Thermal limits for the establishment and growth of populations of the invasive apple snail Pomacea canaliculata

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Thermal limits for the establishment and growth of populations of the invasive apple snail *Pomacea canaliculata*

María E. Seuffert · Pablo R. Martín

Abstract *Pomacea canaliculata* is a South American freshwater snail considered as one of the world's worst invasive alien species. A temperature of around 25 °C has usually been considered to be optimal for rearing *P. canaliculata*. Nevertheless, snails have not been reared under a wide range of temperatures to reveal the optimum for performance in terms of population increase. We investigated the effect of temperature on growth, survival and reproduction, estimating demographic parameters for *P. canaliculata* in the wide range of temperatures at which these snails are active (15–35 °C). No reproductive activity was evidenced for the snails reared at 15 °C, probably explained by the small sizes attained at this temperature. Temperatures above 25 °C did not promote a significant acceleration in growth so higher temperatures will not result in a reduction in time to reach maturity. In fact, snails from 25 and 30 °C began reproduction at the same age. We report here for the first time a detrimental effect of high temperatures that provoked a significant decrease in the contribution of snails to the next generation: the viability of eggs from the snails reared at 30 °C was very low and the snails exposed to a constant water temperature of 35 °C were unable to produce eggs. Our findings reveal a new environmental constraint that could be a determinant of the range limits of this species in invaded regions, especially during the coming decades, anticipating the scenario predicted from global warming.

Introduction

Aquatic invasive species are a growing concern because of their diverse impacts on biodiversity, ecosystem services and associated eradication costs, and freshwater molluscs constitute one of the most represented groups among invasive alien species (Strayer 2010). Understanding the response to temperature is critical for predicting the spread and impacts of invasive species, given the likely increase in the temperature of wetlands due to global warming (Burlakova et al. 2010; Diamond et al. 2012). A recent study revealed that the impacts of invasive alien species in freshwater environments are higher at temperatures that more closely match their thermal optima (Iacarella et al. 2015).

Pomacea canaliculata (Lamarck 1822) is a freshwater snail belonging to the family Ampullariidae (commonly known as apple snails); it is native to South America and its range extends naturally from southern Brazil to Buenos Aires province in Argentina

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(Martín et al. 2001; Hayes et al. 2012). *Pomacea canaliculata* and *P. maculata* Perry 1810 have been introduced to several Asian countries and become major pests of aquatic crops (Cowie 2002; Horgan et al. 2014a). These two species and other South American apple snails have been introduced to the United States, where they may compete with native congeners and where many areas are still susceptible to invasion (Rawlings et al. 2007; Karatayev et al. 2009). Apple snails have been recently reported in Europe (López et al. 2010), Chile (Jackson and Jackson 2009) and Ecuador (Horgan et al. 2014b), indicating that they are still spreading worldwide. Notably, the African continent remains hitherto free of established populations of these invasive apple snails although many tropical, subtropical and temperate areas are probably suitable for apple snail invasion.

Besides its importance as a crop pest, apple snails can cause significant changes in the diversity and functioning of invaded natural wetlands, resulting from the depletion of macrophytes and filamentous algae and an increase in phytoplankton biomass with an associated change in algal composition (Horgan et al. 2014a). All these features have promoted the including of *P. canaliculata* among "100 of the world's worst invasive alien species" (Lowe et al. 2000). Problems caused by *P. canaliculata* have not been completely solved, partly because despite the great amount of information on apple snail control (e.g., Wada 2006; Yusa 2006; Yoshie and Yusa 2008), many aspects of their biology and ecology remain unexplored. Greater understanding of their biology, especially their ecology, is essential for designing monitoring and management plans based on sustainable ecological criteria (Estebenet and Martín 2002).

One of the features contributing to the success of *P. canaliculata* as an invader is its high level of plasticity in several life history traits (Tamburi and Martín 2009). Different thermal regimes can change its life cycle, from a single reproductive season when reared under a constant temperature of 25 °C, to several reproductive seasons when growing under seasonally fluctuating temperature (Estebenet and Cazzaniga 1992; Estebenet and Martín 2002). Proteomic analyses revealed that the invasive *P. canaliculata* is more resistant to heat stress than one of its non-invasive congeners, *Pomacea diffusa* Blume 1957 (Mu et al. 2015).

Several studies concerning the influence of temperature on diverse aspects of the biology of *P.*

canaliculata, including activity, survival, growth and reproduction, have been conducted in recent decades (e.g. Estebenet and Cazzaniga 1992; Albrecht et al. 2005; Matsukura and Wada 2007). However, only two studies have investigated the effect of temperature on more integrative aspects of the performance of *P. canaliculata* at the population level. Using a life table approach, Estebenet and Cazzaniga (1992) determined the demographic parameters (reproductive rate, intrinsic rate of increase and generation time) under two thermal regimes (constant at 25 °C, and fluctuating between 9 and 29 °C). Besides, Lv et al. (2011) estimated the number of generations per year on the basis of a degree-days model in order to forecast the distribution of *P. canaliculata* in mainland China.

A temperature around 25 °C has usually been considered to be optimal for rearing on the basis of growth, survival and reproduction analyzed separately (Seuffert and Martín 2013). Nevertheless, to date, *P. canaliculata* has not been reared from birth to death under a wide range of temperatures to reveal the temperature for optimum performance in terms of population increase. Here we report an experiment that lasted four years, from hatching until the natural death of all snails. In addition to growth and survival, we investigated the effect of temperature on a range of reproductive and demographic variables. From these variables we estimated selected demographic parameters for *P. canaliculata* in the wide range of temperatures (15–35 °C) at which these snails are active (Seuffert and Martín 2010; Seuffert et al. 2010) in order to reveal the thermal limits for the establishment and growth of populations of this invasive snail. Hitherto, most studies have focused on the effect of low temperatures as a limiting factor for apple snail populations (e.g. Matsukura et al. 2009; Yoshida et al. 2014; Deaton et al. 2016) but little is known about the effect of long term exposure to temperatures above 25 °C. The response of these life history traits and demographic parameters to temperature may help us to understand the success of *P. canaliculata* as an invader and to forecast its global distribution and impacts.

Materials and methods

All the snails used in the trials originated from a group of ten egg masses collected during February 2012 in El

Huáscar stream (36°55′3″S, 61°35′50″W, Buenos Aires Province, Argentina). Mean monthly air temperature in this region fluctuates between 7 and 21 °C and mean maximum temperature during summer is around 30 °C (Servicio Meteorológico Nacional, 2016). Water temperature in the streams in this region frequently surpasses 30 °C (up to 36.2 °C; Seuffert et al. 2010).

The snails used in the trials were reared from hatching until their natural death. The eggs hatched during late February 2012 and, thereafter, hatchlings were pooled and raised for 3–4 weeks in groups of ca. 30 in ten 3 L aquaria kept in a rearing room at 25 ± 2 °C under a photoperiod of 12L: 12D. On March 15th, 144 hatchlings (shell length = 4.97 ± 0.55 mm; mean ± SD) were randomly selected from the 3 L aquaria and subgroups of 12 individuals were placed in 12 plastic aquaria of 20 L (30 × 35 × 20 cm). Ten aquaria were maintained at five constant water temperatures with electric thermostats (15, 20, 25, 30 and 35 °C; two aquaria for each temperature treatment) and the other two aquaria were kept at room temperature, which was recorded hourly with a Hobo® data-logger (accuracy = ±0.67 °C). Room temperature reached an absolute minimum of 9.4 and an absolute maximum of 31.9 °C, with a mean global temperature of 23.2 °C. Despite this wide range, in 95 % of the hourly records temperature was between 16.4 and 27.1 °C.

Once a week the aquaria were cleaned, the water was changed and snails' shell length (SL, from the apex to the farthest point of the aperture) was measured with a Vernier caliper to the nearest 0.1 mm; the number of live snails per aquarium was also recorded. The snails were fed with fresh lettuce, supplied two to three times a week in sufficient amounts that all the lettuce was consumed in order to avoid bacterial growth and water fouling. The schedule was the same throughout the experiment.

Pomacea canaliculata lays its egg masses above the water on hard substrates. The appearance of egg masses on the aquarium walls was checked at the same time as the addition of lettuce. Every new egg mass was removed and incubated in a room with controlled temperature (25 ± 2 °C) in a Petri dish that was located above a receptacle of water into which the hatchlings fell. The egg masses were checked daily to record the appearance of hatchlings. After one week without any further hatching, the egg masses were disintegrated in water with sodium hypochlorite. For each treatment, the total number of egg masses and the number of hatchlings, eggs with unhatched embryos (white eggs) and undeveloped eggs (pink eggs) in each mass were counted.

After 120 weeks, the temperature in one of the two aquaria corresponding to each of the 15 and 20 °C treatments (in which there had been no reproduction; see Results) was increased to 25 °C to investigate whether growth could accelerate and whether the snails would still be able to initiate reproductive activity.

Several reproductive and demographic variables were calculated for each treatment, including:

- Fecundity (eggs snail^{-1}): total number of eggs divided by the initial number of snails [a 1:1 sex ratio was assumed for all treatments following Estebenet and Cazzaniga (1992), since population sex ratio is unbiased and independent of temperature (Yusa 2004)].
- Egg mass size (eggs egg mass^{-1}): ratio of the total number of eggs to the total number of egg masses.
- Duration of embryonic development (d): number of days between egg laying and hatching of the first egg of each egg mass.
- Egg mass viability (%) of each egg mass: percentage of eggs that hatched.
- Embryonated eggs (%) of each egg mass: percentage of eggs that hatched plus unhatched embryonated eggs.
- Mean shell length (mm) and mean age (weeks) at laying of first egg mass.
- Mean shell length (mm) at death.
- Mean survival time (weeks), maximum longevity (weeks) and survival rate (%).

Life tables were calculated according to Stearns (1992) for a pooled cohort from the two aquaria of each treatment, based on the following age-specific parameters:

- Survival: $l_x = N_x/N_0$, where N_x is the number of snails of each age class (x) and N_0 is the initial number of snails; each age class comprised a period of four weeks.
- Age-specific fecundity: m_x = number of hatchlings per snail of age x (also estimated with the number of embryonated eggs and with the total number of eggs; see below). A 1:1 sex ratio was assumed for all age classes.

The number of hatchlings produced by an average snail that lives up to the maximum age k (raw reproductive rate RRR, hatchlings ind^{-1}) was estimated on the basis of the age-specific fecundities (m_x). Besides, two demographic parameters were estimated for each pooled cohort taking also into account the survivorship at different ages (l_x): the average number of hatchlings produced per each of the initial snails of the cohort (net reproductive rate R_0, hatchlings ind^{-1}) and the average age at which the snails produced their hatchlings (mean generation time GT, months):

- $RRR = \sum_{x=0}^{k} m_x$

- $R_0 = \sum_{x=0}^{k} l_x \cdot m_x$

- $GT = \frac{\sum_{x=0}^{k} x \cdot l_x \cdot m_x}{\sum_{x=0}^{k} l_x \cdot m_x}$

The intrinsic rate of natural increase (r, individuals $individual^{-1}$ $month^{-1}$) for a population formed by cohorts, with life table parameters estimated as above, was calculated by iteration from the equation of Euler-Lotka (Stearns 1992):

- $\sum_{x=0}^{k} l_x \cdot m_x \cdot e^{-rx} = 1$

Differences in the reproductive variables among temperatures were analyzed with one-way ANOVAs; demographic variables were analyzed with nested ANOVAs with the aquaria being the nested factor and water temperature the main fixed factor. These variables proved to be homoscedastic when investigated with Levene's test. Since there was no significant component of variance due to the different aquaria ($p > 0.05$ in all cases), differences among temperatures were analyzed considering the MS_{pooled} (that combines the $MS_{aquaria}$ and the MS_{error}); means were compared with LSD post hoc tests.

Results

Growth and survival curves of snails in the five temperature treatments are shown in Fig. 1. Mean shell lengths at the beginning of the trial were not significantly different among treatments ($F_{5,138} = 0.651$, $p = 0.661$). Growth curves were very similar in the 25, 30 and 35 °C treatments during the pre-

reproductive phase; after the onset of reproductive activity, growth slowed for all three treatments. Growth for the snails reared at 15 and 20 °C was always considerably slower.

Mortality was highest in the 35 °C treatment, with all snails dead after one year. Mean survival time was significantly different among treatments ($F_{5,119} = 53.271$, $p < 0.001$) and correlated negatively with temperature (Spearman's $\rho = -0.821$, $p < 0.001$), being highest at 15 and 20 °C (Table 1; Fig. 1). At these temperatures there was no mortality during the first two years. Mean survival time for the snails reared at room temperature was intermediate between those at 20 and 25 °C. Length at death was significantly different among temperatures ($F_{5,119} = 6.178$, $p < 0.001$), the snails from 15 °C being smaller than the snails from all the other temperatures ($p < 0.001$; Table 1).

Viable egg masses were obtained from the 20, 25, 30 °C and room temperature treatments. No reproductive activity was evidenced for the snails reared at 15 °C whereas snails at 35 °C were found in copula a few times although females never laid eggs. The first egg masses were recorded almost simultaneously in the 30 and 25 °C treatments, at 13 and 14 weeks, respectively (Table 1). Several months later the first egg masses from the snails reared at room temperature appeared and the egg masses from the 20 °C treatment appeared at 21 months. Shell length at the date of the first egg mass did not differ significantly among treatments ($F_{3,76} = 2.039$, $p = 0.115$; Table 1).

Fecundity at 20 °C was low (Table 1; 1605 eggs in 13 egg masses) while at 25 and 30 °C the total number of eggs was considerably higher (9391 eggs in 75 masses and 11,319 eggs in 85 masses, respectively). Fecundity of the snails reared at room temperature was intermediate between those at 20 and 25 °C (Table 1). The mean number of eggs per mass was not significantly different among treatments ($F_{3,212} = 0.589$; $p = 0.623$), with an overall mean of 127 eggs per mass (Table 1). Egg mass viability was lower for the eggs in the 20 and 30 °C treatments than those at 25 °C and room temperature as it was the percentage of embryonated eggs (Table 1). There was no relation between viability and the order in which the egg masses were laid (Spearman's $\rho = -0.104$; $p = 0.128$). The mean duration of embryonic development differed among treatments ($F_{3,186} = 3.621$; $p = 0.014$), being shortest in the 30 °C treatment and longest in the 20 °C

Fig. 1 Growth, survival and oviposition patterns for the five cohorts reared at different constant temperatures (15, 20, 25, 30 and 35 °C)
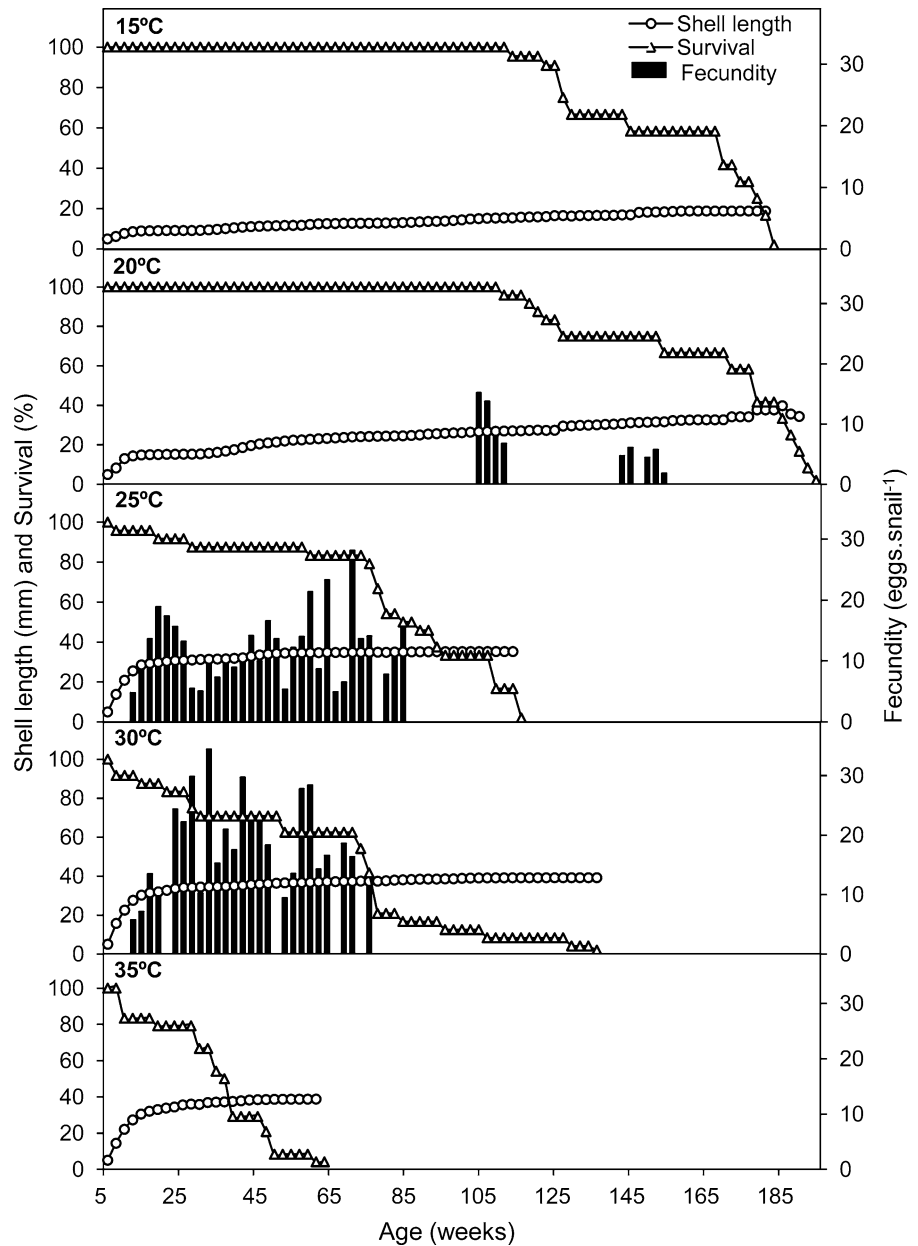
treatment (Table 1); the overall mean duration was 15.74 days.

A substantial increase in shell length was recorded in the snails from the two aquaria in which temperatures were raised from 15 and 20 to 25 °C at 120 weeks, relative to those whose temperature remained unchanged (Fig. 2). This growth was faster for the snails previously at 15 °C, which after 12 weeks exhibited the same mean shell length as the snails kept at 20 °C. Also, two egg masses were recorded in the

aquarium in which temperature was raised from 15 to 25 °C. These eggs were laid at 203 weeks (almost four years) by a female that grew considerably after the temperature was changed, reaching a maximum shell length of 61 mm. No egg masses were produced in the other aquarium (20–25 °C).

Demographic parameters were estimated for the 20, 25, 30 °C and room temperature treatments. The net reproductive rate (R_0) reached a maximum of 472 eggs produced per snail in the 30 °C treatment, with m_x

Table 1 Summary of the reproductive and demographic variables estimated from the five cohorts reared at different constant temperatures (15, 20, 25, 30 and 35 °C) and the cohort reared at room temperature

Temperatures	15	20	25	30	35	Room
Mean survival time (weeks)*	151.19	165.57	80.48	60.54	28.27	93.67
Maximum longevity (weeks)	186.14	201.71	107.14	127.57	52.00	139.71
Shell length at death (mm)*	15.03	31.83	34.03	36.44	33.34	29.70
Age at first egg mass (weeks)	N/A	90.00	13.71	12.86	N/A	40.00
Shell length at first egg mass (mm)*	N/A	27.29	29.24	30.63	N/A	25.92
Fecundity (eggs snail^{-1})	0	66.88	391.29	471.63	0	210.25
Egg mass size (eggs mass^{-1})*	N/A	123.46	125.21	133.16	N/A	117.35
Egg mass viability (%)*	N/A	17.76	52.37	8.74	N/A	62.16
Embryonated eggs (%)	N/A	36.99	74.53	39.12	N/A	79.52
Duration of embryonic development (d)*	N/A	17.00	16.25	15.11	N/A	15.40
Net reproductive rate (R_0, hatchlings ind^{-1})	0	14.79	214.25	36.42	0	140.46
Raw reproductive rate (RRR, hatchlings ind^{-1})	0	23.56	277.74	52.92	0	175.99
Mean generation time (GT, months)	N/A	27.73	12.28	9.25	N/A	14.17
Intrinsic rate of increase (r, ind ind^{-1} month^{-1})	N/A	0.0995	0.8155	0.5201	N/A	0.3853

The values of egg mass viability, R_0, RRR, GT and r correspond to the estimations made with the number of hatchlings

* The values shown are the means obtained from all the snails or egg masses of each treatment

Fig. 2 Increase in mean shell length (SL) of snails from the 15 and 20 °C aquaria (*black* and *grey lines*, respectively) in which the temperature was raised to 25 °C. The plain lines show the mean shell length for the snails maintained with unchanged temperature; the *arrow* indicates the date when water temperature was increased
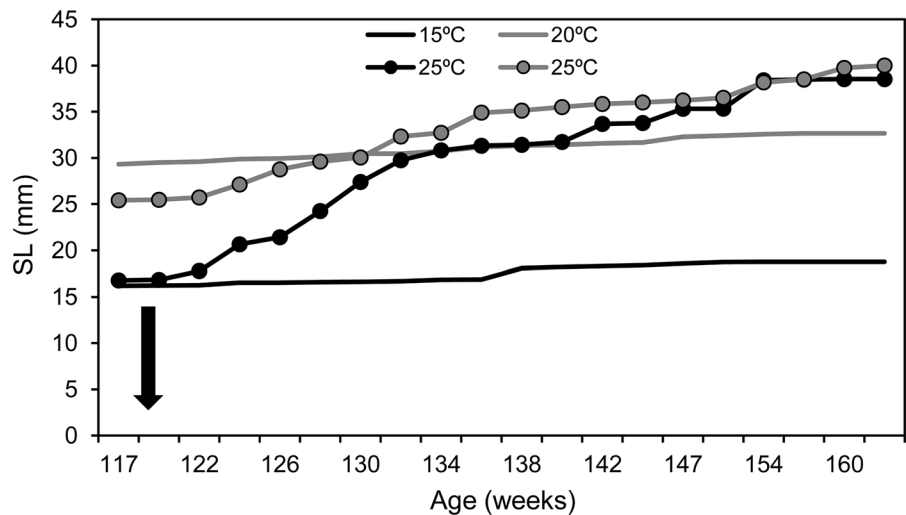
estimated based on the total number of eggs. When m_x was calculated considering only the embryonated eggs or the hatchlings, R_0 was maximum at 25 °C and considerably lower (298 embryonated eggs and 214 hatchlings per snail of the cohort on average, respectively; Table 1; Fig. 3a). The results obtained for the snails reared at room temperature were intermediate between those of 20 and 25 °C. The raw reproductive rate (RRR) estimated with hatchlings followed the same pattern as R_0 (Table 1). The mean generation time (GT) estimated with m_x based on hatchlings ranged between 9.25 weeks at 30 °C and 27.73 weeks at 20 °C, with intermediate values for 25 °C and room temperature (Table 1; Fig. 3b). GT calculated with the three different estimates of m_x gave essentially the same results, with a maximum variation among estimates of only one month (7.9 %) for 25 °C (Fig. 3b).

Fig. 3 **a** Net reproductive rate (R_0), **b** generation time (GT) and **c** intrinsic rate of natural increase (r) for three constant temperatures (20, 25 and 30 °C) and room temperature (mean: 23.21 °C). The three parameters were estimated from a value of fecundity (m_x) calculated with the number of hatchlings, number of embryonated eggs and total number of eggs (*white, grey* and *black circles*, respectively)
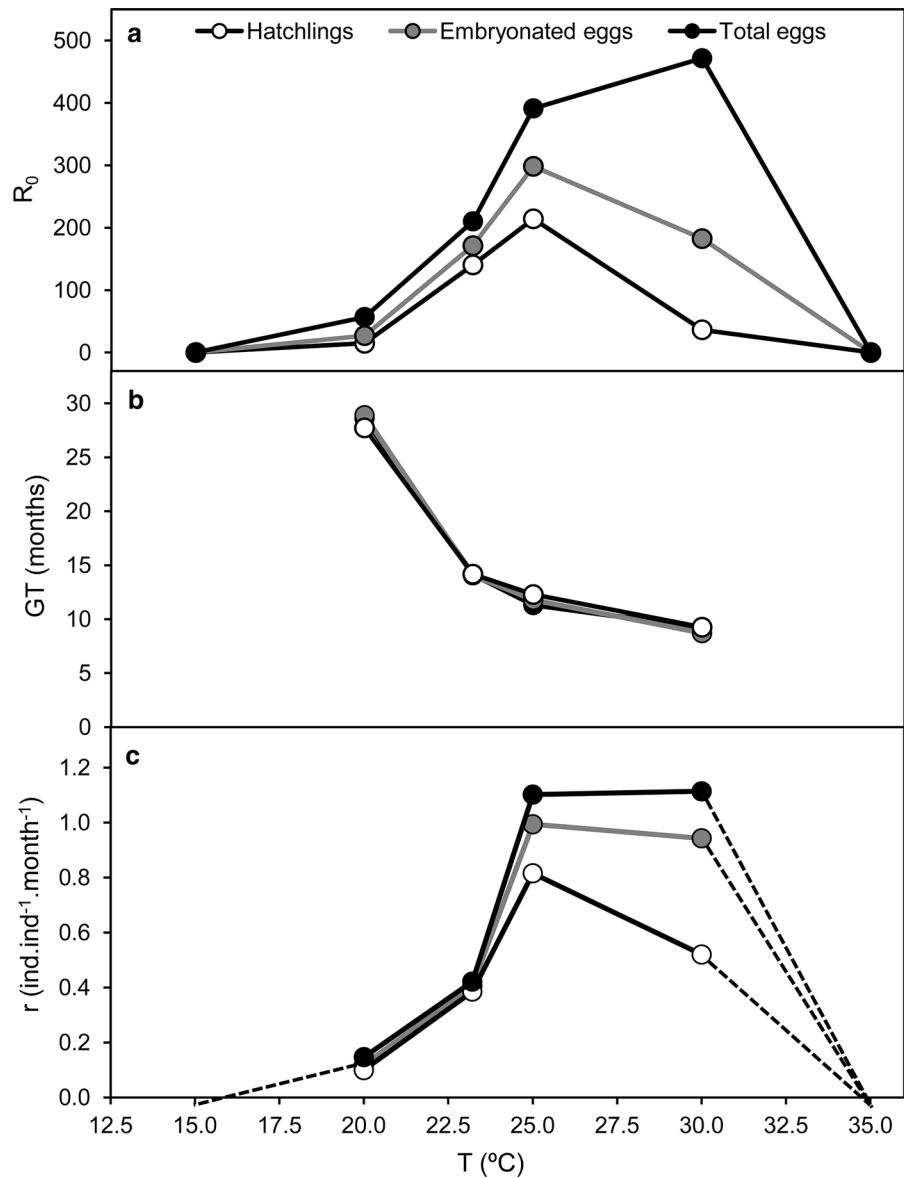
The intrinsic rate of natural increase (r, hatchlings individual^{-1} month^{-1}) was maximum at 25 °C, with intermediate values for 30 °C and room temperature and the minimum at 20 °C (Table 1; Fig. 3c). Since no eggs were produced at 15 and 35 °C, r was estimated based on the instantaneous mortality rate, plotting Ln(N) vs. time and calculating the slope with linear regression (r = −0.0005 and −0.0088 individual individual^{-1} month^{-1}, respectively; Fig. 3c). All the estimates of r were very similar at 20 °C and room temperature but for 25 °C and especially for 30 °C the estimates were higher when based on all eggs or on

embryonated eggs; in these two cases the maximum values were recorded at 25 and 30 °C (Fig. 3c).

Discussion

Growth and survival of *Pomacea canaliculata* showed opposite responses to temperature, as has been previously reported for the pre-reproductive phase of this species (Seuffert and Martín 2013). Growth patterns at 25, 30 and 35 °C were very similar, with a rapid increase in shell length during the pre-reproductive

period and constant but notable decelerated growth afterwards, which continued until death. A similar pattern has been previously reported for this species reared under a constant temperature of 25 °C (Estebenet and Cazzaniga 1992). Tamburi and Martín (2011) found that only females slowed growth with the beginning of reproduction, which could be attributed to the allocation of energy to copulation, egg laying and especially provision of energy reserves to the eggs. Temperatures above 25 °C did not promote significant acceleration in growth and, in consequence, higher temperatures will not result in a reduction in time to reach maturity for females since they need to reach a minimum size to mature (Tamburi and Martín 2009). In fact, snails from 25 and 30 °C began reproduction at the same age.

The growth rate for the snails reared at the three highest temperatures was clearly higher than that recorded at 15 and 20 °C. This shows that the differences reported between those two groups during the pre-reproductive phase (Seuffert and Martín 2013) are still evident during the breeding period, even with the reduction in growth rates that naturally occurs during reproduction (this work; Estebenet and Cazzaniga 1992, 1998; Estebenet and Martín 2002; Tamburi and Martín 2011). The snails reared at 15 and 20 °C grew considerably slower than the snails in all other treatments. The snails reared at 20 °C reached the same mean shell length as the snails in the higher temperature treatments (ca. 33 mm), even though it took them much longer (two and half years). Conversely, the snails reared at 15 °C only reached half the mean size (15 mm) relative to all the other snails after three and a half years, their maximum longevity. This is probably due to reduced ingestion of food by the snails kept at 15 °C relative to the other temperatures, as reported for both *P. canaliculata* (Seuffert et al. 2010) and *P. maculata* (Gettys et al. 2008). The small size that the 15 °C snails reached during their entire lifespan probably explains the lack of reproduction in this treatment, since snails reared at 15 °C were still able to reproduce when the temperature was raised to 25 °C and females attained the size required (see below).

Pomacea canaliculata matured at a mean shell length between 25 and 30 mm, irrespective of the temperature at which they were reared. This agrees with previous reports (Martín 1986; Estebenet and Cazzaniga 1992; Estebenet and Martín 2002) although

it was recently discovered that a minimum size of ca. 32 mm is required only for females to reach maturity, while size is irrelevant for males (Tamburi and Martín 2009). In the present study, treatments included both sexes, hence the range of snail size was wide because of mass rearing (Seuffert and Martín 2013) and the only females able to laid egg masses are 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 of shell length at first egg mass.

Survival rate correlated negatively with temperature, with the lowest survival at 35 °C. The deleterious effects of high temperatures were evidenced after the first week of exposure (Seuffert and Martín 2013; this work). All the snails reared at 15 and 20 °C survived for two years; thereafter survival decreased very slowly. Survival of the snails reared at 25 °C was high until week 71, when it began to decrease steadily, whereas for the snails reared at 30 and 35 °C mortality was quite constant across all ages, though the life span of the snails at 30 °C extended longer.

The snails in the 25 °C treatment showed a maximum longevity of 25 months while Estebenet and Cazzaniga (1992) recorded a maximum longevity of 13.5 months for a strain of *P. canaliculata* obtained from the same region and also reared at a constant temperature of 25 °C. These differences could be due to deleterious effects of crowding on growth and survival (Cazzaniga and Estebenet 1988; Estebenet and Martín 2002), since the latter were reared at a higher density (4 snails/L) than in the present study (0.6 snails/L). Crowding may also explain the differences in age at first egg mass, since our snails laid eggs for the first time long before the snails of Estebenet and Cazzaniga (1992) (three and ten months, respectively), despite mean shell length in both studies being similar (29.24 and 25.75 mm, respectively). Our snails grew faster and hence reached the minimum size required for reproduction sooner.

Water temperature above 30 °C is suboptimal for apple snails, and results in various responses to thermal stress, including behavioral responses (McClary 1964; Wada and Yoshida 2000; Seuffert et al. 2010; Mu et al. 2015) and deleterious effects on hatchability, growth and survival (Ramakrishnan 2007; Pan et al. 2008; Liu et al. 2011; Mu et al. 2015). However, it had not been previously reported that high temperatures could hinder reproduction and

hence reduce population increase. Our results show that a detrimental effect of temperatures above 25 °C on some reproductive functions led to a significant decrease in the contribution of snails to the next generation, since the viability of the egg masses of snails reared at 30 °C was very low (only 8.74 % of the eggs developed normally and hatched) and the snails at 35 °C did not lay eggs. The low viability at 30 °C could not be attributed to a sudden decrease in temperature since the egg masses were laid on the aquarium walls in a rearing chamber in which air temperature was maintained at 25 °C during all the experiment. Low viability and not a low fecundity explains the low value of R_0 estimated for 30 °C relative to 25 °C, since the number of eggs was maximum at 30 °C.

On the other hand, *P. canaliculata* snails exposed to a constant water temperature of 35 °C were unable to produce egg masses. These snails were seldom available for dissection after death because of their rapid decomposition, but a recently dead female had an atrophied albumen gland. Probably, the sterility at 35 °C and the very low viability at 30 °C was due to an irreversible damage to the reproductive tissues of the females and not to a behavioral alteration, since copulations occurred spontaneously. Liu et al. (2011) reported that *P. canaliculata* produced egg masses in aquaria with water temperatures of 35 °C. However, those snails were reared within the range 25–30 °C, conditions at which they reached sexual maturity and were exposed to 35 °C only during a period of 30 days at most.

The patterns of growth, survival and egg production were very similar for the snails reared at 25 and 30 °C, indicating that, at first, the performance of *P. canaliculata* would be the same if water temperature fluctuated around those values. The intrinsic rate of natural increase and both the net and raw reproductive rates peaked at 30 °C, as the generation time reached its minimum and the highest egg production occurred at 30 °C. However, when these parameters are based on the number of hatchlings or on the number of embryonated eggs, rather than total number of eggs, they all peaked at 25 °C. This is because of the low viability of eggs of snails reared at 30 °C. Based on these results we conclude that temperatures above 25 °C would not result in an increase in the performance of *P. canaliculata* in terms of population increase, especially when high temperatures persist for long periods.

The increase in temperature to 25 °C had an immediate effect on growth of the snails previously maintained at 15 and 20 °C, even after 30 months of almost no increase in shell length, as for the snails reared at 15 °C. In addition, these snails were able to start reproductive activity, though egg viability was extremely low, probably related to the old age of the only female still alive (almost four years) as well to the suboptimal temperatures during pre-reproductive stages. Therefore, the main consequence of low temperatures seems to be the slowdown of growth of the snails, delaying the attainment of size needed for reproduction (Tamburi and Martín 2009), but growth can be easily reactivated when water temperature increases.

A considerable difference exists between the intrinsic rate of natural increase estimated by Estebenet and Cazzaniga (1992) and by us for *P. canaliculata* reared at 25 °C (0.203 and 0.82 individuals individual^{-1} month^{-1}, respectively). This could be explained by the earlier and more intense reproduction and the higher survivorship of our snails. Raw and net reproductive rates were much higher for our snails, especially the latter (two and ten fold higher, respectively). At the beginning of reproduction, survival was only 45 % for the snails of Estebenet and Cazzaniga (1992), while 92 % of our snails were still alive.

The mean generation time was, as expected, maximum at 20 °C, minimum at 30 °C and intermediate at 25 °C. The generation time was almost the same within each treatment, regardless of whether it was estimated based on total number of eggs or only hatchlings. This is because there was no relation between viability and the order in which the egg masses were laid, with essentially the same values across the entire reproductive life. Given the same number of eggs, a decrease in viability with time will result in a shorter generation time when estimating it with hatchlings than with the total number of eggs. The mean generation time for the snails reared at 25 °C was around 12 months, which agrees with the estimates of Estebenet and Cazzaniga (1992), indicating that this parameter is less density-dependent than the other demographic parameters.

Water temperature must increase above 40 °C to be lethal for *P. canaliculata*, and the actual lethal temperature is inversely related to the duration of the exposure (Zhou et al. 2003; Pan et al. 2008; Mu et al. 2015). This indicates that, only exceptionally an

increase in water temperature would be a factor influencing survival of invading populations of *P. canaliculata*. This contrasts with the limiting effect that low winter water temperatures have on expansion of this species to higher latitudes (Ito 2003; Kwong et al. 2008; Yoshida et al. 2009). However, temperatures do not need to reach lethal levels to restrict its expansion, as hindering reproduction may suffice. We report here for the first time that temperatures above 30 °C would reduce the increase of a newly introduced population of *P. canaliculata*, by either reducing the viability of the eggs or completely inhibiting egg production, as also happens below 20 °C.

Our findings reveal a new environmental constraint that could limit the range of this species in invaded tropical regions, especially during the coming decades under scenarios predicted from global warming. Temperature is a key factor mediating the impact levels of invasive alien species in inland waters (Iacarella et al. 2015), so knowing the demographic response of *P. canaliculata* to temperature will be useful in forecasting invasion and ensuing impacts in wetlands and aquatic crops, particularly by focusing on those regions that more closely match the thermal optima of this invader. Some of our present results have already been incorporated in a population dynamics model of *P. canaliculata* that has been used to forecast establishment and abundance of this invader (EFSA 2013) and its impacts on the structure, functioning and services provided by recipient ecosystems in the European Union (EFSA 2014). The incorporation of our population dynamics parameters in forthcoming models will help to refine predictions of the impacts of this invader in regions considered suitable by climate matching approaches.

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