REACTION NORMS OF SIZE AND AGE AT MATURITY OF *POMACEA CANALICULATA* (GASTROPODA: AMPULLARIIDAE) UNDER A GRADIENT OF FOOD DEPRIVATION

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ABSTRACT

Pomacea canaliculata, an apple snail native to South America, has become a serious pest of aquatic crops and a promoter of ecosystem changes in natural wetlands worldwide. Its success as an invader has been attributed to its great phenotypic plasticity in life-history traits. Our aims were to determine the reaction norms of size and age at maturity under a gradient of food deprivation. Full sibling experimental snails were reared in isolation from hatching and maintained until maturity under seven different levels of relative food deprivation based on size-specific ingestion rates. To detect the onset of sexual activity of experimental snails, fully mature virgin snails reared in the laboratory were used as consorts. The reaction norms for age and size at maturity of *P. canaliculata* showed marked sexual dimorphism. Shell length was the main component of variation in the male reaction norms for both copulation and egg-laying by female consorts, whereas age was the main component of variation for females. Irrespective of the intensity of food deprivation, males mature at the same age at the expense of size, since size is apparently irrelevant in the access to females and male fitness can be maximized through fast maturation. In contrast, a minimum size is required for females to reach maturity, perhaps as a result of their higher reproductive costs. The highly dimorphic reaction norms lead to an increasing lag between male and female maturity as deprivation increases; in temperate regions, males born early in the reproductive season would mature in the same season irrespective of food availability, while most females would have to overwinter before attaining sexual maturity in unproductive habitats or those dominated by unpalatable macrophytes. The great life-history plasticity reported in invaded areas could be a heritage from populations in the native range.

INTRODUCTION

Pomacea canaliculata (Lamarck, 1822) is a freshwater snail native to South America whose natural distribution ranges from subtropical Southern Brazil to the temperate Southern Pampas (Buenos Aires Province, Argentina). This macrophytophagous species, and other congeneric apple snails, have invaded Eastern Asia and North America, becoming pests on Asian aquatic crops and promoting ecosystem changes in natural wetlands (Carlsson, Brönmark & Hansson, 2004; Cowie, Hayes & Thiengo, 2006; Rawlings *et al.*, 2007).

Pomacea canaliculata shows a high degree of inter- and intrapopulation variation in conchological (Estebenet, Martín & Burela, 2006) and life-history traits (Estebenet & Martín, 2002), most of which can be attributed to phenotypic plasticity (Martín & Estebenet, 2002; Estebenet & Martín, 2003). From an evolutionary viewpoint, size and age at maturity are two of the most significant life-history traits. Estoy *et al.* (2002a), working with field-collected juvenile *P. canaliculata* from Japan, showed that food deprivation differentially affects the time that males and females require to reach maturity and the size attained at this state.

Reaction norms are an interesting approach to phenotypic plasticity describing the different phenotypes a single genotype produces over a range of environmental conditions (Van Dooren, 2001). For a snail that lives in environments so varied and variable as does *P. canaliculata* (Martín, Estebenet & Cazzaniga, 2001), the evolution of reaction norms optimizing age and size at maturity under different conditions would be expected. Stearns (1992) proposed three basic rules for the

maturation event across a range of growth rates (e.g. imposed by food availability). Rule one is to mature always at the same size, even at the risk of dying before reproducing; rule two is to mature always at the same age at the cost of a diminished size and fecundity; rule three is a compromise between age and size at maturity that results from the evolutionary trade-off between these risks and costs. For the last case, a number of theoretical reaction norms have been developed on the basis of fitness optimization models under precise assumptions about the relationships between mortality, growth and fecundity rates (e.g. Perrin & Rubin, 1990; Stearns, 1992). Among the empirical approaches to the study of phenotypic plasticity evolution, the manipulation of environmental variables to expose reaction norms provides relevant information about past selective pressures and potential performance under different conditions (Schlichting & Pigliucci, 1998).

A reaction norm model for female maturity in *P. canaliculata* has been previously proposed on the basis of the first egg mass laid by laboratory cohorts from different studies (Estebenet & Martín, 2002), suggesting that both a minimum age and size are required and that maturity occurs when both have reached their respective minima. The aims of our study were to investigate the shape of reaction norms for age and size at maturity of male and female *P. canaliculata* when subjected to a wide range of food deprivation levels from the early stages of their independent life.

MATERIAL AND METHODS

Pomacea canaliculata is a dioecious snail whose females lay aerial egg masses composed of hundreds of calcareous eggs on

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emergent substrata. Copulations are long lasting (8–20 h; Burela & Martín, 2007) and double paternity occurs in a single egg mass (Yusa, 2004). To minimize genetic variation among experimental snails, hatchlings were obtained from a single egg mass laid by a laboratory female that had been coupled during all her life with the same male. Both parents were obtained from egg masses collected at the Curamalal stream (Encadenadas del Oeste basin), a short permanent watercourse located near the southern natural distribution limit of this species, which has been the subject of previous studies (Martín & Estebenet, 2002; Estebenet & Martín, 2003).

Rearing conditions were the same for all the snails: tap water saturated with calcium carbonate (renewed once a week), temperature of $25 \pm 3^{\circ}C$ and a 14:10 (light:dark) photoperiod. Fresh lettuce was the only food source used during the two main phases of the experiment: Isolation Phase (without access to mates; first 12 weeks of life) and Pairing Phase (with access to mates; 13 weeks of life onwards). Experimental hatchlings were reared for 3 weeks in a 20-l aquarium and then 84 snails were randomly selected (mean shell length $\pm$ SE = 4.96 $\pm$ 0.056 mm, $n = 25$), assigned to seven different levels of food deprivation (FD%) and reared thereafter individually in 3-l aquaria.

To detect the onset of sexual activity of experimental snails, mature virgin snails fed *ad libitum* were used as consorts. Consort snails were born 3 months earlier than experimental snails (from egg masses of the same stream) and were mass-reared in 20-l aquaria until their sex could be determined (see below). Thereafter males and females were reared in isolation to secure their virginity and identity.

Food deprivation levels were projected relative to the amount of lettuce that a snail of a certain size consumed under *ad libitum* conditions. Daily ingestion of hydrated drained lettuce was estimated through 24 h trials (temperatures of $25 \pm 3^{\circ}C$ and 14:10 (light:dark) photoperiod) under *ad libitum* conditions (unpublished results). Snail size range was 3.54–55.18 mm. A power model for the daily lettuce ingestion was obtained by least-squares linear regression, using shell length as the independent variable. Six levels of relative food deprivation (FD%: 13, 27, 40, 53, 67 and 80) were evenly set using the values predicted by the regression model as the non-deprived level (FD 0%).

For the experimental snails the same rearing regime was maintained throughout the experiment. On Mondays water was changed, aquaria were cleaned and shell length was measured (using a micrometric lens during the first 6 weeks and a calliper thereafter). The weekly ration for each FD% level was calculated according to its mean shell length and provided in two half-doses on Tuesday and Friday, so the snails were able to feed except from 8.00 am on Mondays to 8.00 am on Tuesday.

Each Monday experimental snails were carefully observed to detect as soon as possible the testis through the translucent shell (Takeda, 1999) and the humping of the operculum in males (Estebenet *et al.*, 2006). After a 9-week rearing period, 12 surplus snails from the initial 84 were discarded because of restrictions on rearing facilities. The final number of males was five in each FD% level, but for females it varied from three to six, since it was not possible to balance the design due to male-biased sex ratios.

Sexual maturity of consorts was checked before the onset of the Pairing Phase (six consort–consort couples were formed and all readily copulated). Each of the remaining consort snails was randomly assigned to a marked experimental snail and these couples were maintained up to the end of the experiment. Two supplementary cohorts of consorts were reared to be coupled with the experimental snails taking longer to mature, in anticipation of a possible senescence of the first consorts.

To avoid trophic interference between the experimental snails and their consorts during the Pairing Phase, they were put together for 24 h on Mondays (during which they were not fed). Copulatory behaviour was recorded at least on six occasions; snails were considered to be copulating when the male was tightly attached to the right side of the female's body whorl (Burela & Martín, 2007) on two consecutive observations. The number of egg masses laid by experimental females on their aquarium walls was recorded daily except on weekends. After the onset of the Pairing Phase the consort females were also individually maintained in 3-l aquaria to record their egg masses, while male consorts were collectively maintained in 20-l aquaria (up to 13 snails per aquarium). Both were fed *ad libitum* for the rest of the experiment.

Experimental-consort couples were reared for 4 weeks after their first egg mass. The egg masses were incubated at room temperature and most of them hatched normally; experimental snails were sacrificed and stored for later analysis, results of which will be published elsewhere.

Most variables (five out of six in each sex) showed a significant heterogeneity of variances (Levene's test) that could not be resolved with the general transformations suggested by the Box-Cox method. The prevalent heteroscedasticity precluded the use of parametric multi-factorial analysis so that their statistical analysis was performed through non-parametric tests. The Kruskal–Wallis test was used to test for significant differences in the mean rank of the deprivation levels. In the instances where this test was significant, Cuzick's test (Cuzick, 1985) was used to detect monotonic trends in the variables that showed a significant effect of food deprivation. All non-parametric tests were two-tailed and corrected for ties.

RESULTS

The snails subjected to different food deprivation levels showed differences in the timing of appearance of the first externally noticeable sexual character (i.e. a whitish testicular mass over the dark background of the midgut gland at the apex of males). Most males in the lowest FD% levels (0–54%) could be sexed in the second week of the Isolation Phase, while those of the highest levels (FD 67–80%) could be sexed with certainty only by the fourth week. In addition, the testes at these levels were difficult to observe due to their faintness.

The effects of food deprivation on all the variables studied were very different for males and females of *Pomacea canaliculata*, so separate analyses were performed for each sex. The growth trajectories of males from all FD% levels were linear up to the onset of egg-laying of their consorts (Fig. 1). Some males from FD 0%, FD 13%, FD 27% and FD 53% copulated in the first week of the Pairing phase; most males began to show copulatory behaviour between 12 and 14 weeks of age.

The time required by males to begin to copulate showed a monotonically increasing trend with food deprivation (Fig. 2A; Table 1); the males under the highest level of deprivation copulated at older ages than those under the six other levels (one-tailed Mann–Whitney comparisons corrected by Dunn-Sidak, $P = 0.045$). The shell length at first copulation showed a monotonically decreasing trend with food deprivation (Fig. 2B; Table 1), showing a steeper decrease beyond the FD 40% level.

The age of experimental males at the appearance of the first egg mass laid by their female consorts showed a monotonically increasing trend with food deprivation (Fig. 2A; Table 1); under the highest FD% level the consorts laid their first egg mass at older ages than those of the other six (one-tailed Mann–Whitney corrected by Dunn-Sidak, $P = 0.024$), after approximately 178 days as compared to 91 days (median values) for the consorts of non-deprived males. The shell
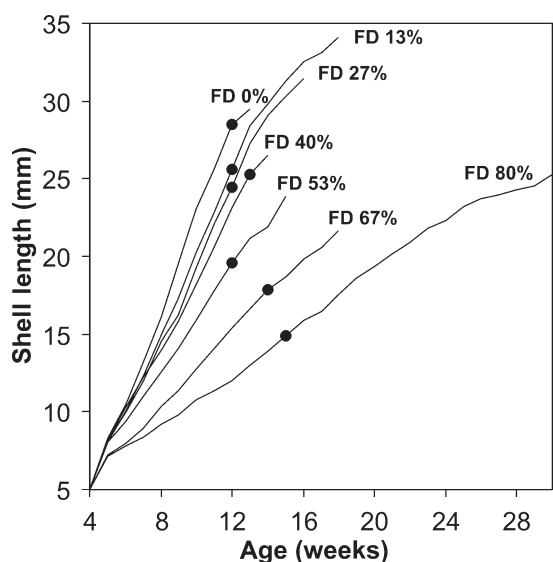
Figure 1. Mean growth curves for *P. canaliculata* males under a gradient of food deprivation. Dots indicate the first copulation of each FD%. Curves extend up to the first egg mass of the last consort female to reach maturity of each FD%.

length of the experimental males at first egg mass showed a predominantly monotonically decreasing trend with food deprivation (Fig. 2B, Table 1), although the most deprived males attained a larger shell length than those at the two immediately lower FD% levels.

For the experimental males the average delay from the first copulation to the first egg mass and the growth during that period both showed a monotonic increase with food deprivation (Fig. 2A, Table 1). The delay ranged from a median value of 7 days (for the FD 0% to FD 67% levels) to 73 days for the highest level of deprivation (FD 80%), which was significantly delayed relative to the other levels (one-tailed Mann–Whitney corrected by Dunn-Sidak, $P = 0.018$). The FD 80% males showed copulatory behaviour on most Mondays during the delay. The growth during the delay was also significantly higher for the most deprived males (one-tailed Mann-Whitney corrected by Dunn-Sidak, $P = 0.015$).

The consort snails, fed *ad libitum*, grew during the two phases of the experiment but their growth rate decreased steadily after maturity (i.e. during the Pairing Phase). Consequently, the ratio of shell length of the experimental males to their corresponding consorts increased during the Pairing Phase, although the increment was slower for the deprived snails (Fig. 3). Many of the differences detected in the analyses of males seem to be due to the most deprived level, probably as a result of this size asymmetry (see
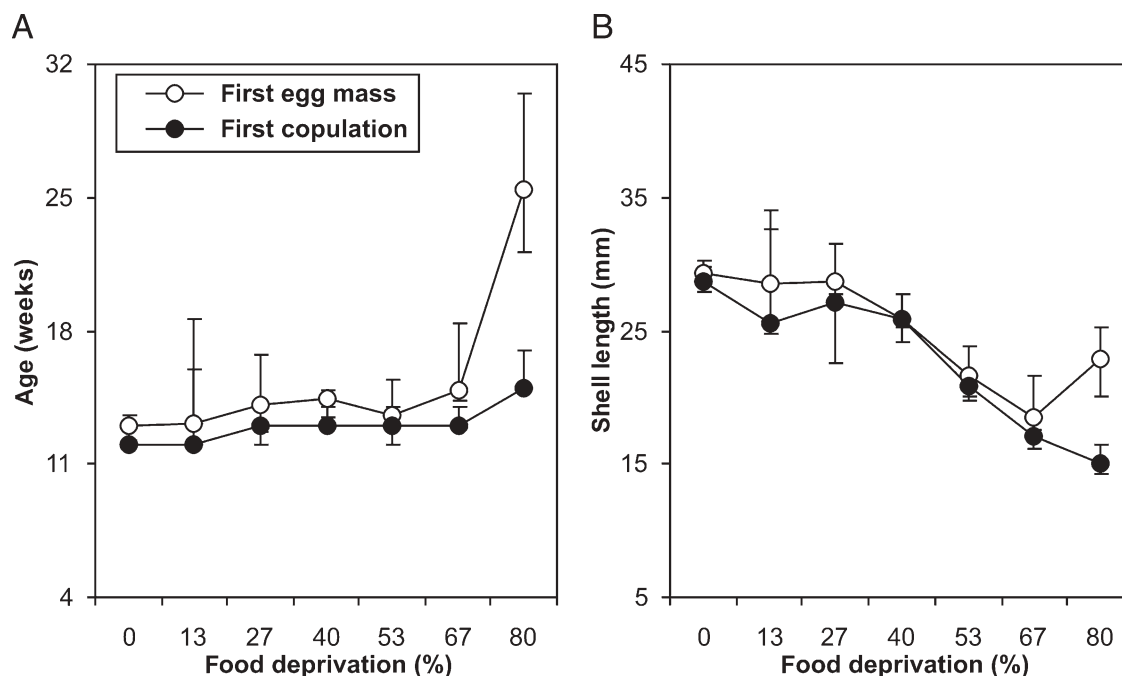

Figure 2. Age and size of *P. canaliculata* males at first copulation and at their consorts' first egg mass under a gradient of food deprivation. **A.** Age; **B.** Shell length. Dots are medians; bars extend between the extreme values ($n = 5$).

Table 1. Non-parametric tests of the variables related to maturity for males of *Pomacea canaliculata* (*P*, probability value; z and X^2, values of normal standardized and Chi-square statistics for the tests, respectively).

		Age at first copulation (weeks)	Shell length at first copulation (mm)	Age at first egg mass (weeks)	Shell length at first egg mass (mm)	Delay (days)	Growth during delay (mm)
Kruskal–Wallis rank test	X^2_6	17.955	29.524	20.291	25.283	19.906	19.674
	P	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Cuzick's trend test	z	3.47	−5.34	4.056	−4.46	3.34	3.43
	P	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
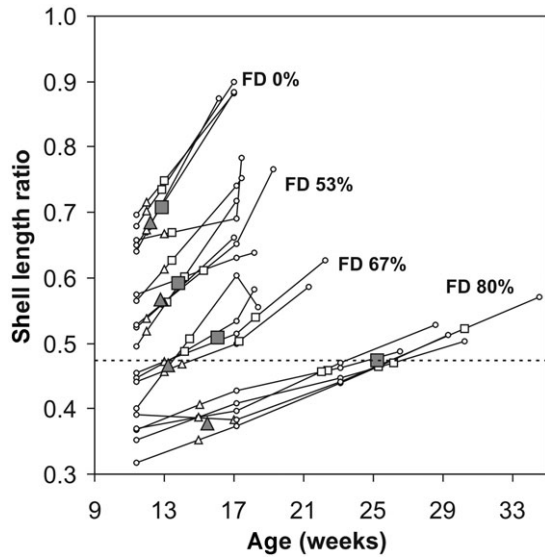
Figure 3. Experimental male-to-consort-female shell length ratios for individual couples during the Pairing Phase (dots). Triangles indicate the first copulation and squares indicate the first egg mass of the female consort (full symbols indicate the mean value for each food deprivation level (FD%); FD 13%, FD 27% and FD 40% occupied positions between FD 0% and FD 53%). Dotted line marks the minimum ratio registered in the field (0.48).
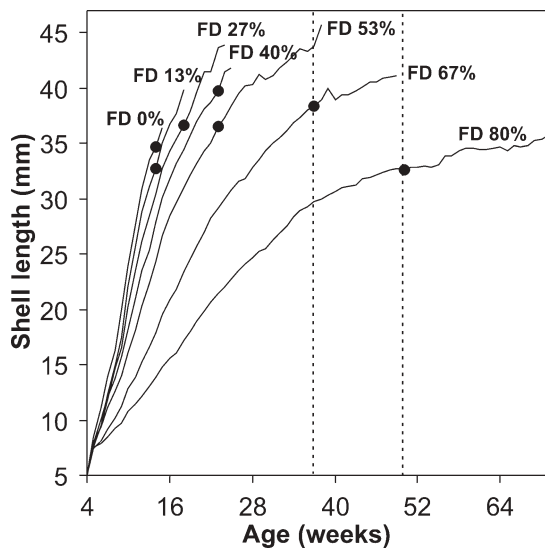
Figure 4. Mean growth curves for *P. canaliculata* females under a gradient of food deprivation. Dots indicate the first copulation of each FD%. Curves extend up to the first egg mass of the last consort female to reach maturity of each FD%. Dotted lines mark the substitution of male consorts.

Discussion). Performing the same tests without this FD% level, the effect of food deprivation on the age at first copulation and at first egg mass, on the delay between them, and on the growth during this delay, all became non-significant (Table 2). In contrast, shell lengths at first copulation and at first egg mass maintained their monotonic decrease.

The growth patterns of experimental females were linear during most of their pre-reproductive life for all FD% levels, but the growth rate showed a decrease after reaching a shell length of approximately 30 mm (Fig. 4). Consort snails were substituted at 37 weeks of age, only for females that had not copulated until then (mostly from FD 67% and FD 80% levels). Most females from the FD 67% level copulated during the first or second week after consort substitution (Fig. 4). After a second substitution at 50 weeks of age, three females from the FD 80% level copulated, while the other three did not show copulatory behaviour up to the end of the experiment (70 weeks). After each substitution, the replaced male consorts were paired with mature females from a laboratory stock (25–45 mm) and all of them then copulated readily.

The age at which experimental females began to copulate showed a monotonic increase with food deprivation (Fig. 5A, Table 3), ranging from 105 to 350 days (median values). The shell length at first copulation displayed a symmetric, non-monotonic response to food deprivation with a maximum between the FD 40% and FD 53% levels (Fig. 5B, Table 3). The delay between the first copulation and the first egg mass showed no influence of food deprivation and was less than a week for more than 80% of the experimental females (Fig. 5A, Table 3). Consequently, the age and shell length at first egg mass showed almost identical values and trends to those of the corresponding variables at first copulation (Figs 5A, B, Table 3).
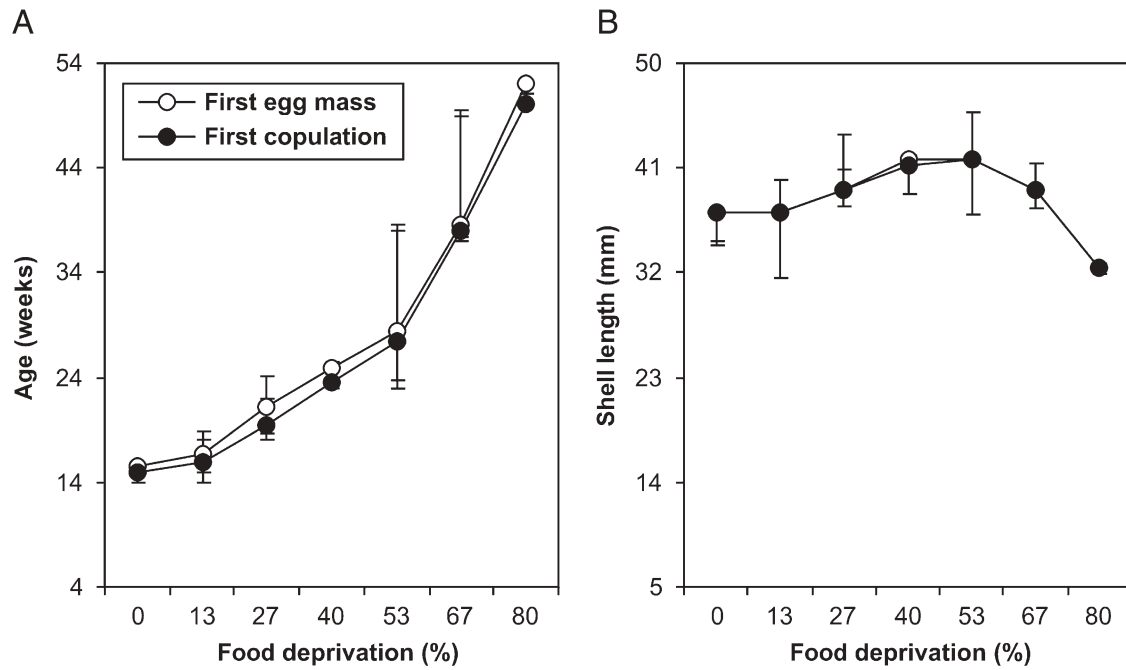
The bivariate reaction norms for age and size at maturity of male and female *P. canaliculata* were highly dimorphic and non-overlapping (Fig. 6). In the female reaction norm of first copulation, age showed a greater relative variation than shell length (coefficient of variation CV = 41% and 9%, respectively). In contrast, for males the reaction norm varied less in age than in shell length (CV = 10% *vs* 27%, respectively). The reaction norm of first egg mass for females showed the same pattern as for first copulation (CV = 40% and 9% for age and length, respectively), whereas for males the pattern was inverted (CV = 28% *vs* 17% for age and shell length respectively). However, when the most deprived males were excluded from the analysis the pattern for copulation and first egg mass (CV = 7% and 11% for age and CV = 19% and 17% for shell length, respectively) was the same.

DISCUSSION

The age at first copulation in *P. canaliculata* males was independent of food deprivation and consequently of size. Only males under the extreme levels of deprivation copulated a little earlier or later than the intermediate males. Many males from

Table 2. Non-parametric tests of the variables related to maturity for males of *Pomacea canaliculata* excluding the FD 80% treatment (*P*, probability value; *z* and X^2: values of normal standardized and Chi-square statistics for the tests, respectively).

		Age at first copulation (weeks)	Shell length at first copulation (mm)	Age at first egg mass (weeks)	Shell length at first egg mass (mm)	Delay (days)	Growth during delay (mm)
Kruskal–Wallis rank test	X^2_6	8.141	23.183	10.502	21.335	9.965	8.458
	P	0.149	<0.01	0.062	<0.01	0.076	0.133
Cuzick's trend test	*z*	–	−4.68	–	−4.39	–	–
	P	–	<0.01	–	<0.01	–	–

Figure 5. Age and size of *P. canaliculata* females at first copulation and at first egg mass under a gradient of food deprivation. **A.** Age. **B.** Shell length. Dots are medians; bars extend between the extreme values ($n = 3, 3, 4, 4, 6, 6$ and 3, for 0–80% of food deprivation, respectively).

Table 3. Non-parametric tests of the variables related to maturity for females of *Pomacea canaliculata* (*P*, probability value; z and X^2, values of normal standardized and Chi-square statistics for the tests, respectively).

|		Age at first copulation (weeks)	Shell length at first copulation (mm)	Age at first egg mass (weeks)	Shell length at first egg mass (mm)	Delay (days)	Growth during delay (mm)
Kruskal–Wallis rank test	X_6^2	26.361	16.527	25.663	16.182	12.389	8.231
	P	<0.01	0.011	<0.01	0.013	0.054	0.222
Cuzick's trend test	z	5.1	0.65	5.03	0.4	–	–
	P	<0.01	0.5174	<0.01	0.6864	–	–

the less deprived levels were probably ready to copulate some time before they had their first chance. Estoy *et al*. (2002a) found no age differences at first copulation among juvenile males of *P. canaliculata* collected from Japanese paddy fields and reared under a somewhat narrower range of food deprivation (0, 40 and 70%, corresponding to 7, 4 and 2 days per week of cabbage *ad libitum*, respectively). The minimum shell length of males at first copulation obtained here (15.34 mm) was very much lower than the 25 mm reported in their study (in both cases for the most deprived level), probably due to an earlier application of deprivation.

Gamarra-Luques *et al*. (2006) suggested that virgin females of *P. canaliculata* do not lay egg masses, a proposition confirmed in our experimental and consort females, which in most cases began egg-laying 1 week after their first copulation. However, the most deprived males showed a marked delay from their first copulation to the first egg mass laid by their consorts (up to 73 days), suggesting that, despite their continuous copulatory activity, this was decoupled from the capacity to inseminate females. This may be the result of the great difference in growth rates between these snails (fed at 20% of their daily ingestion rate) and their consorts (fed *ad libitum*). Their first attempts to copulate occurred when the shell length ratio was approximately 0.38 but their consorts began egg-laying only when a ratio of approximately 0.48 was reached.

The minimum male to female shell length ratio in the Curamalal stream was 0.69 in 153 copulations observed (unpublished results), although ratios as low as 0.48 have been recorded in invaded areas (estimated from a picture in Cowie, 2002). Probably males are unable to reach the female gonopore with the penis sheath when the females are more than twice their size. Estoy *et al*. (2002a) suggested that there is no critical penis sheath size for successful copulation, but the size asymmetry between their experimental males and their consorts was probably very much lower than here, since both experienced the same feeding regimen.

For females at the two higher levels of food deprivation, age at maturity was probably underestimated since they started their reproductive activity after the substitution of consorts by males 3 months younger and generally smaller. Size asymmetry with the male consorts fed *ad libitum* seems not to be the cause, since shell length ratio to their first consorts (0.84–1.34) was below the maximum (1.38) observed in the Curamalal stream. In addition, most replaced males readily copulated with non-virgin stock females, indicating that they were not senescent. Probably a 'novelty effect', independent of size and age of the consort, triggered the copulatory activity. However, this has probably not affected the estimation of shell length at maturity since females' growth rates were already very low.
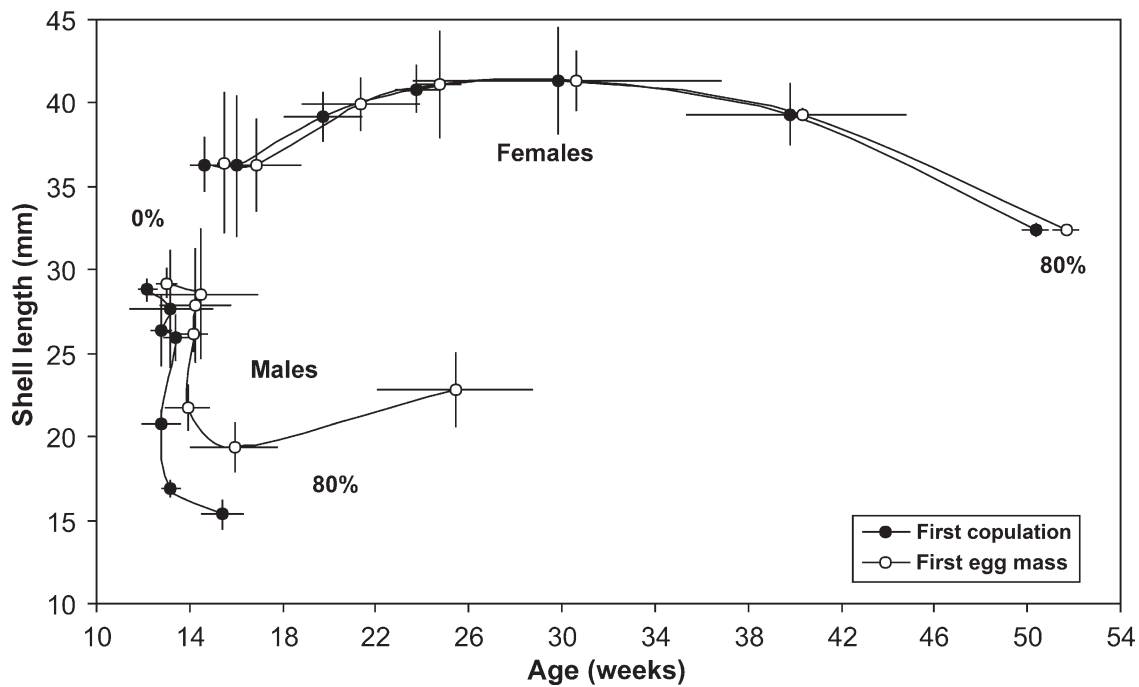
Figure 6. Reaction norms for age and size at first copulation and at first egg mass for both sexes of *P. canaliculata*. Lines connect the means for each sex and reproductive event ordered according to food deprivation level (bars are one standard deviation).

Both age at first copulation and at first egg mass in female *P. canaliculata* steadily increased with food deprivation. Estoy *et al.* (2002a) described a similar trend, with females maturing at older ages as food availability decreases, although they reported a delay of approximately 20 days between first copulation and the first egg mass. The delay estimated here (6.34 ± 0.95 days, mean ± SE) is considerably lower, even adding a bias of 3 days due to the fact that a female ready to copulate in a given day would have the chance to do it only 1–6 days later. In the Estoy *et al.* (2002a) study, consort and experimental snails were permanently together and this could give the consort males greater opportunities to copulate with females not ready to lay eggs, though copulation with immature females also occurs in the paddy fields.

Female shell length at maturity showed a complex response to food deprivation, with a maximum at intermediate levels. Estoy *et al.* (2002a) described a simpler trend, with females starting to copulate and to lay eggs at smaller sizes as deprivation increases. Probably due to methodological differences both studies spanned different parts on the spectrum of growth rates generated by a given food deprivation range. Nevertheless, a point of comparison can be established by comparing the treatments that grew at the same rate. The growth rates in the study by Estoy *et al.* (2002a), graphically calculated for females growing from 20 to 25 mm, ranged from 0.28 to 0.14 mm/day for their temporal food deprivation levels of 0–70%. These values are well within the range obtained in our study for the food deprivation levels of 53 and 80% (0.33 and 0.10 mm/day, respectively). Consequently, at the lower end of the explored range of potential growth rates, both studies showed the same decreasing response in female size at maturity.

In our study the number of eggs laid by the experimental females showed a decreasing trend only for deprivation levels higher than 40% (unpublished results), indicating that the changes in size and age at maturity can compensate for a reduction of up to 60% in ingestion rates. Estoy *et al.* (2002b)

suggested that reductions in food availability would be a better control strategy than direct reductions of density, since the former would decrease population growth due to a decline in egg output and a delay in maturity while the latter could be compensated by an alleviation of crowding. Our study concurs, in that any reduction of food availability would reduce population growth through a delay in female maturity, but suggests that a reduction in fecundity would appear only at high levels of deprivation.

The minimum shell length of females at first egg mass (31.9 mm) was very similar to the 32.9 mm obtained by Estoy *et al.* (2002a), in both cases for the lowest food level. A considerably lower minimum size of 25 mm has been reported in previous studies (Estebenet & Cazzaniga, 1992; Tanaka *et al.*, 1999), but these figures were based on the mean shell length of bisexual or female-only cohorts, respectively. For these mass-reared snails it is likely that the size range was very wide due to crowding and the only females laying egg masses were the biggest ones. On the other hand, the smaller shell length of males at a given age (Estebenet *et al.*, 2006) would have also lowered the mean value in bisexual cohorts.

Males of *P. canaliculata* seem to follow Stearns' Rule Two for maturation across a range of growth rates, sacrificing body size in order to attain the fastest maturation (Stearns, 1992). However, there is probably no significant fecundity loss, since females seem not to choose mates by their size (Estebenet & Martín, 2002) and the consort females inseminated by the males reared under different FD% showed no significant differences in egg production (unpublished results). Estoy *et al.* (2002a) also suggested that size is unimportant in male access to females and that males can maximize their fitness through fast maturation. An early start of mate searching would be favoured if scrambling is the main mechanism of sexual selection (Andersson & Iwasa, 1996). The minimum age is probably limited only by the time required for cell differentiation from zygote to gametes at a certain temperature. Only the most deprived males showed a slightly higher age at first

copulation, probably related to the 2-week lag in the start of external sexual differentiation.

Estebenet & Martín (2002) proposed that females mature when both age and size have reached their respective minima. These rules would generate an L-shaped reaction norm, which is clearly not the case for females in our study (Fig. 6); it probably resulted from 'averaging' the reaction norms for males and females under the incorrect assumption that they were similar. However, it could still apply to bisexual cohorts as a whole.

Females of *P. canaliculata* seem to show an evolutionary compromise between mortality risks and fecundity costs, leading to a convex or dome-shaped reaction norm. Perrin & Rubin (1990) developed a theoretical optimization model that predicts such dome-shaped reaction norms, under the critical assumption that mortality and growth rates are positively correlated. Field and laboratory experiments have shown that crowding effects on growth rates are quite important in *P. canaliculata* (e.g. Cazzaniga & Estebenet, 1988; Tanaka *et al.*, 1999); therefore, high mortalities provoked by crowding (Cazzaniga & Estebenet, 1988) or predation (Carlsson, 2006) would result in an increment of the survivors' growth rate. As compared to females under intermediate rates of growth and mortality, the fast growing females should mature at a smaller size to reduce the time of exposure to a high mortality risk. On the other hand, the slow growing females should do so to avoid a much extended pre-maturity period, even if they are exposed to a low mortality rate. In females, the minimum size at maturity is probably imposed by a minimum weight of the albumen gland necessary to start egg-laying (Estoy *et al.*, 2002a), perhaps in turn related to a certain minimum viable size of the aerial egg mass. Photo-protective and anti-desiccation functions have been attributed to the perivitelline fluid and to the calcareous shell (Heras *et al.*, 2007) of the complexly-structured eggs (Catalán, Fernández & Winik, 2002). As the female clusters the eggs in a compact mass, these functions scale up with egg number, potentially rendering very small egg masses almost unviable under the harsh conditions to which they are continuously exposed.

According to our results, males always begin to copulate earlier than females of the same food deprivation level and the females' lag increases with deprivation, ranging from 20 to more than 180 days (Fig. 6). Estoy *et al.* (2002a) reported qualitatively similar results, but the lag ranged from only 20 to 40 days. In Southern Buenos Aires province the reproductive period extends for 5 months (from mid-November to mid-April). Independent of food availability, males born early in the reproductive season (before mid-January) would mature in the same season (at 90–100 days of age). On the other hand, only in highly productive habitats would the females born early in the reproductive season do so (at 100–141 days of age), while in unproductive habitats most females would probably have to overwinter before attaining maturity. Assuming lower growth rates in the field than in the laboratory (e.g. due to suboptimal water temperatures), females would mature in the same reproductive season under an even narrower range of food availabilities than males.

Pomacea canaliculata is a polyphagous snail able to gather food by shredding, scraping and ciliary feeding (Cazzaniga & Estebenet, 1984), raising the question as to whether its growth could be ever seriously limited by trophic availability in the field. However, despite its wide trophic spectrum, some aquatic plants are totally unpalatable to *P. canaliculata*. For example, they may starve for a month or even to death when *Elodea canadensis* (Estebenet, 1995) or *Eichhornia crassi*pes (Lach *et al.*, 2000) are offered as the only food. Chemical defences seem to be involved for *Eichhornia crassi*pes (Boland *et al.*, 2008). Hence, severe food deprivation can appear even within dense macrophyte stands, especially due to the grazing-promoted replacement of palatable species. Conversely, depending on the palatability of the species present, ampullariids can deplete the macrophyte biomass shortly after introduction (Horne, Arsuffi & Neck, 1992; Carlsson *et al.*, 2004), leaving survivors or their offspring a barren bottom, where they must endure starvation or utilize less preferred food items.

Our environmental manipulation uncovered a highly significant plasticity in the age and size at maturity in *P. canaliculata* and revealed that this species is able to complete its life cycle across a very wide range of trophic availability. The strong sexual dimorphism in the reaction norms indicates that they are not merely the collateral result of the variation in growth rates, but an adaptive response to variable trophic resources. The diverse and flexible feeding mechanisms and the wide dietary spectrum of *P. canaliculata* also suggest a long evolutionary history coping with highly variable and unpredictable food resources. The great life-history plasticity reported in invaded areas (Estoy *et al.* 2002a, b) seems not to be a spontaneous development (Guo, 2006) or a trait selected by management practices (Estebenet & Martín, 2002), but a legacy from populations in the native range.

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