to peaks of conductivity or to a rapid change in this parameter (Martín and Estebenet 2002). The highest levels of pH were recorded in the Venado stream, reaching values of up to 9.94 in VE1; at this site *P. canaliculata* was recorded at a very low density (only four snails). Moreover, in subsequent visits to site CC1 we could not find any live apple snails or egg masses. Therefore, it is likely that *P. canaliculata* would be able to survive and reproduce in both streams during a relatively short period, but unfavorable conditions make them adverse environments for long term colonization and subsequent dispersal. From the evidence found in the Cochicó Chico and Venado streams we conclude that the snails from sites CC1 and VE1 constitute sink populations and their persistence would depend on the downstream immigration of individuals from source populations.

P. canaliculata populations were recorded in all the long streams, with the exception of Sauce Corto, characterized by its greater width and its lower levels of $SO_4^{=}$, $PO_4^{\equiv}$, conductivity and tree cover. However, it seems possible that the absence of apple snails and also some of these features result from the dredging works that took place along 90% of its length between 1960 and 1972 to increase the discharge capacity during flooding (Dirección Provincial de Saneamiento y Obras Hidráulicas, Provincia de Buenos Aires). These operations, which were only applied to the Sauce Corto stream in this basin, involved a large movement of sediments and an extended "smoothing" of the margins, probably reflected in its wider channel and the scarcity of riparian trees. At the time of sampling, a dense population of *P. canaliculata* was found in a nearby man-made channel with scarce stagnant water, located at less than 200 m to the east of site SC1. From this information we deduced the presence of snails prior to the dredging works in this sub-basin and hypothesized that the direct impact (mass remotion of snails) and the resulting increase in current velocity (especially during floods) contributed to the gradual extinction of *P. canaliculata* populations from the Sauce Corto stream.

P. canaliculata was not found in reaches of higher altitude of the long streams. Its absence from the headwaters was also reported in a Brazilian subtropical stream (Pereira et al. 2011) and it was also more frequent in wetlands located at low altitudes in southern Brazil (Maltchik et al. 2010). Martín et al. (2001) found that eight out of the 11 sites uninhabited by *P. canaliculata* (located in the northern slopes of Tandilia and Ventania mountains) were in proximity of the headwaters. Intense floods are common in this region and heavy rainfall over a short period of time might result in the local eradication of *P. canaliculata* populations (Martín and Estebenet 2002; pers. obs.). Indeed, the headwaters of the streams are the most affected sites when precipitation falls in the mountain area and, consequently, they would not constitute favorable habitats for the persistence of this species.

The inhabited sites by *P. canaliculata* within the long streams showed a higher mean content of organic matter though there was no evidence of a threshold minimum value since the lowest records were similar in both the inhabited and the uninhabited sites (1.66% and 1.78%, respectively). On the other hand, some sites presented relatively high organic matter contents (e.g. 5.73% in CG5) but had no snails, though this might be due to the lack of colonization or to local extinction processes. At the microhabitat level, *P. canaliculata* was also generally associated with substrata rich in organic matter (i.e. sapropel, see below). It has been shown that the density of *P. canaliculata* is correlated with water chemical oxygen demand (Ichinose et al. 2000) indicating some tolerance, if not preference, for sites with high organic and nutrient loads.

The higher concentrations of Na^+ in the inhabited sections does not seem to be a determinant for the presence of *P. canaliculata*, since the levels recorded in the long streams (0.89–7.87 mequiv l^{-1}) fall within the range previously described as habitable for this species in southern Buenos Aires province (0.85–19.84 mequiv l^{-1}; Martín et al. 2001), with the exception of an uninhabited site on the Curamalal Grande stream (CG5, where the concentration of this ion was only 0.36 mequiv l^{-1}). In contrast to Ca^{++}, the concentration of Na^+ has not usually been considered as a determinant of the distribution of freshwater gastropods (e.g. Lodge et al. 1987; Crowl and Schnell 1990; Utzinger et al. 1997b), but *P. canaliculata* is a hyperionic regulator and Na^+ is the first ion in importance in its plasma (Cueto et al. 2011). Therefore, within habitable waterbodies with low electrolytic content, those with higher levels of Na^+ would implicate lower energetic costs when it is incorporated into the plasma.

The significance of the lower levels of suspended organic matter in the inhabited sections is not clear but may also reflect the absence of snails near the headwaters, where turbulence is higher and hence more substratum particles become suspended, including organic material. The dissimilar models selected for at the section and site levels are probably due to multicolinearity among independent variables (for instance, the concentration of Na^+ and altitude are negatively correlated; $r = -0.592$, $p < 0.010$).

In the Encadenadas del Oeste basin, egg masses are a good indicator of the presence of *P. canaliculata* (Martín et al. 2001) but apparently not of the densities of snails or females since there was no relationship with the density of egg masses. A similar situation was described for *Pomacea paludosa*, suggesting that the number of egg masses is not a reliable index of the density of snails due to its high variability and to the influence of variables such as temperature and vegetation on oviposition (Darby et al. 1997). On the other hand, snail density or catchability may be affected by short term variation in some environmental factors, such as high water discharge or extreme temperatures (Seuffert et al. 2010), that have a minor influence on egg masses (Pizani et al. 2005; Dreón et al. 2006).

At the microhabitat level, the points occupied by *P. canaliculata* individuals differed in all the environmental variables recorded in relation to their availability, with the exception of depth. A decrease in density with water depths greater than 0.5 m has been reported for *P. canaliculata* in Japan (Ichinose et al. 2000), *P. paludosa* (Darby et al. 2002) and *P. insularum* (Burlakova et al. 2010). Even though we recorded deeper water in some places than those mentioned above, the mean depth for all the systematic points was only 0.47 m. It is probable that depth is not a determinant for habitat use in the streams of the Encadenadas del Oeste basin since most of them are shallow waterbodies.

In our study apple snails were most frequently recorded in places located close to the shore that were also characterized by lower current velocities, fine inorganic substratum rich in organic matter and abundance of macrophytes. However, as all these variables are naturally correlated at a small spatial scale in the streams, it is difficult to interpret their effects separately. Experimental studies with *P. canaliculata* have only dealt with some of these variables, such as the influence of access to atmospheric air on individual performance (Seuffert and Martín 2010) and its resistance to current (Seuffert and Martín 2012). From the evidence found by Seuffert and Martín (2010) it can be inferred that the association of snails with microhabitats in proximity of the shore or with available emergent substrata is due, at least in part, to the periodical need to ventilate the lung, as was also suggested for *P. paludosa* (Darby et al. 2002; Karunaratne et al. 2006).

Current velocity may have an important role in habitat use, since strong currents can provoke the detachment of snails or the substratum where they lie (Seuffert and Martín 2012) and this could cause death by crushing or abrasion, a decrease in population size (Lysne and Koetsier 2006) or a shift to unfavorable habitats (Holomuzki and Biggs 2006). In a laboratory flume it was determined that *P. canaliculata* can withstand current velocities of up to $1.64\,\mathrm{m\,s^{-1}}$ (albeit during a few minutes; Seuffert and Martín 2012). However, almost all snails in both streams were found at points with current velocities below $0.3\,\mathrm{m\,s^{-1}}$. Similarly, Ichinose et al. (2000) reported that the density of *P. canaliculata* decreases to almost zero in places with velocities greater than $0.5\,\mathrm{m\,s^{-1}}$. In Brazil, *Pomacea* sp. is mainly found in lentic habitats or in places with low current velocities in the inhabited lotic waterbodies (0.2–$0.3\,\mathrm{m\,s^{-1}}$; Camargo Maia 2005; Giovanelli et al. 2005). Therefore, in spite of the current velocities that the snails are able to resist if they become exposed, they will tend to avoid fast-flowing places probably due to the interference of current with their activities and movements (Seuffert and Martín 2012). In addition, the sites with fine substrata (such as sapropel), where *P. canaliculata* was frequently found, were associated with very low or nil currents while the less used points with pebbles and boulders were characterized by relatively higher current velocities.

The association of *P. canaliculata* with sites with an abundance of macrophytes and plant debris could be due to the use of macrophytes as food (Estebenet 1995) or as an emergent substratum for spawning and aerial respiration (Seuffert and Martín 2010) and as a refuge from currents (Guimarães 1981). Kwong et al. (2010) mentioned that in the inhabited lentic water bodies from Hong Kong, *P. canaliculata* is mainly limited to the margins where macrophytes are very abundant. A greater abundance of snails in shallow areas along the vegetated shores was also reported in other *Pomacea* spp. (Guimarães 1981; Giovanelli et al. 2005; Karatayev et al. 2009; Burlakova et al. 2010). In the streams of this basin, we never found the snails actually feeding on the most common macrophytes present. However, it is likely that they exploit the biofilm that forms on vegetation and decaying parts of macrophytes (even of those unpalatable when fresh; Qiu et al. 2011).

In southern Buenos Aires province, a series of physical and chemical parameters determine the presence of *P. canaliculata*, both among different waterbodies (Martín et al. 2001) and at the microhabitat level (this work; Seuffert and Martín 2010). On the other hand, some environmental variables influenced the distribution of *P. canaliculata* among and within the streams of the Encadenadas del Oeste basin, but none of them seem to be crucial for the survival of this species, probably on account of the relative homogeneity of these variables and so their ranges fall within the ecological tolerance of most species of gastropods (Tietze and De Francesco 2010). Moreover, the sites in this region identified as uninhabitable by *P. canaliculata* (10 alkaline lakes located in western Buenos Aires province; Martín et al. 2001) were already excluded from the study area.

Floods and dry downs, very common in this basin, can provoke the eradication of apple snails from suitable places and the gathering of them at unsuitable places. Given their high resistance and slow active dispersal (Martín et al. 2001; Martín and Estebenet 2002; Seuffert and Martín 2012), this mismatch between the snails' preferred habitat and their actual location might persist for long enough to be sampled and to interfere with correlative studies. On the other hand, the environmental conditions at inhabited sites may be consequence of the presence of a promoter of ecosystemic changes, such as *P. canaliculata*, rather than determinants of it. For instance, high organic matter in the sediment of inhabited sites may result from the local depletion of palatable submerged macrophytes by this apple snail (Carlsson et al. 2004).

All the streams belonging to the Encadenadas del Oeste basin would be, at first, habitable for *P. canaliculata*, but the populations could only persist autonomously in the long term in the low and medium reaches within the longer streams. Even though the distribution of *P. canaliculata* in this basin had time to reach a state of equilibrium, this does not imply a static state. Therefore, the distribution of *P. canaliculata* within the long streams is probably governed by stochastic patterns of extinction-colonization as a consequence of the variability in the climatic and hydrological conditions of this region (Montesarchio 1989; Scian and Donnari 1997).

Acknowledgments

This work was funded with Grants from CONICET ("Consejo Nacional de Investigaciones Científicas y Técnicas", PIP 6150 and PIP 112 200901 00473) and UNS ("Universidad Nacional del Sur", PGI 24B/108 and PGI 24B/144). MES is a postdoctoral fellow in CONICET. PRM is a researcher in CONICET. We are grateful to Nicolás Tamburi for his assistance with the surveys.

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