



Life cycle of the South American apple snail *Asolene platae* (Maton, 1811) (Caenogastropoda: Ampullariidae) under laboratory conditions

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ABSTRACT

Reproductive mode, life cycle and fecundity are relevant to understand and predict the spread and impacts of invasive freshwater molluscs. Ampullariids or apple snails have been intensively studied in recent decades due to the fast global expansion and severe impacts of two species of *Pomacea*, a genus with a peculiar reproductive mode (aerial egg masses). We investigated the life cycle and fecundity of *Asolene platae*, an apple snail with a different reproductive mode (aquatic egg masses) from the Río de la Plata basin by following three cohorts from hatching to death under laboratory conditions. Growth of *A. platae* remained continuous during the 4-year lifespan and the snails reached 80% of their asymptotic size at an age of 1 year. In terms of the von Bertalanffy model, females attain higher asymptotic sizes (26.02–25.72 mm) than males (23.01–24.89 mm), but males grow to their asymptotic sizes at slightly higher rates than females (0.047–0.054 vs 0.050–0.057 week⁻¹). Males matured at a smaller size (21.16 vs 24.53 mm) and much earlier (55.02 vs 84.88 weeks) than females. The survivorship curves showed 63% mortality during the first 2–8 weeks, almost no mortality for the following 2 years and finally a steady decline in the number of survivors, with at least 7% of the snails still alive after 3 years. The life-span fecundity of females included 20.61 egg masses and 1429.9 eggs. The tertiary sex ratio of the three cohorts was balanced, but varied from 0.25 to 0.76 among egg masses. Our laboratory data indicated that, in temperate environments, *A. platae* males would mature in their second summer and females during their second or third summer, and that the survivors would reproduce again during the three following summers. Several attributes of the life cycle of *A. platae* (slow growth, high posthatching mortality, late maturation and relatively low fecundity) indicate lower invasive potential and population resilience than those of invasive apple snails.

INTRODUCTION

The characteristics of the reproductive mode, life cycle and fecundity of invasive freshwater molluscs are relevant to understand and predict their spread and impact (Keller, Drake & Lodge, 2007; Cowie *et al.*, 2009; Horgan, Stuart & Kudavidanage, 2014). Apple snails (family Ampullariidae) are large-sized freshwater snails with macrophytophagous habits. They have both a gill and a lung, with which they are able to breathe both in water and air. Apple snails have been the focus of intense research during the last two decades due to the fast expansion around the world of several ampullariid species, which have become successful invaders (Horgan *et al.*, 2014; Hayes *et al.*, 2015). Most investigations about the life cycle of apple snails have focused on two genera (*Pomacea* and *Pila*) that exhibit a very peculiar and specialized reproductive mode for a freshwater snail. These genera produce masses of eggs protected with calcareous shells and laid on hard substrates out of the water (Hayes *et al.*, 2015). The remaining genera (*Lanistes*, *Afropomus*,

Saulea, *Felipponea*, *Asolene* and *Marisa*), which lay gelatinous egg masses under water (Hayes *et al.*, 2009), have received considerably less interest, with the possible exception of *Marisa*. The representative species *M. cornuarietis* has frequently been used as a biological control agent (e.g. Pointier & David, 2004) and as a model for ecotoxicological studies (e.g. Oehlmann *et al.*, 2006).

Asolene is a monophyletic genus endemic to South America, where eight species are currently recognized. It appears to be closely related to *Felipponea* and *Marisa*, the other two Neotropical genera with subaquatic egg masses (Hayes *et al.*, 2015). *Asolene platae* (Maton, 1811), an apple snail native to the Río de la Plata basin, likely represents a senior synonym of *A. pulchella* (Maton, 1838), based on their conchological, anatomical and genetic similarity (Hayes *et al.*, 2009; Léon, Hayes & Cowie, 2014).

Recently, the thermal biology, copulation, oviposition and development of *A. platae* have been investigated (Tiecher, Burela & Martín, 2014; Tiecher, Seuffert & Martín, 2015). Information about its gonadal cycle and its size-frequency distribution has been obtained for a population from a tributary stream of the

Río de la Plata (Martín, 1984a, b, 1987). However, such histological and size-frequency data are difficult to interpret, because many basic traits of the life cycle (age and size at maturity, longevity, survivorship and growth curves) remain unknown. Some apple snails appear sexually dimorphic in secondary aspects of their morphology, behaviour and life-history traits (Estebenet, Martín & Burela, 2006; Hayes *et al.*, 2015). Among apple snails with subaquatic egg masses, sexual dimorphism (involving pigmentation, shell size and shape) has been reported only in a distant relative of *Asolene*, *M. cornuarietis* (Demian & Ibrahim, 1972), but no information exists about differences in growth, survivorship or maturity. Thus, we sought to investigate the life cycle and fecundity of *A. platae* under laboratory conditions to gain insight on their invasive potential and demographic resilience. We followed three cohorts of *A. platae* from hatching to death to determine the survivorship and growth curves, the age and size at maturity and the reproductive activity (RA) for each sex. We also estimated the lifespan fecundity of females and the tertiary sex ratio of the cohorts.

MATERIAL AND METHODS

Origin and rearing of snails

Unless stated otherwise, the snails were reared in tap water saturated with CaCO_3 and maintained under a photoperiod of 14/10 h (light/dark) at $25 \pm 2^\circ\text{C}$. The snails were supplied with fresh lettuce *ad libitum*. We cleaned aquaria and changed the water once a week.

Snails used in this study came from egg masses laid in the laboratory by snails from a population in Regatas Lake ($34^\circ 34' 24''$ S, $58^\circ 24' 53''$ W, Ciudad Autónoma de Buenos Aires, Argentina). We reared seven males and seven females in common aquaria (20 l) and collected the egg masses, which were then put individually in 15-cm Petri dishes filled up to 1 cm. We maintained the hatchlings for 3 weeks in the same Petri dish in which they hatched, together with the remains of the egg mass. These egg mass remnants served as food during the first week, after which the snails received small pieces of thawed lettuce in the second week (Tiecher *et al.*, 2014).

We set up three asynchronous cohorts of *A. platae*, using the hatchlings that survived the 3-week periods in the Petri dishes. After this period, we reared snails individually in 200-ml plastic aquaria and fed them with fresh lettuce *ad libitum*. At around the 28th week, we transferred snails to 3-l glass aquaria. Cohort 1 began on April 17, Cohort 2 on July 7 and Cohort 3 on August 18 of the year 2010, using 108 hatchlings (from four egg masses), 77 hatchlings (three egg masses) and 72 hatchlings (two egg masses), respectively; the identity of the parents was unknown. A Hobo® data-logger recorded the temperature of the air in the rearing room hourly.

We measured the shell length (SL, in mm, from the apex to the farthest point of the aperture) of all the snails every 2 weeks during the water change. To avoid damage to the snails, especially during the first weeks of life, we obtained a digital photograph in dorsal view while the snail was resting on the bottom of the plastic aquarium. A 1-cm bar drawn on the outer side of the translucent plastic aquarium served as reference to scale each photograph for the estimation of SL (Fig. 1A). Once in the 3-l glass aquaria, we marked the snails with a number on the shell and measured SL with a calliper (Fig. 1B) until the end of the experiment. During the first weeks, when the shell still appeared translucent, the observation of heart beats helped determine if a snail was alive. In older snails, when the shell turned opaque, we determined death by the absence of ciliary and muscular movements of the foot and the lack of reaction to touches with a blunt needle.

Asolene platae males and females do not show any signs of external sexual dimorphism (unpublished results). To sex the snails of

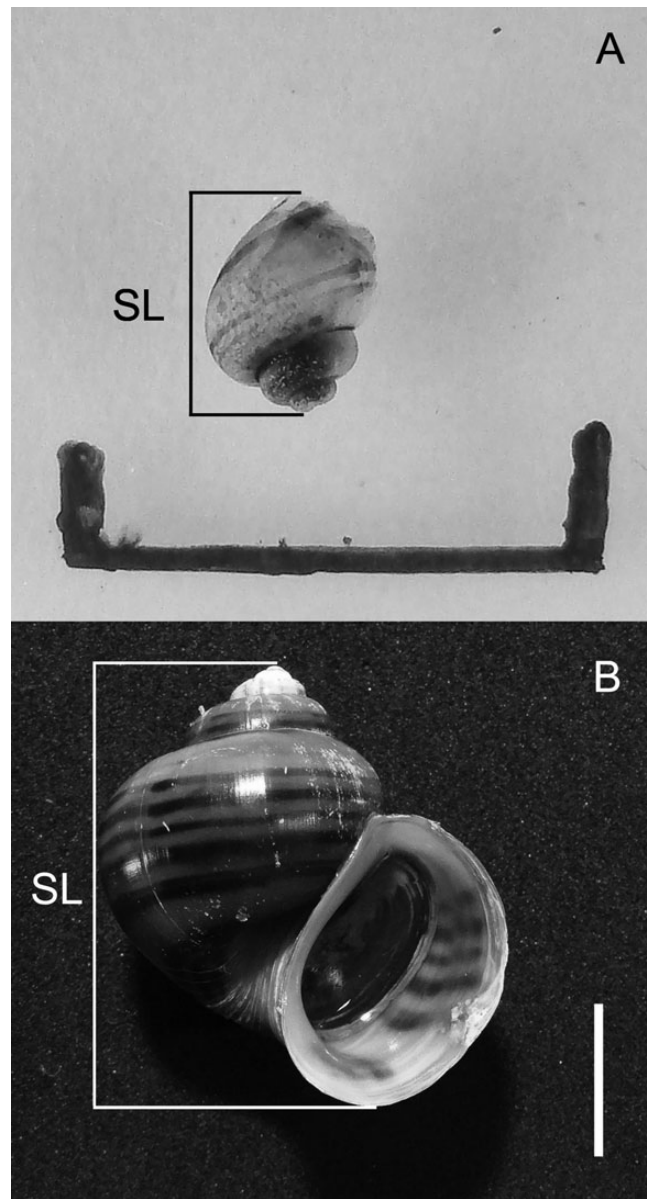


Figure 1. Measurement of shell length (SL) in *Asolene platae* during rearing experiment. **A.** For snails younger than 28 weeks. **B.** For snails older than 28 weeks. Bracket and bar are 1 cm long.

the three cohorts and to determine their sexual maturity, we allowed them to mate under controlled conditions, from the time they reached a mean size of 18 mm until the end of the experiment. Fourteen to 17 snails were placed together once a week for 8 h (the mean duration of copulation is 2.62 h; Tiecher *et al.*, 2014) in cylindrical aquaria (32 cm diameter, 6 cm depth). During the first weeks we also placed three mature females from a laboratory stock into the cylindrical aquaria to make sure the males had the possibility of copulation.

We made observations every 10 min and recorded precopulatory and copulatory behaviours for each snail. Snails that showed mounting behaviour on the shell of other snails (Tiecher *et al.*, 2014) or for which we observed the intromission of the penis sheath into the partner's mantle cavity were categorized as males. As homosexual pairings between males are common, being mounted by a male cannot be used to recognize females (Tiecher *et al.*, 2014). Hence, after the snails were returned to

their individual aquaria we recognized a female when we detected an egg mass within it.

For males, we used the time of first copulation to determine the SL and age at maturity (SLM, in mm, and AM, in weeks, respectively). For females, we used the time of first laying of an egg mass. Dissections after death provided sex determination for the snails that died before showing copulatory behaviour or egg laying. Five snails could not be sexed, because they were partially decomposed when found dead and were categorized as undifferentiated individuals. We also recorded both the age and SL at death of each mature snail (AD, in weeks, and SLD, in mm, respectively).

Once a snail attained sexual maturity, we monitored its RA until the end of the experiment. Once a week we randomly paired mature males and females by putting the male in the female's aquarium and observing copulatory behaviour every 10 min for 8 h. We checked aquaria of females daily for the presence of egg masses, because females are highly cannibalistic with their own egg masses (Tiecher *et al.*, 2014). We counted the number of eggs in each egg mass under a stereoscopic microscope and calculated the total number of eggs laid for each female.

We estimated RA separately for each cohort. For males, RA was estimated as the proportion of males showing copulatory behaviour relative to the number of males alive in a given week. For females, RA was the number of egg masses laid by all the females in a given week relative to the number of females alive. We calculated tertiary sex ratios (number of males that reached maturity relative to the number of mature snails) separately for each of the egg masses of each cohort.

Statistical analysis

Levene's tests performed in advance of two-way ANOVAs for SLM and AM, and for SLD and AD, indicated that there was no homoscedasticity among them; no transformation allowed the assumption of homoscedasticity. Hence we used Welch's unequal variances *t*-test to compare the means of these variables between sexes for each cohort separately and applied the Bonferroni correction for these multiple comparisons ($\alpha = 0.0166$). The deviation from equality of the overall tertiary sex ratio of the three cohorts was tested with a X^2 test.

We fitted the von Bertalanffy model to the growth curves of males and females of each cohort separately. The parameters of the von Bertalanffy model (SL_{∞} , asymptotic SL; K , specific growth rate; t_0 , intercept) were estimated following the maximum likelihood method (Aubone & Wöhler, 2000).

RESULTS

Similar growth patterns of SL occurred for males and females of the three cohorts (Fig. 2). Growth remained continuous during the lifespan of the snails, but the net growth rates decreased steadily and the mean SL reached an asymptotic value (SL_{∞}) of around 26 mm in the case of females and 24 mm in the case of males (Table 1). The K values of females ranged from 0.047 to 0.054 week⁻¹ and those of males from 0.050 to 0.057 week⁻¹. The three cohorts reached 80% of their asymptotic size at the end on their first year of life. The average SL of the females exceeded that of males after 34–40 weeks of life, although the values were not significantly different except for cohort III at the end of the experiment (Fig. 2C). The maximum SL recorded for females and males were 29.6 and 28.7 mm, respectively.

The start of RA showed some variation among cohorts, with values of 40, 60 and 55 weeks for cohorts I, II and III, respectively. One male of cohort III attempted to copulate at 31 weeks of age, but no female of this cohort laid egg masses until week 64. In almost all cases, the males tried to copulate first with the older mature females from the laboratory stock and not with the

females of the same cohort. In two cases, the males mounted snails that proved to be males. The RA of males and females of the three cohorts was mostly continuous throughout the lifespan, albeit with fluctuations in intensity, especially in cohort I (Fig. 2). Part of this variation was related to short-term fluctuations of the temperature of the rearing room beyond the usual range due to extreme meteorological events; the lowest minimum weekly mean was 20.95 °C and the highest maximum weekly mean was 26.83 °C. The RA of females showed a weak, but significant, correlation with the minimum weekly mean temperature of the air recorded in the rearing room ($r = 0.30$, $P < 0.001$, $n = 147$). No significant correlation between RA and mean temperature was found for males ($r = 0.12$, $P > 0.140$, $n = 147$).

The AM and SLM were significantly lower for males than for females ($t_{45.81} = -5.60$, $P < 0.0001$ and $t_{76.03} = -6.59$, $P < 0.0001$, respectively). Males showed a significantly lower AM (Fig. 3A) than females in cohort I ($t_{14.32} = -4.72$, $P < 0.001$), but the difference was nonsignificant in cohorts II and III after Bonferroni correction ($t_{16.20} = -2.33$, $P < 0.033$ and $t_{6.75} = -2.25$, $P < 0.061$, respectively). Males of the three cohorts were significantly smaller than females at maturity (Fig. 3B; $t_{21.13} = -5.03$, $P < 0.001$, $t_{24.0} = -2.24$, $P < 0.004$ and $t_{6.97} = -4.79$, $P < 0.002$ for cohorts I, II and III, respectively). The number of eggs laid per female during the whole lifespan totalled 1635, 961 and 1748 for the three cohorts (grand mean: 1429.9 eggs per mature female), compiled from 26.52, 12.42 and 22.19 egg masses (grand mean: 20.61 egg masses per mature female). The average oviposition rates of cohorts I, II and III during the reproductive phase were 0.39, 0.26 and 0.34 egg masses and 10.62, 8.35 and 11.27 eggs per female per week.

The survivorship curves of the three cohorts exhibited similar declines (Fig. 4), with three differentiated phases: a high mortality phase (53–76%) during the first 2–8 weeks, an almost zero mortality phase up to 100–118 weeks of age and a final phase with a steady decline in the number of survivors until the end of the experiment (201 and 188 weeks for cohorts I and II, respectively) or, in the case of cohort III, until the death of the last snail at 184 weeks. The survivorship curves of males and females showed no consistent differences. The age at death did not differ between sexes for any of the cohorts (*t*-tests, $P > 0.073$ in all cases). The SLD differed significantly only for males and females of cohort III ($t_{15.0} = -3.20$, $P < 0.006$). Only 43, 40 and 24% of the snails of cohorts I, II and III, respectively, reached maturity.

The tertiary sex ratio of the three cohorts showed some variation, being 0.60, 0.53 and 0.44 for cohorts I, II and III, respectively. Most of the variation in the tertiary sex ratio appeared associated with the different egg masses used to initiate the cohorts (Fig. 5). The sex ratio of the egg masses varied from 0.25 to 0.76, but the overall ratio for the nine egg masses (0.52) did not differ significantly from 0.5 ($X^2 = 0.383$; $P = 0.536$).

DISCUSSION

Growth of *Asolene platae* remained continuous during the 4-year lifespan, although the growth rates decreased steadily and the snails reached 80% of their asymptotic size ($SL_{\infty} = 24.87$ mm on average) at an age of 1 year. The growth curves of other apple snails under constant conditions also show an asymptotic tendency after several months of life (Hayes *et al.*, 2015), but quasi-asymptotic sizes are attained in a shorter period than in *A. platae*. The specific growth rates of *Pomacea patula* under laboratory conditions at 25–26 °C and with artificial diets (Espinosa-Chavez & Martinez-Jeronimo, 2005; Vazquez Silva *et al.*, 2012) were higher ($K = 0.055$ – 0.071 week⁻¹) than the average observed here ($K = 0.052$ week⁻¹).

The growth patterns of males and females of *A. platae* appeared similar, with the latter attaining slightly larger sizes at the same age. In terms of the von Bertalanffy model the females

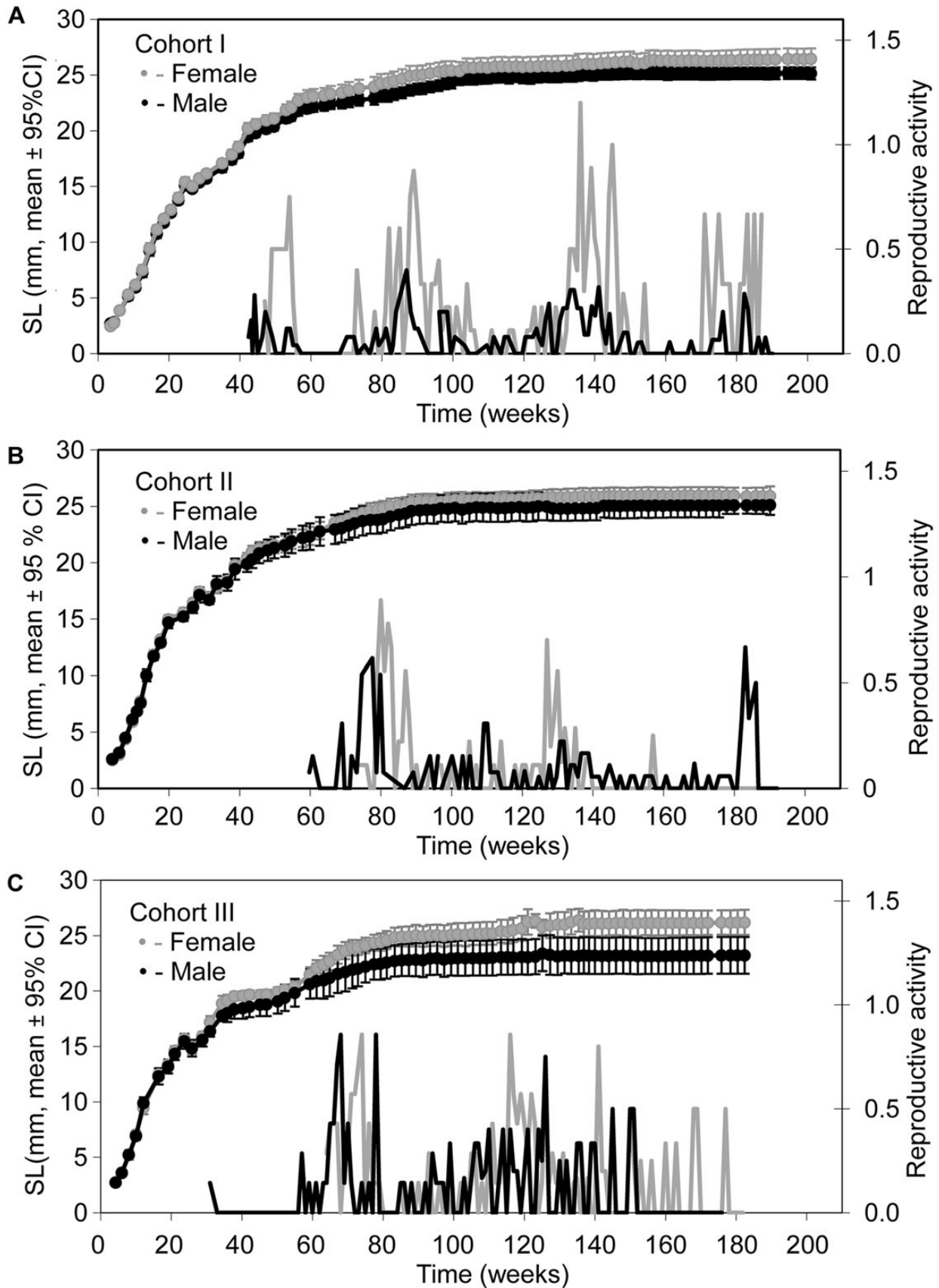


Figure 2. Growth and reproductive activity of males and females of *Asolene plataea*. **A.** Cohort I. **B.** Cohort II. **C.** Cohort III. Left y-axis: maximum shell length (SL) attained by males and females that reached maturity; right y-axis: reproductive activity (proportion of males that copulated each week or mean number of egg masses per female per week).

attain higher asymptotic sizes than the males, but the latter grow to their asymptotic sizes at a slightly higher specific rate than the females. The sexual dimorphism in the growth of curves is less marked than in *P. canaliculata* (Estebenet & Cazzaniga, 1998; Estebenet & Martín, 2003). Males of *A. platae* mature at a smaller size than females (21.16 and 24.53 mm, respectively). Martín (1987) observed in a natural population of *A. platae* that the mean sizes of males with mature gametes were slightly smaller than those of females in the same condition (20.3 and 22.06 mm, respectively). In a related genus, Demian & Ibrahim (1972) reported smaller sizes at maturity for males (23–24 mm) than for females (24–25 mm) of *Marisa cornuarietis*. Within the Ampullariidae, females usually attain large sizes more frequently than males (Estebenet *et al.*, 2006; Hayes *et al.*, 2015).

On average, males of *A. platae* matured much earlier (at 55.02 weeks) than females (84.88 weeks). To date, sexual dimorphism in age at maturity in ampullariids has been studied only in *P. canaliculata* (Tamburi & Martín, 2009). For *P. canaliculata* reared under the same conditions (individual aquaria at 25 °C), the delay between the first copulation of males and the first egg mass of females was shortest (3 weeks) when food availability was high, but reached values between 27 and 38 weeks when food availability was low. The age at maturity for females of *A. platae*

Table 1. Parameters of the von Bertalanffy growth model for females and males of the three cohorts of *Asolene platae* and correlation coefficient (*r*) between the observed values of SL and those predicted by the model.

	Cohort I		Cohort II		Cohort III	
	Females	Males	Females	Males	Females	Males
SL _∞ (mm)	26.025	24.894	25.723	24.853	25.850	23.010
<i>K</i> (week ⁻¹)	0.049	0.050	0.054	0.057	0.047	0.057
<i>t</i> ₀ (week)	15.954	15.478	14.492	13.970	14.365	12.465
<i>r</i>	0.996	0.995	0.993	0.994	0.989	0.991

(84.88 weeks) is five times higher than that estimated for *P. canaliculata* females (15 weeks; Tamburi & Martín, 2009) and also higher than those of *M. cornuarietis* and *P. bridgesii* reared in groups under similar conditions (25 °C and high food availability): 18–21 weeks (Aufderheide *et al.*, 2006) and 27 weeks (Coelho, Calado & Dinis, 2012).

A mature *A. platae* female laid on average 20.61 egg masses during its whole lifespan, for a sum total of 1429.9 eggs. The number of eggs is lower than those of *P. maculata* (2066 eggs per egg mass with 16–18 egg masses per warm period; Barnes *et al.*, 2008) and *P. canaliculata* (4407–4641 eggs per female; Martín &

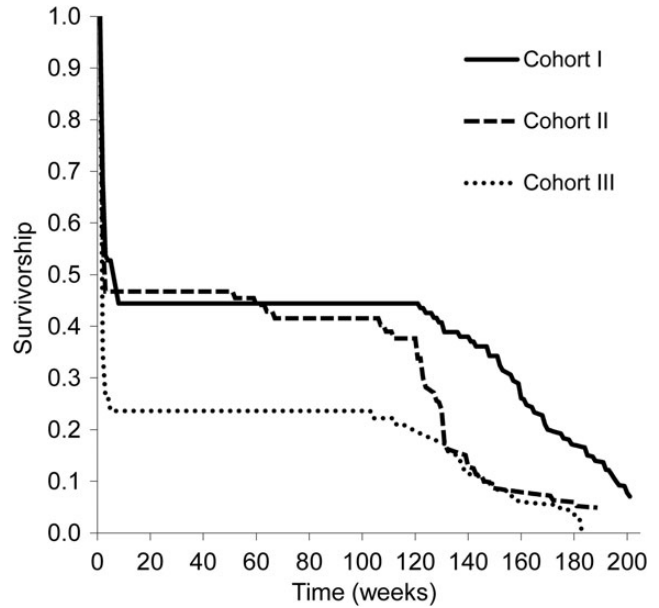


Figure 4. Survivorship curves of *Asolene platae* from cohorts I, II and III.

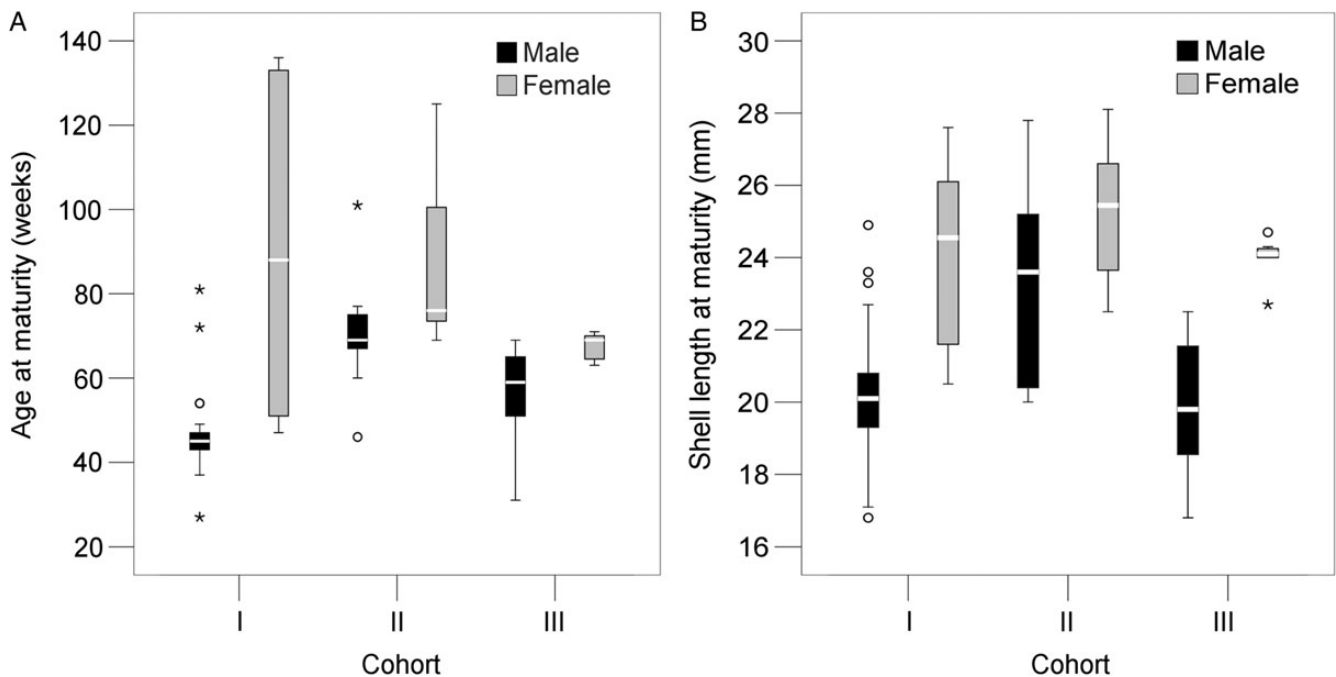


Figure 3. Maturity of males and females of *Asolene platae* from cohorts I, II and III. **A.** Age at maturity. **B.** Shell length at maturity. Graphical conventions: box, interquartile range; white line, median; bars, minimum and maximum values; circles and asterisks indicate outliers and extreme values (values between 1.5 and 3, or more than 3 box lengths from upper or lower edge of the box, respectively).

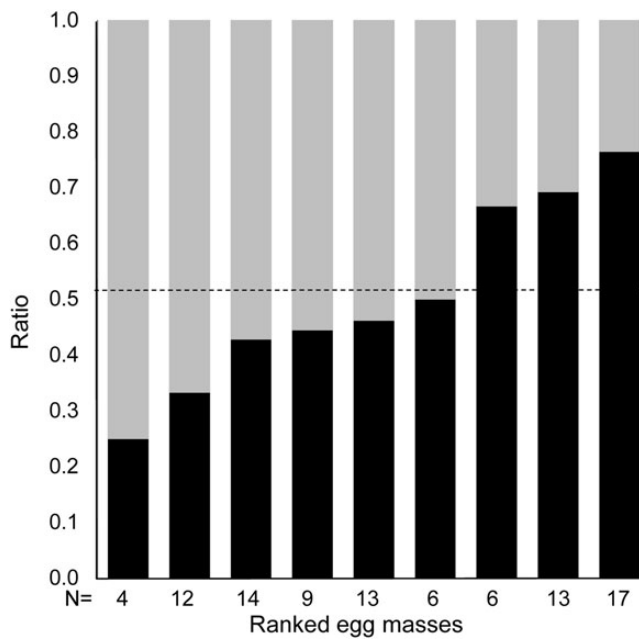


Figure 5. Tertiary sex ratio for each egg mass of *Asolene platae* used to constitute cohorts I, II and III. Grey bars indicate females and black bars, males; dashed line shows the average sex ratio of all egg masses; N is the number of snails that reached maturity and were sexed.

Estebenet, 2002), but the number of egg masses appears similar (19–28 on average). Lifetime estimations of fecundity remain rare in apple snails with subaquatic egg masses, but the oviposition rates of 0.24 egg masses (Aufderheide *et al.*, 2006) and 7–42 eggs (Oehlmann *et al.*, 2006) per female per week reported for *M. cornuarietis* approach the lifetime averages for *A. platae* (0.33 egg masses and 45.06 egg per female per week, respectively).

The survivorship curves of *A. platae* showed a high mortality (63% on average) during the first 2–8 weeks, followed by 2 years of almost zero mortality and finally by a continuous and steady fall in the number of snails that remained alive. At least 7% of the snails in each cohort lived past 3 years in culture. In cohort I, 7% of the snails survived up to 4 years. The cohort survivorship curves of *A. platae* corresponded to Dewey's Type III, while those of the *P. canaliculata* studied to date belong to Type I (i.e. almost all mortality concentrated at the advanced ages) when reared under optimum conditions (Estebenet & Martín, 2002; Tamburi & Martín, 2009; Seuffert & Martín, 2013). Contrary to the hatchlings of *Pomacea* species (Seuffert & Martín, 2009; Coelho *et al.*, 2012), those of *A. platae* do not seem fully competent during the first weeks of independent life, because they start to feed on thawed lettuce only in their third week of age and to breathe air at 8–10 weeks of age (Tiecher *et al.*, 2014). Food quality seems crucial for posthatching survival, since for *M. cornuarietis* high mortality rates (up to 55%) were observed during the first 14 weeks of life when fed on some aquatic plants but not on others (Arsuffi *et al.*, 1993).

The survival values at 700 d for *M. cornuarietis* (24–45%) (Arsuffi *et al.*, 1993) are similar to those observed here for *A. platae*, but they may have been somewhat increased by the lower temperature (21 °C, compared to our study at 25 °C; Seuffert & Martín, 2013). Between 5 and 17% of the *A. platae* snails survived after 3 years and 9 months (180 weeks) and 7% survived 4 years in cohort I. These figures exceed those of *P. canaliculata* at 25 °C, where the average longevity ranged from 8.4 to 11.4 months and the maximum longevity recorded was less than 2 years (21.7 months; Martín & Estebenet, 2002).

The tertiary sex ratio of the three cohorts did not differ significantly from 0.5, but the sex ratio of the nine egg masses used to initiate them varied greatly, from 0.25 to 0.76. Martín (1984b) also reported a balanced sex ratio of 0.49 in a natural population of *A. platae*. Such variation in sex ratio among egg masses, combined with a balanced ratio in the population, reflects the situation observed in *P. canaliculata*, in which sex determination depends on a few genes located on different chromosomes (Yusa, 2007). Conversely, in laboratory and outdoor experimental populations of *M. cornuarietis*, a female-biased sex ratio occurred (0.41–0.43; Demian & Ibrahim, 1972).

The evidence obtained here under laboratory conditions allows inference of some of the characteristics of the life cycle of *A. platae* under field conditions. According to Martín (1987, 2002), the reproductive period of *A. platae* in the Río de la Plata extends from November to March (late spring-summer) and the snails remain buried in mud during the colder months. Little to no growth, feeding and general activity occurs for *A. platae* at 15 °C (Tiecher *et al.*, 2015). The climate in the Río de la Plata area is warm and temperate with monthly mean temperatures fluctuating between 23.6 °C (January) and 10.6 °C (July) and below 15 °C from May to September. As the minimum absolute age at maturity for a female was 11 months (19.8 months on average) under laboratory conditions (25 °C \pm 2), it is highly unlikely that under field conditions *A. platae* females mature in their first summer. Probably most of them mature in their second or third summer.

The maximum longevity observed in the laboratory was 4 years, although in temperate regions this would probably be extended due to the low temperatures during the winter months. The same occurs in *P. canaliculata*, in which mortality drops almost to zero during cold months and longevity increases to 4 years when reared under fluctuating room temperatures (9–29 °C) as compared to 1 year at 25 °C (Estebenet & Cazzaniga, 1992; Estebenet & Martín, 2002). Temperatures of 15 °C for 25 d does not affect mortality of *A. platae* (Tiecher *et al.*, 2015), but perhaps temperatures below this limit would reduce the percentage of snails surviving up to a certain age. In general we expect higher maximum longevities in the field, but at the same time a lower percentage of snails to survive to those extreme ages.

The RA of *A. platae* females, but not of males, seems to be very sensitive to temperature. Although egg laying was mostly continuous in our rearing room at 25 °C, we observed some fluctuation that was correlated with uncontrolled drops in temperature during the winter. In the same rearing room as the one used in the present study, *P. canaliculata* never showed an effect of temperature variations (e.g. Martín & Estebenet, 2002; Tamburi & Martín, 2009; Burela & Martín, 2011; personal observation). Janer *et al.* (2006) observed that *M. cornuarietis* snails kept under constant conditions nevertheless display a clear reproductive seasonality.

Estebenet & Cazzaniga (1992) showed that the life cycle of *P. canaliculata* changes from annual and semelparous (one reproductive period in the lifespan) at 25 °C to tetra-annual and iteroparous (more than one reproductive period) at room temperature (9–29 °C). On the basis of our laboratory data for *A. platae*, it seems possible that, in temperate environments, males mature in their second summer and females during their second or third summer, and that both could reproduce again during the following summers. The total number of reproductive periods during the lifespan of *A. platae* depends on the survival rates and longevity in the field. If one assumed the same longevity as in the laboratory, some snails would reproduce at least during three consecutive summers. The proposed life cycle of *A. platae* seems to fall in the category *Hi* of Dillon (2000: 157), established for “populations that require 24–35 months to mature and reproduce iteroparously”.

Martín (1984b) reported a unimodal size-frequency structure for a stream population of *A. platae* in the Río de la Plata basin, with snails between 20 and 25 mm usually being the most abundant all the year round and only a few snails reaching sizes between 25 and 30 mm. The continued presence of size classes corresponding to mature snails (Martín, 1987) indicates that *A. platae* snails were probably iteroparous, with a life cycle longer than 1 year. This size structure agrees with our data showing a 4-year lifespan and asymptotic growth up to 25 mm. As their growth is low and their survivorship high, snails tend to accumulate in the modal size class (20–25 mm), which thus represents a multicohort group of mature snails able to reproduce in several successive summers.

The scattered information for apple snails indicates a dominance of iteroparous and multiannual life cycles, like the one proposed here for *A. platae*. In tropical areas with a dry season, lifespans of 2.5–3.5 years and two to three reproductive seasons have been reported for *Pomacea* species (Burky, 1974; Lum-Kong & Kenny, 1989; Ocaña *et al.*, 2015). A similar life cycle has been proposed for the southernmost populations of *P. canaliculata*, although in this case the snails remain inactive during the cold months (Estebenet & Martín, 2002; Martín & Estebenet, 2002). In a permanent artificial pond in India, *Pila globosa* attained its maximum size after 4 years, but the lifespan was supposed to be longer in natural waterbodies considering the periods of dormancy during the dry season (Haniffa, 1980). *Pomacea paludosa* in Florida wetlands seems to be an exception, because it represents an annual species with a strong postreproductive die-off (Darby, Valentine-Darby & Percival, 2003), thus revealing a semelparous life cycle. In the genera with subaquatic egg masses there is also great variation: a lifespan of 5–10 years was estimated for *Lanistes nyassanus* in Lake Malawi (Louda & McKaye, 1982), whereas an AM of 4 months and a survival of only 0.03% after 1 year of life were reported for *M. cornuarietis* introduced to Sudan (Haridi, El Safi & Jobin, 1985).

Specimens of *Asolene* obtained from natural populations within the natural range of *A. platae* (Lower Paraná river and the southern shore of Río de la Plata) are traded as ‘zebra apple snails’ in pet shops and on aquarist websites in Argentina (PRM, personal observations; Tiecher *et al.*, 2015). These practices open the gate to introduction of this species to other regions of Argentina, South America and to other continents in the future, as has happened with other apple snails (Cowie *et al.*, 2009; Horgan *et al.*, 2014). Several attributes of the life cycle of *A. platae* (slow growth, high posthatching mortality, late maturation and relatively low fecundity) indicate that its invasive potential may be low relative to that of *P. canaliculata* and of *M. cornuarietis*. On the other hand, the ability to store viable sperm for up to 169 d (Tiecher *et al.*, 2014) appears comparable with that of *P. canaliculata* (up to 140 d) and probably increases the chances of successful establishment. The long lifespan and iteroparous strategy may be traits increasing the probability of persistence once a population gets established. On the whole, the life-cycle strategy of *A. platae* seems less suited to unstable or unpredictable environments than that of the invasive apple snails (*P. canaliculata*, *P. maculata* and *M. cornuarietis*) and indicates that the high population resilience of the latter cannot be taken for granted for all apple snails.

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