A lentic dweller in lotic habitats: the behavior of the invasive South American apple snail Pomacea canaliculata in flowing water

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A lentic dweller in lotic habitats: the behavior of the invasive South American apple snail *Pomacea canaliculata* in flowing water

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Abstract The aim of this study was to test the hypothesis that positive rheotaxis and anti-detachment behaviors contribute to the persistence of *Pomacea canaliculata* in lotic environments. This invasive apple snail is commonly considered a lentic dweller. In a first series of trials in a laboratory flume, current velocity was gradually increased until snails' detachment. Detachment velocity was highly variable, with some snails able to withstand strong currents during short periods. Sexually undifferentiated snails were the most resistant to detachment; most of the snails that resisted high velocities were facing flow before detachment. In a second series of trials, snails' net displacement was estimated at three fixed velocities (0, 0.15, and 0.30 m s^{-1}). Current velocity did not influence mean net displacement, which was not different from zero. Marked snails were released in a stream and recaptured 24 h later estimating their net displacement. Most recovered snails dispersed a short distance from the release point and crawled through sites with very low current velocities. A small proportion of snails drifted downstream, indicating the existence of different dispersal mechanisms. Snails were able to resist current velocities that are among the highest recorded in streams in the Pampas region. *P. canaliculata* did not show a positive rheotactic response; in flowing water, snails crawl more often upstream, but at a slower pace than downstream. At the population level, a slow upstream spread seems possible in plain's streams, probably being enough to compensate drift, but not to colonize headwaters. Irrigation systems are feasible pathways for the spread of this species in invaded regions.

Keywords Streams · Current velocity · Detachment · Dispersal · Rheotaxis · Drift

Introduction

Pomacea canaliculata (Lamarck 1822) is a freshwater snail (commonly known as golden apple snail) whose natural range of distribution extends from La Plata river basin (27°S, Paraguay and southern Brazil) southwards to the Tandilia and Ventania mountains (37°S, Buenos Aires Province, Argentina; Martín et al. 2001; Hayes et al. 2008). This species has been either intentionally or accidentally introduced in several countries around the world (Cowie 2002; Rawlings et al. 2007; Hayes et al. 2008; Jackson and Jackson 2009; Karatayev et al. 2009) and is considered as one of the 100 worst invaders worldwide (Lowe et al. 2000). *P. canaliculata* is a serious pest of rice and other aquatic crops (especially in Southeast Asia;

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Cowie 2002) and can also produce serious changes in the diversity and functioning of invaded natural wetlands (Carlsson et al. 2004; Fang et al. 2010). Problems caused by this species have not been fully solved partly because, despite the dozens of reports available on apple snails' control (e.g., Ranamukhaarachchi and Wickramasinghe 2006; Wada 2006; Yusa 2006), many aspects of their biology, ecology, and behavior, especially in their natural ranges, remain unexplored.

Water current is one of the main factors influencing the small-scale distribution of aquatic invertebrates in general (Malmqvist 2002) and of lotic freshwater snails in particular (e.g., Huryn and Denny 1997; Johnson and Brown 1997; Utzinger et al. 1997). Hydraulic forces affect the snails and their behavior directly or indirectly through their influence on the physical structure of the habitat, food availability, as well as predation and competition processes (Johnson and Brown 1997; Sagnes et al. 2008). *P. canaliculata* has been usually considered as a species characteristic of lentic environments (Hylton-Scott 1958; Castellanos and Fernández 1976), but it has been shown that it is also common and reaches the highest densities in plain's streams of Encadenadas del Oeste basin (southern Buenos Aires Province; Martín et al. 2001). In these water bodies, it is usually found in areas with little current and rarely in the steepest sections near the Ventania mountains. As in other gastropods (Dussart 1987), routine activities of *P. canaliculata*, such as crawling and lung ventilation (Seuffert et al. 2010), can be altered by the movement of water. The increase in the cross-section of the shell suggests that critical velocities for these activities will probably decrease with size, making the behavior of larger snails more prone to be affected by current. However, the current velocities that snails of this species are able to resist and the possible behaviors enhancing their resistance have not been investigated.

The floods that frequently occur in the streams of Encadenadas del Oeste basin have been considered as a major disturbance to *P. canaliculata* populations, since they are able to eradicate them locally by downstream drifting (Martín and Estebenet 2002; Martín, P.R., unpublished results). In *Pomacea*, the air located inside the lung confers the snails with some buoyancy (Burky and Burky 1977; Heiler et al. 2008), while isolated snails and mating couples have also been observed floating downstream (Martín, P.R.,

personal observation). Therefore, it is possible that the snails exhibit some mechanism of differential upstream dispersion to compensate for accidental or catastrophic drift. The existence of positive rheotaxis has been reported for several species of freshwater snails, with multiple hypotheses being proposed to explain this behavior such as the search for food (Bousfield 1979), a decrease in predation risk (Schneider and Lyons 1993), the compensation for downstream drifting during larval stages (Schneider and Frost 1986; Kano 2009), and biomechanical hypotheses related to shell hydrodynamics (Huryn and Denny 1997). Other *Pomacea* snails also inhabit lotic environments (e.g., *Pomacea insularum,* Hylton-Scott 1958; *Pomacea curumim*, Simone 2004), though there is no information concerning the dispersal patterns of ampullariids in flowing waters; the possible rheotactic responses of *P. canaliculata* in streams are so far unknown.

Our study was based on the hypothesis that positive rheotaxis and anti-detachment behaviors are two of the main mechanisms allowing the persistence of *P. canaliculata* in flowing waters. In order to test this, we determined detachment velocities, investigated the effect of current velocity on dispersal rate and direction, and estimated the net displacement of the snails in a stream belonging to Encadenadas del Oeste basin. This study will contribute to the comprehension of the factors influencing the distribution and dispersal of ampullariids in lotic systems.

Materials and methods

Origin, maintenance, and sexing of snails

All the snails used in this study were collected from populations belonging to Encadenadas del Oeste basin (Buenos Aires Province, Argentina): one in an artificial channel that diverts water from Pigüé stream to Venado stream ($37°11'26''$S, $62°40'26''$W) and the other in Guaminí stream ($37°02'59''$S, $62°25'26''$W). All snails were kept until use in 20-L aquaria with $CaCO_3$-saturated tap water, located in a breeding room at $25 \pm 2°C$ under a constant photoperiod of 14L/10D and fed fresh lettuce (Martín and Estebenet 2002). The day before each experiment, eight snails were randomly selected from a group of 200 individuals (shell length: 7–70.4 mm) and separated in a 5-L container

provided with lettuce. Before the start of each trial, the snails' shell length (SL, mm) was measured from the apex to the extreme lip of the aperture with a Vernier caliper to the nearest 0.1 mm, and they were also sexed. Males were externally recognized by the presence of a convex operculum (Estebenet et al. 2006) or the observation of the testicle through the translucent shell (Takeda 1999). The convex operculum is always evident in males larger than 25 mm, so snails without these male traits were considered as sexually undifferentiated if smaller than 25 mm and as females if larger than that size.

Detachment velocity

Trials were conducted in a laboratory flume 9-m long, 35-cm wide, and 50-cm high supplied by a 150-m^3 cistern filled with tap water. The flume bottom was made of painted iron, and the walls were transparent glass. The flume was provided with a collimator or rectifier grid in the water entrance, which decreases turbulence and makes flow more linear (Muschenheim et al. 1986). A 5-cm high weir at the exit allowed the maintenance of that water level without circulation. The flume was filled with water, and with current velocity zero, one snail was placed in the center. Once the snail got hold onto the bottom, it was observed during 1 min without current to confirm that it was attached or started to crawl. Then, current velocity was gradually increased at intervals of 1 min (at an average rate of 0.068 m s^{-1} per minute) until the snail's detachment. At each step, actual current velocity was recorded a few centimeters downstream from the position of the snail with a digital flowmeter (FP101 Global Water®); the detection threshold of the flowmeter was 0.1 m s^{-1}, so velocities below this value were read as zero. During these trials, water temperature in the flume was 20.1°C on average and ranged between 18 and 21°C.

The snails used in these trials were collected at the artificial channel between Pigüé and Venado streams. The size ranges of males (n = 32), females (n = 42), and undifferentiated snails (n = 15) were 26.8–62.5, 26.8–70.4, and 7–19.6 mm, respectively. During the whole trial, the time spent in different activities (crawling, lung ventilation, attaching, and clamping) was continuously recorded. Attached snails were those immobile and fastened to the substratum with the cephalic tentacles and labial palps extended, while in clamped snails, these body parts were withdrawn under the shell and the foot was contracted and firmly fixed to the substratum. The orientation of the snails relative to the current (with the cephalopodium facing downstream, upstream, or perpendicular to the direction of flow) was also recorded. As control of the snails' behavior in still water, the same experiment was conducted without water circulation (n = 13), recording the activity of each snail during a 15-min period (the mean duration of the trials with water flow).

The detachment velocity (DV, m s^{-1}) was analyzed in relation to snail size using linear regression analysis; the velocities recorded for males and females were compared with a t test. The percentage of time spent in different activities during the trials was compared with those recorded for controls using a Mann–Whitney (non parametric) test, since for these variables, the assumption of homoscedasticity was rejected (Levene tests, $P < 0.010$ in all cases).

Effects of current velocity on dispersal rate and direction

This experiment was performed in the same flume described above, using three fixed current velocities (CV, m s^{-1}): (1) without flow, (2) 0.15 m s^{-1}, which is within the range in which snails are commonly found in their natural habitat, and (3) 0.30 m s^{-1}, since above this velocity a very low frequency of snails is recorded in the streams of Encadenadas del Oeste basin (Seuffert and Martín, submitted); 25 snails (collected at Guaminí stream) were assigned to each treatment. The size ranges of males (n = 25), females (n = 26), and undifferentiated snails (n = 24) used in these trials were 23.1–45.7, 25.4–54.0, and 11.0–24.3 mm, respectively. Water temperature was 20°C on average and fluctuated between 19 and 21°C.

As in the previous experiment, the snails were placed one at a time in the center of the flume with still water (5-cm deep). Except for the treatment without flow, once a snail became attached to the bottom, current velocity was gradually increased. Once the required velocity was achieved, we recorded at 1-min intervals (during 1 h) the longitudinal position of the snail in the flume (used afterwards to calculate the distance covered; see below), the direction of its movement relative to current, and its activity. After each trial, the bottom and sides of the flume were

thoroughly brushed while water was flowing to remove the mucus trails left by snails in successive trials, thus avoiding the possible interference between them (Takeichi et al. 2007).

From the data recorded for each snail, we calculated: (1) the net displacement (ND, m) as the difference between the final and initial positions, (2) the total displacement (TD, m) as the accumulated displacements recorded during the whole observation period, and (3) the displacement rate (DR, cm min^{-1}) as the quotient between the total displacement and the time elapsed, which was variable because some individuals reached one of the flume ends in less than an hour. For each snail, we also calculated the number of times that it changed direction of crawling (CD) and the difference between the number of stretches covered either in downstream or upstream directions (DU). Finally, the quotient between the total displacement and the time during which the snails were crawling was used to calculate the average crawling velocity (AV, cm min^{-1}); the upstream (UP, cm min^{-1}) and downstream (DO, cm min^{-1}) crawling velocities were calculated accordingly. The average crawling velocity and the displacement rate were identical only for the snails that crawled continuously during the experiment (16 out of 75 snails).

To examine the possible differences between treatments, ANCOVAs were performed using shell length as covariate. For the dependent variables in which the covariate was not significant, we performed one-way ANOVAs or a non-parametric test (Kruskal–Wallis or Mann–Whitney) for those that did not meet the assumption of homoscedasticity (Levene tests, $P < 0.010$ in all cases). No variable was significantly different between males and females in preliminary analyses, thus sex was not included as a factor in the final analyses.

Dispersal in a pampasic stream

This study was conducted during February 2010 in a reach of Guaminí stream (37°09′04″S, 62°26′50″W), selected for its shallowness and uniform width; depth ranged between 0.37 and 1.1 m and width between 4.78 and 6.64 m. The reach is inhabited by a natural population of *P. canaliculata,* and the bottom is composed mainly of mud, with patches of calcareous bedrock and mats of *Potamogeton striatus*. During the study, water temperature fluctuated between 15.6 and

24.8°C (mean: 19.8°C), pH was 8.57, and conductivity was 0.746 mS cm^{-1}.

Fifty males (SL: 36.3–61.4 mm) and 50 females (SL: 36.1–57.0 mm) were collected from the artificial channel running from Pigüé stream to Venado stream and brought to the laboratory. Their shells were wholly painted with yellow synthetic paint, to allow easier localization underwater, and marked individually with a number. After that, snails were maintained under the laboratory conditions mentioned earlier and did not show any sign of stress (e.g., crawling out of water or persistent withdrawal). Three days later, they were released in a 1 m-wide transect at the centre of the reach of Guaminí stream. Water chemistry is quite similar in the channel and the reach: the similitude estimated through the correlation coefficient (using the concentrations of eight ions, conductivity, pH, turbidity, and total suspended matter) is very high ($r = 0.989$, $P < 0.0001$). The snails were placed by hand near the margins (lower current velocity) to reduce the chances of being immediately dislodged. After 24 h, the snails were carefully sought in upstream direction (visually and by touch on the bottom and the submerged vegetation), starting at a point located 25 m downstream from the release point and up to a point located 25 m upstream from it. For each recovered snail, the longitudinal distance from the release point and the distance to the nearest shore were recorded. The net displacement vector for each snail (i.e., the straight line joining the initial and final positions, irrespective of the path actually followed by the snail) was estimated by trigonometry. Afterward, current velocity was recorded at systematic points spaced 1 m apart on 26 transects perpendicular to the shore and evenly distributed along the reach. The final position of each snail was superimposed with the values of current velocity corresponding to the systematic points, and the net displacement vectors were correlated with the current velocities encountered along it.
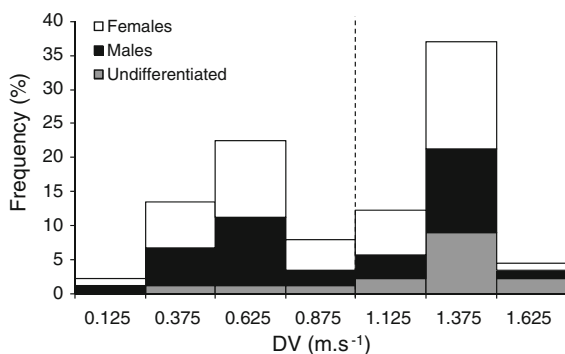
Results

Detachment velocity

The mean detachment velocity (VD) was 0.98 m s^{-1}, but showed a wide variation (range: 0.07–1.64 m s^{-1}; Fig. 1). When all snails were analyzed together by

regression analysis, the detachment velocity showed no significant relationship to snail size ($F_{1,87} = 2.674$, $P = 0.106$). Mean detachment velocity was not significantly different between males and females (t test, $P = 0.960$; Fig. 1).

The frequency distribution of detachment velocities was bimodal (Fig. 1), with two distinct groups of snails, one below and one above the mean detachment velocity (ca. 1 m s^{-1}). The association between low and high detachment velocities (0.57 and 1.33 m s^{-1} on average, respectively) and different characteristics of the snails was investigated through contingency tables.

The frequency of undifferentiated snails was higher in the group of high detachment velocities. For this reason, we explored the association between sexual differentiation (differentiated and undifferentiated snails) and resistance to detachment, which was significant ($\chi^2 = 4.934$, $P = 0.026$, Fig. 2a). The proportion of differentiated snails was similar in both groups (51% for low and 49% for high detachment velocities), whereas the undifferentiated snails showed a significantly higher proportion in the group of high detachment velocities (20 and 80%, respectively).

Detachment velocity was significantly associated with the orientation of the snails just before detachment ($\chi^2 = 19.669$, $P < 0.001$; Fig. 2b), but not with the orientation most frequently recorded ($\chi^2 = 4.026$, $P = 0.134$). The proportion of snails positioned perpendicular to the flow before detachment was similar in both groups of low and high detachment velocities (43 and 57%, respectively). By contrast, most of the snails orientated with the cephalopodium facing upstream before detachment (79%) resisted high current velocities, while 89% of the snails facing downstream only resisted low velocities (Fig. 2b). Given the high proportion of undifferentiated snails recorded in the group of high detachment velocities, we also investigated whether the orientation of the snails before detachment was related to sexual differentiation and did not find an association between these variables ($\chi^2 = 3.403$, $P = 0.182$).
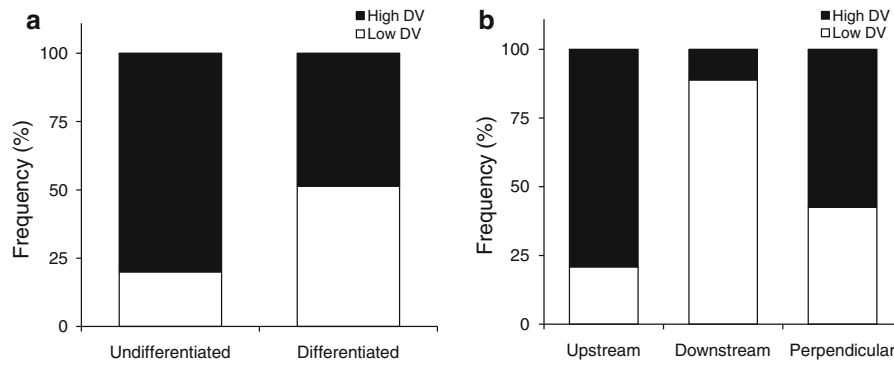
The percentage of time spent crawling and attached to the substrate was significantly different between the snails subjected to running water and still water; the former spent more time attached (33 and 4%, respectively; Mann–Whitney $U = 176.5$, $P < 0.001$) and less time crawling (62 and 95%, respectively; Mann–Whitney $U = 185$, $P < 0.001$). Lung ventilation frequency varied between 0 and 8 emersions per hour, both in the trials with current and the controls, but it was significantly lower with current (0.67 and 2.15 h^{-1} on average, respectively; Mann–Whitney $U = 384.5$, $P = 0.006$).

Clamping was not observed in the control snails nor in the group of low detachment velocities. Instead, this behavior was recorded in 38% of the snails that resisted high detachment velocities and in all cases in the final stage of each experiment (i.e., with the highest current velocities). The time spent clamped varied between 3 and 65% of the total time of observation. Given this result, we searched for an association between clamping and the position before detachment. Most of the snails that were clamped (72%) were also facing upstream before detachment ($\chi^2 = 23.535$, $P < 0.001$), and in 22% of the cases, the clamped snails were positioned perpendicular to flow.

Effects of current velocity on dispersal rate and direction

Three snails corresponding to the treatment of 0.15 m s^{-1} and three to that of 0.30 m s^{-1} detached spontaneously from the bottom sometime during the experiment and drifted downstream, reaching the end of the flume in 2–28 min; these individuals were not considered in the analyses. The minimum time spent to reach one of the extremes of the flume by crawling was 26 min, although most snails (81%) took more than 45 min.

The net displacement (ND) of the snails was not influenced by the different water velocities nor by size (Table 1). The mean net displacement was slightly

Fig. 1 Frequency of detachment velocities (DV) for females, males, and undifferentiated snails ($n = 42$, 32, and 15, respectively); the *dotted line* indicates the value that separates the groups of low and high detachment velocities (1 m s^{-1})

Fig. 2 Percentage of snails in groups of low and high detachment velocity (DV) ($n = 41$ and 48, respectively) against: **a** sexual differentiation and **b** orientations relative to flow before detachment

Table 1 ANCOVAs for the net displacement (ND), total displacement (TD), and displacement rate (DR) of the snails with shell length (SL) as covariate; the different groups were the three current velocities (0.00, 0.15, and 0.30 m s^{-1})

|	Slope equality	Common slope	Covariate (SL)	Intercept equality	Adjusted means
ND	$F_{2,63} = 0.488$	-0.0329	$F_{1,65} = 1.076$	$F_{2,65} = 0.725$	#
	$P = 0.616$		$P = 0.303$	$P = 0.488$	
TD	$F_{2,63} = 0.570$	0.0548	$F_{1,65} = 10.042$	$F_{2,65} = 2.537$	*0.00*: 2.99
	$P = 0.568$		$\mathbf{P = 0.002}$	$P = 0.087$	*0.15*: 3.72
					0.30: 2.65
DR	$F_{2,63} = 0.706$	0.1159	$F_{1,65} = 8.142$	$F_{2,65} = 2.330$	*0.00*: 5.46
	$P = 0.497$		$\mathbf{P = 0.006}$	$P = 0.105$	*0.15*: 7.49
					0.30: 5.29

Adjusted means were not estimated for ND since the slopes were not significantly different from zero

Bold typing indicates $P < 0.05$

biased to the downstream direction (1.04, 1.19, and 0.20 m from the center of the flume for 0.00, 0.15, and 0.30 m s^{-1}, respectively), but it was not statistically different from zero (though for the treatment without current, the *P value* of the *t* test was marginal: $P = 0.057$; $P > 0.105$ for the other two treatments). In the experiments without current and with 0.30 m s^{-1}, the frequency distribution of net displacement was quite uniform across all distances (11 and 13% on average, respectively; Fig. 3), although no snail reached the upstream end. With 0.15 m s^{-1}, the most frequent net displacement (41%) was the maximum distance in downstream direction. On the whole, 56 and 44% of the snails ended downstream and upstream from the release point, respectively (these percentages are not significantly different from the 50% expected with random crawling; $\chi^2 = 0.941$, $P = 0.332$).

The total displacement (TD) and the displacement rate (DR) were not significantly different between
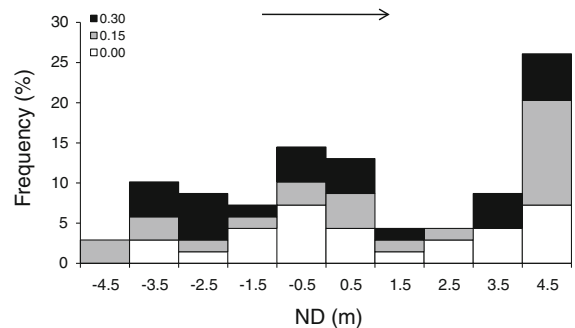

Fig. 3 Frequencies of net displacement (ND) recorded in the three treatments: 0.00 ($n = 25$), 0.15 ($n = 22$), and 0.30 m s^{-1} ($n = 22$); the *arrow* indicates the direction of flow

treatments, though, in both cases, a higher average value was associated with 0.15 m s^{-1} (Table 1). The maximum total displacement for the snails without current and with 0.30 m s^{-1} was 4.76 and 5.21 m, respectively, whereas in those with 0.15 m s^{-1}, the

maximum was 9.04 m. For both variables, there was a positive correlation with snails' size. The displacement rate was rather variable, with a maximum value of 18.23 cm min^{-1} with 0.15 m s^{-1}.

The number of times that snails changed direction during the course of each trial (CD) significantly decreased with the increase in current velocity (Kruskal–Wallis test, $H_2 = 14.304$, $P < 0.001$), reaching a minimum of 1.18 in the treatment of the highest velocity (0.30 m s^{-1}; Fig. 4). On the other hand, the difference between the number of stretches covered in downstream and upstream directions (DU) was 9.72, 3.14, and −15.18 for the 0.00, 0.15, and 0.30 m s^{-1} velocities, respectively, indicating that in the latter the
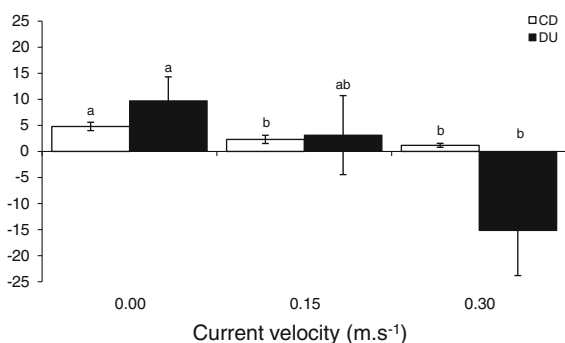
Fig. 4 Number of changes in direction (CD) and difference between the number of stretches covered in downstream and upstream directions (DU; means ± SE) for the snails of the three treatments (positive values indicate greater number of stretches in downstream direction). *Different letters* indicate significantly different means (after Bonferroni correction for three comparisons); $n = 25$, 22, and 22 for 0.00, 0.15, and 0.30 m s^{-1}, respectively

number of stretches covered in upstream direction was higher than those in the opposite direction. However, the differences among the three treatments were only marginally significant (Kruskal–Wallis test, $H_2 = 4.627$, $P = 0.099$); with pairwise comparisons, we found significant differences between the treatments of 0.00 and 0.30 m s^{-1} (Mann–Whitney $U = 178$, $P = 0.039$; Fig. 4).

The average crawling velocity (AV) and the velocities in downstream (DO) and upstream (UP) directions differed significantly among treatments and were positively related to size (Table 2). The first two variables were significantly lower in the 0.30 m s^{-1} treatment, while upstream crawling velocity was lower in both treatments with current.

Crawling velocities in upstream and downstream directions were not significantly different for the treatment without current. For the treatments with current, crawling velocity in upstream direction was lower than the velocity in downstream direction (Fig. 5). For the 0.15 m s^{-1} treatment, both velocities were significantly different (paired t test: $t_{21} = 3.405$, $P = 0.003$), while with 0.30 m s^{-1}, the differences were only marginally significant ($t_{21} = 1.939$, $P = 0.066$).

Dispersal in a pampasic stream

After the period of 24 h from the release of the 100 snails in the reach of Guaminí stream, we recovered 38 individuals (21 males and 17 females); we also found another 51 unmarked snails from the resident population (all sexually differentiated). The frequencies of

Table 2 ANCOVAs for the average crawling velocity (AV) and the velocities in downstream (DO) and upstream (UP) directions with shell length (SL) as covariate; the different groups were the three current velocities (0.00, 0.15 and 0.30 m s^{-1})

	Slope equality	Common slope	Covariate (SL)	Intercept equality	Adjusted means
AV	$F_{2,63} = 2.266$ $P = 0.112$	0.1402	$F_{1,65} = 14.824$ **$P < 0.001$**	$F_{2,65} = 5.133$ **$P = 0.009$**	*0.00*: 8.45[a] *0.15*: 8.99[a] *0.30*: 5.93[b]
DO	$F_{2,63} = 2.341$ $P = 0.105$	0.1204	$F_{1,65} = 6.151$ **$P = 0.016$**	$F_{2,65} = 4.526$ **$P = 0.015$**	*0.00*: 9.06[a] *0.15*: 9.45[a] *0.30*: 5.74[b]
UP	$F_{2,63} = 0.519$ $P = 0.598$	0.1183	$F_{1,65} = 10.819$ **$P = 0.002$**	$F_{2,65} = 11.004$ **$P < 0.001$**	*0.00*: 7.74[a] *0.15*: 4.89[b] *0.30*: 3.21[b]

[a,b] Different letters indicate significantly different means (t tests, $P < 0.015$)

Bold typing indicates $P < 0.05$
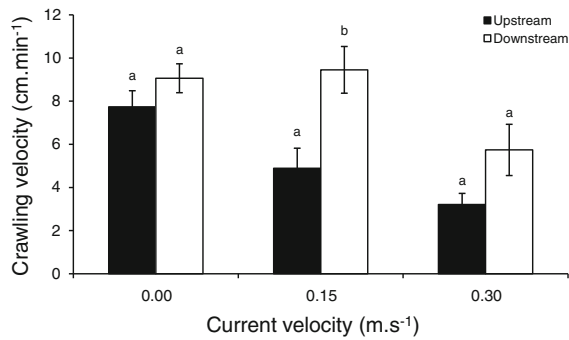
Fig. 5 Crawling velocities (adjusted means ± SE) in upstream and downstream direction for the three current velocity treatments ($n = 25$, 22, and 22 for 0.00, 0.15, and 0.30 m s^{-1}, respectively)

net displacement did not differ between males and females (Kolmogorov–Smirnov $Z = 0.481$, $P = 0.975$). The maximum net displacement recorded in downstream and upstream directions was 17.83 and 6.14 m, respectively (Fig. 6a). Most individuals (71%) dispersed only a short distance (between 0.6 and 4 m) downstream from the release point; only two snails were found upstream from the release point. The frequency of recovered marked snails recorded in each transect was significantly different from that of the resident snails (Kolmogorov–Smirnov $Z = 1.838$, $P = 0.002$; Fig. 6a), which were more evenly distributed along the reach (although relatively concentrated near the margins; Fig. 7).

The final position of each snail relative to the values of current velocity from the systematic points indicated that most marked snails were found in sites with low current (Fig. 7). The current velocities recorded in each transect were highly variable (Fig. 6b); the mean velocity of the reach was 0.13 m s^{-1} and ranged between 0 and 0.4 m s^{-1}. In general, the transects with relatively low current velocities presented a higher concentration of snails. We determined that 84% of the net displacement vectors of recaptured snails crossed exclusively through sites with current velocities below the flowmeter detection threshold (considered here as zeros) and the rest through sites with relatively low velocities (0.099 m s^{-1} on average). Current velocity recorded at the points where the snails were found was significantly lower than the available velocities along the reach (Kolmogorov–Smirnov $Z = 3.201$, $P < 0.001$), with only three snails found in sites where the nearest systematic point showed a current velocity higher than zero.
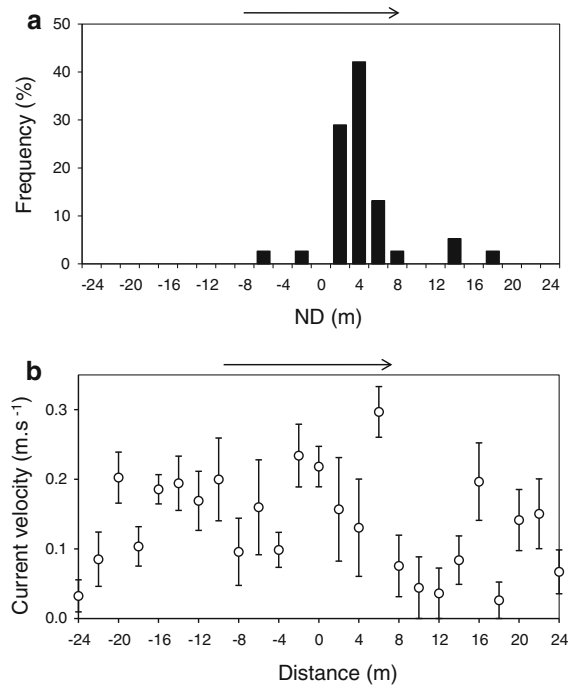
Fig. 6 a Frequency of net displacement (ND, m) for the marked snails recovered 24 h after their release ($n = 38$) in the 50-m-reach of Guaminí stream; **b** current velocity (mean ± SE) recorded in systematic transects at different distances from the release area; the *arrows* indicate the direction of flow

Discussion

The mean detachment velocity determined for *Pomacea canaliculata* was 0.98 m s^{-1} and ranged from 0.07 to 1.64 m s^{-1}. Lysne and Koetsier (2006) studied the short-term resistance to current in three very small freshwater snails and reported maximum detachment velocities of 0.41, 0.58, and 0.51 m s^{-1}, respectively. Dussart (1987) also determined the current velocities resisted by several species of pulmonates, which ranged between 0.70 and 0.86 m s^{-1}. However, all those records correspond to relatively small species, making this experimental study of detachment velocity the first conducted with snails of very large size (up to 70.4 mm of shell length). Although *P. canaliculata* is not commonly found in fast flowing environments (Martín et al. 2001; Camargo Maia 2005; Seuffert and Martín, submitted), this is a species that has a comparatively high resistance to flow, being able to resist, during a short period of time, velocities that are among the highest recorded in the streams of Encadenadas del Oeste basin (1.61 m s^{-1}; Seuffert and
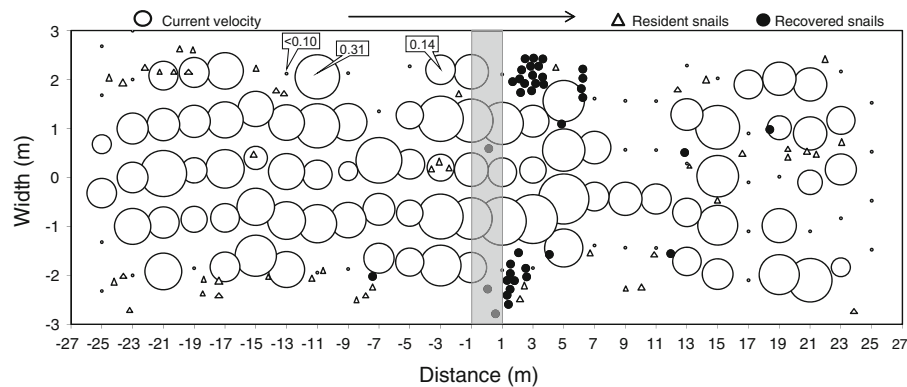
Fig. 7 Final position of the marked snails recovered 24 h after their release (*black circles*, n = 38) and location of the resident snails (*white triangles*, n = 51) in the reach of Guaminí stream. The area of the *circles* is proportional to the current velocity (m s^{-1}) of each systematic point (three current velocities are shown as examples in the call out *boxes*; the smallest *circles* represent current velocities below 0.1 m s^{-1}). The central *shaded rectangle* indicates the release area and the *arrow* the direction of flow

Martín, submitted). This capacity is probably useful when the snails face a sudden increase in current velocity, as might be the case in a flood of small magnitude, allowing them to reach hydraulic refuges. However, self-dislodgment, instead of a persistent attachment, is an alternative strategy, since the consequences of detachment are probably worse when it occurs at high than at low velocities (e.g., impact against an obstacle during drifting).

During the estimation of detachment velocities, two distinct groups of snails were recognized: one with velocities below and one above the mean detachment velocity. Sexually undifferentiated snails showed a clear association with the group of high detachment velocities, suggesting that smaller snails would have a greater resistance to current. Similarly, Moore (1964) reported that smaller individuals of the pulmonate snails *Stagnicola palustris* and *Physa propinqua* showed the smallest number of detachments. Current velocity decreases when approaching the bottom of the flume, indicating that a small snail would not endure the same current and would face different hydraulic forces than bigger snails (Statzner 1988; Huryn and Denny 1997). Statzner and Holm (1989) suggested that because of the opposite effects of body size on different hydraulic forces, young individuals should be differently shaped to fully grown ones to optimize their performance in flowing waters. In spite of the wide size range of *P. canaliculata* (2.5–80 mm), ontogenetic changes in shell shape are subtle (Estebenet 1998; Estebenet et al. 2006), so an effect on

hydrodynamic properties is unlikely. Another factor related to this greater resistance to current could be the decrease in the foot area/shell cross-section ratio with size, giving the smaller snails a greater relative area of adhesion (Moore 1964; Dussart 1987). For instance, the increase in shell drag in the adult snails of the pleurocerid *Elimia semicarinata* restricts their movements if current velocity exceeds 0.32 m s^{-1} (Johnson and Brown 1997). In *P. canaliculata*, the foot area/shell length ratio also decreases with size (Saveanu L., personal communication), suggesting that both the abovementioned factors could be jointly involved in the greater resistance to current of smaller snails.

On the other hand, snail behavior is important in regard to detachment velocity. Most of the snails that resisted high current velocities were facing against the flow, while many of them were also clamped to the substrate during the period of greatest increase in velocity. Dussart (1987) described the general behavior of a snail with increasing current velocity: at first, the snails crawled randomly, but eventually they ended up with the cephalopodium facing upstream. In this position, the columellar muscle is contracted, pushing the shell towards the foot. After some point, the snails lose control of this muscle and the shell begins to be swept downstream, until it eventually detaches. This exactly matches the behavior observed in the snails of *P. canaliculata* that resisted high current velocities and can be considered as an anti-detachment behavior. However, some snails (7%) made no attempt to resist drift and soon left the

observation section of the flume. One possible explanation is that, since the snails used in the trials were collected in the field, they had had different life experiences. For instance, a snail that had previously faced a situation of sudden increase in flow by forceful attachment will probably have more chances to adopt such behavior again, since *P. canaliculata* is capable of associative learning (Aizaki and Yusa 2010). In addition, factors such as age, parasitism or different flow-facing strategies cannot be discarded.

The snails subjected to increasing current spent less time crawling, and consequently more time attached or clamped to the substrate, than the controls. It seems that there is no limiting velocity for crawling, since some snails crawled with velocities up to 1.52 m s^{-1} at the moment of detachment. However, the crawling velocity under strong currents was extremely low but still noticeable. Lung ventilation frequency was on average 0.67 and 2.15 emersions per hour for the experiments with and without current, respectively. The frequency of emersions for the snails subjected to current was lower than the expected according to the water temperature recorded in the flume (ca. 20°C), since a snail of 40 mm of shell length would surface 1.26 times on average during 1 h (Seuffert and Martín 2009). Lung ventilation was recorded under relatively high velocities (up to 1.15 m s^{-1}), but the snails were always attached to the vertical walls of the flume and with the extreme of the aperture shell at the same level as the water surface. This suggests that the drag exerted by water in places with strong currents would not allow the normal extension of the siphon and force the snails to crawl to the surface to breathe air.

In lotic waterbodies, sites with high current velocities are commonly associated with coarse or consolidated substrata like pebbles, boulders, or limestone. These substrata allow a better attachment than fine grained, non-consolidated substrata and consequently a higher resistance of snails to current (Moore 1964). On the other hand, sand and mud are rapidly swept downstream when water velocity increases, and hence the attachment capacity of the snails becomes useless there. Therefore, the hard and smooth floor of the flume would adequately mimic the substrata on which the snails may become exposed to high currents and have the opportunity to resist detachment.

Current velocity did not influence the mean net displacement, which was not different from zero at any of the three levels tested. For the treatment with the highest current velocity (0.30 m s^{-1}), the fewest number of changes in direction were recorded together with the greatest number of stretches covered in the upstream direction. This shows that under this velocity, the snails are at least partially limited in their movements and crawl less frequently downstream, probably to reduce the risk of becoming detached. In the zero current treatment, both the net displacement and the crawling direction were slightly, although not significantly, biased downstream. This was probably caused by some factor external to the flume (such as a heterogeneous illumination or vibration) which perhaps also provoked an underestimation of the tendency to crawl more frequently upstream at the highest velocity.

The crawling velocity, and thus the total displacement and the displacement rate, positively correlated with snails' size, which is in agreement with previously reported results for this species (Seuffert and Martín 2010). The average crawling velocity recorded here in the zero current treatment (8.3 cm min^{-1}) compares relatively well with the value of 10.5 cm min^{-1} recorded by Seuffert and Martín (2010) with a water temperature of 20°C. However, it is much greater than the velocity of 2.5 cm min^{-1} reported at the same temperature for an aquarium strain of *P. canaliculata* (Heiler et al. 2008), probably because non-crawling time was not excluded from the estimations. The highest values for the total displacement and the displacement rate were recorded with 0.15 m s^{-1}, presumably because crawling velocity reached its maximum in this treatment. This intermediate current velocity would be the most favorable for the active dispersal of this species, since it apparently would not limit the snails' movements as observed with 0.30 m s^{-1} and it promotes the covering of greater distances compared to a still water habitat. However, it is important to note that for upstream dispersal, a reach of calm water is possibly the most favorable situation.

According to the results obtained in the flume, it was expected that the snails released in Guaminí stream would be found quite evenly distributed in the reach after the period of 24 h. However, most of the recovered snails were in the proximity of the release point and much more concentrated than the resident snails also found in the reach, probably indicating that a stable microdistribution was not yet attained. This also suggests that the potential dispersal of the snails

during a day may have been overestimated by the 1-h trials performed in the flume, a frequent bias in dispersal studies of freshwater snails (Kappes and Haase 2011).

In addition, the net displacement vectors suggest that the snails crawled across sites with very low velocities or mostly without current or, otherwise, they crossed through sections with higher velocities and then changed their direction to avoid those conditions. The snails were found in points with velocities much lower than the average of those available. This indicates that, despite the relative high current velocities that the snails are able to resist, they apparently tended to remain in the first suitable place they found. Despite their great dispersal capacity, even under high current velocities, adult *E. semicarinata* also selects hydrodynamic refuges within high-flow habitats, a behavior that probably reduces bioenergetic costs (Johnson and Brown 1997; Dussart and Pointier 1999). The present results were probably also influenced by the fact that the snails were released at the margins of the stream, a microhabitat preferred by *P. canaliculata* due to their dependence on emergent substrata to reach the water surface to ventilate the lung (Seuffert and Martín 2010), a tendency that was also apparent for the resident population.

Given the relatively low proportion of recaptured snails, it is likely that after 24 h, some individuals had reached sites located beyond the limits of the reach, either by crawling or drifting. As an estimation of the minimum time required to leave the recovery area by crawling, it would take just 8 h 31 min and 4 h 25 min (from values in Table 2) to surpass the limits of the reach (assuming that a snail crawls always upstream or downstream with a current of 0.15 m s^{-1}, close to the average of 0.13 m s^{-1} recorded in the stream). In fact, a few hours after the release a pair of marked snails was noticed crawling upstream and substantially away from the release point (ca. 10 m). On the other hand, a few minutes after the release, some snails could be seen drifting away, although it was not possible to determine their final location. During the experiments performed in the flume, a small proportion of snails (8%) also detached and drifted. Therefore, spread of *P. canaliculata* would depend on two different mechanisms of dispersal: crawling exclusively and drifting, accidentally or not. The results of the detachment trials showed that differentiated snails usually detach at lower velocities, a characteristic that

could be enhanced by reproductive behavior, since Kwong et al. (2008) observed that snails are more prone to drift during mating.

Studies dealing with dispersal of ampullariids are very scarce, mostly from lentic waterbodies, and, as in the present study, based on net displacement estimations. Louda and McKaye (1982) reported for *Lanistes nyassanus* values of 2.8 m per day, although crawling seemed to occur mostly during nocturnal or twilight hours. For *P. paludosa* from Central Florida, Darby et al. (2002) estimated mean net displacements of up to 6 and 11.85 m per day. *P. canaliculata* can disperse within drainage channels of Japan (current velocity not reported) up to 71.4 and 14.3 m per day in downstream and upstream direction, respectively (Ozawa and Makino 1989 *fide* Ito 2003). Given the marked differences between the dispersion distances in either direction, it is likely that also in those populations a proportion of snails commonly drifts or floats downstream, probably covering several meters in a few seconds. When disturbed, *P. insularum* withdraws into the shell and rolls or floats for 20 m or more, even under low current velocities (0.1 m s^{-1}; López et al. 2010). The rates recorded for *Pomacea* snails are higher than those recorded in Guamini stream (3.73 m on average), although our displacements seem to be an underestimation of the actual rates, since a significant fraction of the snails crawled or drifted beyond the recovery area. These results, however incomplete, suggest that dispersal is faster in lotic systems, although strongly skewed downstream. Nevertheless, extreme caution has been advised when extrapolating the results of laboratory or short-term studies to long-term and wide-scale dispersal (Kappes and Haase 2011) such as invasion processes.

Upstream crawling was reported by López et al. (2010) for *P. insularum* in irrigation channels with slow current (about 0.1 m s^{-1}). Our flume results indicate that a definite positive rheotaxis is not present in *P. canaliculata,* since the percentage of snails that ended upstream of the release point after one hour was not higher than the expected by random, non-directional crawling. In the freshwater snail *Elimia,* upstream migration has been explained as a by-product of the hydrodynamic drag that tilts the tall shell downstream, and therefore forces the snails to face the flow to reduce drag (Huryn and Denny 1997). Similar hydrodynamic constraints seem to operate upon the globose shell of *P. canaliculata*, since snails

exposed to increasing current velocity tend to face the flow, though this directionality is apparently counterbalanced by the decrease in crawling velocity.

In the streams of Encadenadas del Oeste basin, *P. canaliculata* is not found in the upper sections near the headwaters at Ventania mountains (Martín et al. 2001; Martín and Estebenet 2002). This may be related to the upstream decrease in water alkalinity and abundance of macrophytes in the streams running from Ventania mountains (Limbozzi and Martín 2003; Martín 2003) or to the increase in hydraulic stress due to the higher slopes of the headwaters (Martín 2003). However, *P. canaliculata* is able to colonize waterbodies with lower alkalinities (42 mg $CaCO_3$ L^{-1}, Kwong et al. 2008) than those recorded in the headwaters (111 mg $CaCO_3$ L^{-1}, Martín 2003) and is an herbivore-omnivore with a wide trophic spectrum (Estebenet 1995). The snails are probably able to surmount reaches of moderate water velocity, especially crawling near the water edge where current is slower, but unable to trespass riffles or small waterfalls whose frequency increases upstream. Similarly, Ichinose and Yoshida (2001) found that *P. canaliculata* from southern Japan is not able to spread to highlands due to the high current velocities at the boundaries between paddy fields and rivers. The evidence gathered in our study suggests that a slow upstream spread, resulting from both displacement and population growth, may be possible in the long term in Encadenadas del Oeste basin, probably being enough to compensate catastrophic or accidental drift, but not to colonize the headwaters. The aerial egg masses in this genus are probably immune to floods of moderate magnitude and duration and constitute an input of new colonizers.

Since its introduction and subsequent establishment as a pest species in southern and eastern Asia, many efforts have been made trying to find effective measures to eradicate, or at least control, the populations of invasive apple snails in natural wetlands and especially in paddy fields (e.g., Cowie 2002; Wada 2004; Yusa et al. 2006). The information obtained here indicates that drainage basins located in plains and irrigation systems are feasible pathways for the spread of this species in invaded regions. Irrigation channels constitute refuges from which apple snails can reinvade paddy fields (Ito 2002). These artificial environments seem suitable places to practice control measures, as might be the capture with nets of drifting snails (drift caused by natural or induced pulses of

water discharge) or the construction of fast flowing sections to deter upstream crawling, and thus prevent the re-colonization of paddies where control measures have been applied.

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