

THRESHOLD TEMPERATURES AND DEGREE-DAY ESTIMATES
FOR EMBRYONIC DEVELOPMENT OF THE INVASIVE APPLE SNAIL
POMACEA CANALICULATA (CAENOGASTROPODA: AMPULLARIIDAE)

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ABSTRACT

Pomacea canaliculata is a freshwater snail native to subtropical-temperate South America that has invaded several countries around the world. Temperature is probably one of the main limitations to the expansion of this and other apple snails to higher latitudes in invaded regions. Egg masses are aerial, and the duration of embryonic development varies greatly with air temperature. We compared different methods for determining the lower temperature thresholds and the cumulative degree-days (DD) required for the completion of the embryonic development of *P. canaliculata*. The lower temperature threshold was estimated with four methods: the least standard deviation from the mean of degree-days, the least standard deviation from the mean of days, the coefficient of variation in days and the linear regression coefficient method. The cumulative degree-days were estimated using hourly records and daily averages (calculated according to the single triangle and the single sine methods) of air temperature. The lower temperature thresholds ranged between 15.8°C and 18.3°C and the cumulative DD between 88.8°C.d and 133.8°C.d. The estimations obtained with the single triangle and the single sine methods were exactly the same. The values obtained with the method of the least standard deviation in degree-days and the corresponding cumulative DD were the poorest estimations. The estimates obtained with daily mean temperatures were close to those obtained with hourly records, indicating that recording only maximum and minimum temperatures should be sufficient. The use of degree-day models for egg development in *Pomacea* will serve to increase the effectiveness and efficacy of control measures targeted to egg masses through a better timing in their application, especially in localities with highly variable temperatures.

Key words: eggs, hatching, lower threshold, cumulative degree-days, developmental rate.

INTRODUCTION

Pomacea canaliculata (Lamarck 1822) is a freshwater snail native to subtropical-temperate South America naturally distributed from Paraguay and southern Brazil southwards to southern Buenos Aires Province, Argentina (Martín et al., 2001; Hayes et al., 2008). This species and a few congeners are serious pests in several countries around the world where they have invaded different types of freshwater systems, such as paddy fields and natural wetlands (Cowie, 2002; Rawlings et al., 2007; Hayes et al., 2008; Lv et al., 2012), prompting the listing of *P. canaliculata* among the 100 worst invaders worldwide (Lowe et al., 2000). Temperature is probably one of the main limitations to the

expansion of apple snails to higher latitudes in invaded regions (Baker, 1998; EFSA, 2012).

Many aspects of the biology of *P. canaliculata* depend on temperature, such as growth rate, reproduction, lung ventilation frequency, feeding rate and activity (Estebenet & Martín, 2002; Seuffert et al., 2010). In temperate climates, *P. canaliculata* reproduces more than once during its lifespan, whereas under tropical conditions it behaves as semelparous, showing only one reproductive period (Estebenet & Cazzaniga, 1992). Females deposit aerial, pink calcareous eggs, arranged in clusters of 30 to 300 eggs (Albrecht et al., 1996; Tamburi & Martín, 2011). Embryonic development occurs within the calcareous egg capsules and hatching usually occurs two weeks after oviposition, but this

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period varies greatly (Estebenet & Cazzaniga, 1992; Pizani et al., 2005; Liu et al., 2012), most of this variation being probably caused by the inverse relationship of air temperature and developmental rate.

The developmental rate of ectotherms is dependent on temperature, so that the cooler the temperature, the slower is the rate of growth and development. As temperature increases above a specific minimal threshold, development time progressively decreases, until the temperature becomes high enough to affect growth and development negatively. The lower developmental threshold for a species is the temperature at and below which development stops. The upper developmental threshold is less well defined, but it is commonly considered as the temperature at and above which developmental rate does not increase (Zalom et al., 1983; Snyder et al., 1999; Ruml et al., 2010).

As temperature increases, the duration of a specific physiological process decreases, but the cumulative heat required remained approximately constant (Zalom et al., 1983; Snyder et al., 1999; Lv et al., 2011). Temperature could be constant or fluctuating, but the combination of temperature (above the lower threshold) and time will be the same. This physiological time for development is measured in cumulative degree-days. A bigger difference between the temperature and the lower threshold implies an earlier accumulation of the required degree-days and hence a faster developmental rate.

Zhou et al. (2003) developed a degree-day model for *P. canaliculata* and estimated a threshold temperature for egg development of 14.0321°C. However, this parameter was obtained from populations living in an invaded area (China) and of which the identity is uncertain, because at least another *Pomacea* species coexist with *P. canaliculata* in mainland China (Hayes et al., 2008; Lv et al., 2012), and it is difficult to distinguish them externally (Cowie et al., 2006). Given that the threshold temperature for development may vary considerably as consequence of intrinsic features of the snails and factors related to specific environmental conditions, it is important to investigate the thermal requirements of *P. canaliculata* from data obtained from native individuals in its natural realm. Moreover, studies on the thermal requirements for embryonic development of snails with aerial eggs are very scarce (Liu et al., 1991; Zhou et al., 2001, 2003) and hence this work will contribute to the general knowledge of the thermal biology of gastropods.

Most studies on the degree-days required to hatching in freshwater gastropods have been developed on the basis of the variation of development duration of eggs incubated at different constant temperatures (e.g., Zhou et al., 2001, 2003; Hong et al., 2004). Here we took a different approach, computing thresholds and cumulative degree-days to hatching for *P. canaliculata* on the basis of hourly or daily records of fluctuating temperatures, an approach that has been successfully applied in other ectotherms (e.g., Yang et al., 1995; Snyder et al., 1999; Ruml et al., 2010). Although using hourly data provides a higher accuracy in the calculation of degree-days, daily maximum and minimum temperature data can also be used and they are often the only available records.

The aims of this work are to compare different methods for determining lower temperature thresholds, selecting those that are best supported by the data recorded for numerous egg masses, and to estimate the degree-days required for the completion of the embryonic development of *P. canaliculata*. These results will expand the knowledge of the thermal biology of this invasive species and would be useful for the development of predictive models of distribution both in native and invaded areas and to increase the efficiency of control measures directed towards the egg masses, the most conspicuous stage of the life cycle.

MATERIALS AND METHODS

Egg Masses and Temperature Records

Thirty males and 30 females of *P. canaliculata* were hand-collected in November 2009 at Guaminí stream (37°10'44"S, 62°25'59"W, Encadenadas del Oeste basin, Buenos Aires Province, Argentina). In the laboratory (located 170 km to the SSE from the collection site), 30 couples were formed and put in 3 L aquaria with CaCO₃ saturated tap water and fed with lettuce. From this pool of couples, 24 females that have laid at least one egg mass during the first week were selected for further record of their ovipositions.

From November 25, 2009, to April 26, 2010, the females were reared under the same conditions in a room without control of photoperiod or temperature. The experiment was ended after four weeks had passed without any oviposition. Half of the females received a full ration of lettuce corresponding to an *ad libitum* ingestion

rate (estimated from the equation provided by Tamburi & Martín, 2009) and the others received 50% of that ration. Water was changed and the aquaria were cleaned weekly. Every four weeks, a male was put in the aquarium during one day to maintain sexual activity and to allow replenishment of sperm reserves. The presence of egg masses fastened to the aquarium wall was checked every day in the morning, because egg laying is mostly a nocturnal activity (Albrecht et al., 1996; Estebenet & Martín, 2002). Once an egg mass was detected, the female together with the water, lettuce remains and feces were changed to a new aquarium. The egg mass was incubated in the original aquarium (with 1 cm of tap water in the bottom) in the same room as females; room's air temperature (T_h , °C) was recorded hourly with a Hobo® data-logger. The egg masses were checked daily to record the appearance of hatchlings in the aquarium. The counting of hatchlings was ended after one week without any hatching and the remaining eggs were counted to estimate egg mass viability. The duration of development (d, days) was calculated as the number of days elapsed between egg laying and the date of first hatching.

Determination of Threshold Temperature

The lower temperature threshold (T_l) for embryonic development was estimated with four different methods: (1) the least standard deviation from the mean of degree-days (SD-DD) proposed by Magoon & Culpepper (1932) and Stier (1939), (2) the least standard deviation from the mean observed number of days (SD-day) of Arnold (1959), (3) the coefficient of variation in days (CV-day) of Nuttonson (1958) and (4) the linear regression coefficient method (REG) from Hoover (1955). The different threshold temperatures were estimated using the equations developed by Yang et al. (1995) based on these four methods. To confirm that the three first equations perform properly, an iterative process with different candidate threshold temperatures was performed, as suggested by Snyder et al. (1999). The value that produced the least standard deviation in the mean of DD (1), in the mean of days (2) and the least coefficient of variation in days (3) was compared to the values obtained with the equations proposed by Yang et al. (1995).

For all methods, two sets of temperature data were used (making a total of eight estimations of the lower threshold): the detailed hourly

temperature data and a daily mean calculated averaging the records of maximum and minimum temperatures of each day.

Estimation of Degree-days Requirement

The degree-days (DD, °C.d) for the embryonic development of *P. canaliculata* were calculated using the hourly records of temperature by computing the degree-hours and summing over the 24-h. Degree-hours were calculated as the difference between the recorded hourly mean temperature (T_h) and the lower threshold (T_l):

$$DD = \sum (T_h - T_l)$$

The cumulative DD were estimated by summing the daily DD over the specific period of development (d) of each egg mass. We also estimated the cumulative DD using a mean value of temperature (T_m) obtained from daily highest (T_x) and lowest (T_y) records. This mean temperature was calculated according to the single triangle and the single sine methods described by Zalom et al. (1983). For all estimations, DD was set to zero when $T_l > T_h$ or T_m since it was reported that it generally gave better results than the approach in which DD retained a negative value (Ruml et al., 2010). The three methods were applied in combination with the eight estimations of the lower temperature threshold, giving a total of 24 estimations of cumulative DD.

In this work, we considered the introduction of an upper threshold to be unnecessary since, based on the evidence reported in previous works (e.g., Cowie, 2002; Seuffert et al., 2010), it may be inferred that the highest temperature to which the egg masses were exposed here (31.93°C) almost certainly does not preclude development.

RESULTS

A total of 123 egg masses were laid by the 24 females during the whole period of oviposition (late spring to early autumn). The mean viability of egg masses (number of live hatchlings / total number of eggs) was 35.5% and fluctuated between 0 and 99%. For the estimations of thresholds and degree-days, we decided to use the data obtained from egg masses with viabilities greater than 10%, leaving a total of 88 egg masses. The time required for embryonic development (d) varied from a minimum of only 7 days to a maximum of 30 days (mean \pm SD = 14.67 \pm 3.44 days).

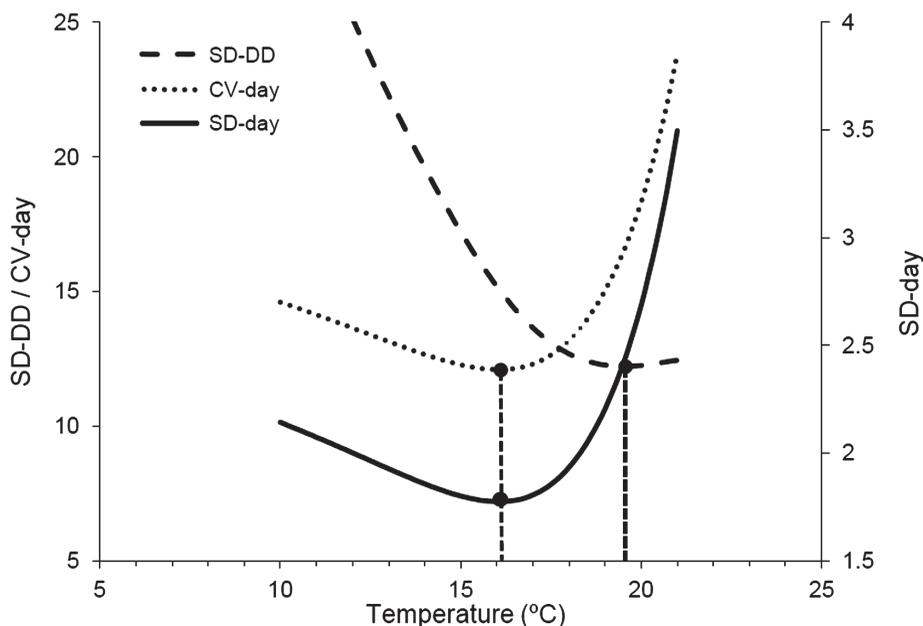


FIG. 1. Standard deviation in degree-days (SD-DD), standard deviation in the observed number of days (SD-day) and coefficient of variation in days (CV-day) for the embryonic development of *Pomacea canaliculata* (estimated with the hourly records of temperature) vs. temperature. The dotted vertical lines show the minimum value for the three methods corresponding to the lower temperature thresholds (19.6°C, 16.1°C and 16.1°C, respectively).

TABLE 1. Threshold temperatures and degree-days (DD) for the embryonic development of *Pomacea canaliculata*. Two data sets of temperature (T°) were used: hourly records and a daily mean of the maximum and minimum records. Threshold temperatures ($^{\circ}\text{C}$) were estimated by different methods: the least standard deviation in DD (SD-DD), the least standard deviation in days (SD-day), the coefficient of variation in days (CV-day) and the linear regression coefficient method (REG); values in parentheses are the thresholds obtained by iteration. The cumulative DD (mean \pm SD; $^{\circ}\text{C}\cdot\text{d}$) were estimated using the hourly temperature records (hourly) and the highest and lowest records (triangle and sine methods).

T° Data sets	Method	Threshold	Cumulative DD		
			hourly	triangle	sine
Hourly records	SD-DD	18.2 (19.6)	90.3 \pm 12.6	94.8 \pm 12.7	94.8 \pm 12.6
	SD-day	15.8 (16.1)	125.0 \pm 15.6	132.2 \pm 15.1	132.2 \pm 15.1
	CV-day	15.9 (16.1)	120.7 \pm 15.0	130.7 \pm 15.0	130.7 \pm 15.0
	REG	16.0	122.1 \pm 15.2	129.1 \pm 14.8	129.1 \pm 14.8
Daily mean	SD-DD	18.3 (18.6)	88.8 \pm 12.5	93.2 \pm 12.6	93.2 \pm 12.6
	SD-day	15.7 (15.8)	126.5 \pm 15.7	133.8 \pm 15.3	133.8 \pm 15.3
	CV-day	16.1 (15.8)	120.7 \pm 15.0	127.6 \pm 14.6	127.6 \pm 14.6
	REG	16.2	119.2 \pm 14.8	126.0 \pm 14.5	126.0 \pm 14.5

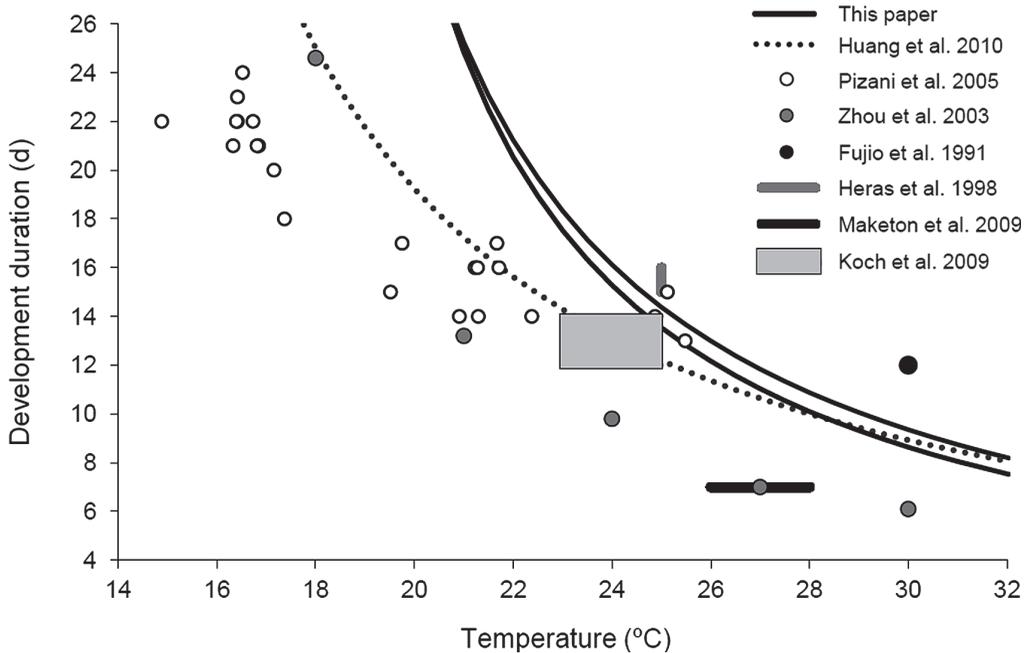


FIG. 2. Duration of embryonic development of *Pomacea canaliculata* at different temperatures (continuous lines) calculated with the extreme estimations obtained in this paper (15.7°C and 16.2°C for the lower temperature threshold and 133.8°C.d and 119.2°C.d for the cumulative degree days) and durations reported by different authors (bars and rectangles indicate ranges of temperatures and/or durations, empty circles represent records for single egg masses and full circles averages for several egg masses; the dotted line was calculated on the basis of the linear regression model from Huang et al., 2010).

The two feeding regimes used here were scheduled as part of another study and will be analyzed elsewhere. However, it is worthy to note that a separate estimation of the mean DD (using the hourly records of temperature and the threshold of 15.8°C obtained with the SD-day method) revealed no significant differences between both treatments (*t*-test, $p = 0.906$).

Determination of Threshold Temperature

The lower temperature thresholds for the embryonic development of *P. canaliculata* estimated with the equations of Yang et al. (1995) for the four methods fluctuated between 15.8°C and 18.3°C (Table 1). The values obtained by iteration (Fig. 1) were very similar to those obtained with these formulae for SD-day and CV-day methods (differences not bigger than 0.3°C) while for the SD-DD method the differences were larger (up to 1.4°C) between both threshold estimations.

Estimation of Degree-days Requirement

The mean cumulative DD estimations ranged between 88.8°C.d and 133.8°C.d (Table 1). The estimations obtained with the single triangle and the single sine methods were exactly the same. The values estimated from the hourly temperature records were 4.72% to 7.65% lower than both cumulative DD obtained from the daily mean of maximum and minimum records.

DISCUSSION

The threshold values obtained with the SD-DD method were higher (between 11.0% and 14.2%) than the other estimations and differed more from the corresponding values obtained by iteration. Besides, a threshold of 18.2°C or 18.3°C seems too high as compared to independent estimations for *Pomacea* species (15.4°C, Liu et al., 1991; 14.03°C, Zhou

et al., 2003). We therefore concluded that the values obtained by this method (with both sets of temperature data) and the corresponding cumulative DD (see below) are the poorest estimations for the embryonic development of *P. canaliculata* and hence will not be considered hereafter. The same situation was reported by other authors: in some cases, the SD-DD method generated negative values (Črepinšek et al., 2006; Ruml et al., 2010) and in others produced poor predictions (Snyder et al., 1999; Yang et al., 1995).

Ruml et al. (2010) showed that the results obtained with the CV and SD in days' formulae from Yang et al. (1995) are almost identical. With our data, the results obtained with those two methods were also very similar when using the formulae and, moreover, were exactly the same when we calculated them by iteration. As such, we infer that any of these two methods would be adequate and will produce very similar results.

On the other hand, the cumulative degree-days estimated using only the highest and lowest daily temperatures were exactly the same when using the single triangle and single sine methods. This situation occurs when temperature records fall within the range comprised by the lower and upper thresholds (Zalom et al., 1983). In our daily temperatures, only four records were below the lower threshold, being recorded at the end of the oviposition period (late April) and were considered for only one egg mass calculation. However, it has been reported that both the single triangle and single sine methods are easily calculated and are good estimators (Zalom et al., 1983). Therefore, even with a wider range of temperatures either of these methods would provide acceptable estimates when only daily temperature measures are available.

The estimates obtained using daily mean temperature values were close to those obtained using hourly records (either for the estimation of the lower thresholds or the calculation of cumulative degree-days). This indicates that they provide the best measure when hourly records are available, but when designing a new experiment, recording only maximum and minimum temperatures should be sufficient (see below).

The simplest way to calculate the cumulative DD is to use 0°C as threshold but this approach seems to be appropriate only for organisms with very low threshold temperatures, as is the case of several plant species (e.g., Snyder et al., 1999; Črepinšek et al., 2006; Ruml et

al., 2010) or the eggs of Siberian freshwater limpets (Shirokaya & Röpstorf, 2003). However, this 0°C-threshold is not adequate for a subtropical-temperate snail species whose feeding, crawling and aerial respiration cease between 10°C and 15°C (Seuffert et al., 2010). The use of 0°C as threshold could result in a significant overestimation of cumulative degree-days requirement for this species, just as the high values obtained with the SD-DD method (18.2–18.3°C) produced very low values of cumulative degree-days relative to the other methods (Table 1).

The range of temperature thresholds for embryonic development reported here (15.7–16.2°C) is just two degrees higher than those reported for nonindigenous populations of this species (14.03°C, Zhou et al., 2003; 14.2°C, Huang et al., 2010), and a half degree higher than the threshold reported for an uncertain *Pomacea* species identified as *Ampullaria gigas* (15.4°C, Liu et al., 1991). The reported cumulative degree-days for *Pomacea* are more variable than those of temperature thresholds and our values (119.2–133.8°C.d) lay well within the range reported (94.87°C and 161.3°C.d; Liu et al., 1991; Zhou et al., 2003; Huang et al., 2010). Our snails came from one the southernmost natural populations of *P. canaliculata*, where low temperatures set a limit to different activities during half of the year (Seuffert et al., 2010) and where a lower threshold would prevent excessively extended development periods. The ecological significance of these differences is difficult to assess. Part of the variation in these parameters may be explained by the different methodology employed as estimates from Chinese populations were obtained from egg masses incubated at different constant temperatures. Furthermore, differences between apple snail populations in the native range and those elsewhere may be due to acclimation, genetic drift or hybridization in the invaded range, different geographic sources of origin in the natural range, or simply species misidentification (e.g., Lv et al., 2012; Hayes et al., 2008).

The duration of embryonic development of *P. canaliculata* at different temperatures predicted by our degree-day models was compared to the durations reported by other authors (Fig. 2). The durations reported for egg masses under constant temperatures in their natural range (Buenos Aires Province, Argentina; Heras et al., 1998; Koch et al., 2009) only differed from our predictions in two days at most. In contrast,

estimates obtained under constant temperatures with populations in the invaded range of Southeastern Asia were generally lower than predicted, from 2 to 13 days shorter at 32°C and 21°C, respectively (Maketon et al., 2009; Zhou et al., 2003). The values predicted by the model proposed by Huang et al. (2010) were the same as ours at high temperature but became increasingly smaller as temperature decreases, reaching a difference of 12 days at 20°C. Again, the information available on thermal ecology of *Pomacea* egg development is not complete enough to determine if the observed differences are methodological, taxonomic or genetic in origin. For instance, the duration of 12 d at 30°C reported by Fujio et al. (1991) is clearly the oddest and was obtained in Japan for a laboratory strain in which low hatchability was associated with inbreeding depression.

Pizani et al. (2005) published data on the mean temperature and duration of development for egg masses incubated under uncontrolled temperature in the same laboratory as those of the present study and deposited by snails from the same geographic area (Encadenadas del Oeste basin). The temperature required to hatch in a certain number of days was clearly lower than that predicted by our degree days models (Fig. 2), especially for the egg masses that developed at lower rates. For instance, at 16°C the eggs hatched in 22–24 days but the predictions of our models indicate that at that temperature hatching would take an infinite time. This is probably due to the use of just one overall mean temperature (estimated over the entire incubation period for each egg mass) as an indicator of the thermal environment. Actual temperatures that fell well below the mean value of 16°C did not further retard development in those egg masses, but those well above 16°C certainly increased development time. Therefore, when temperature actually falls frequently below the threshold, the use of overall mean temperatures during the development indicates a lower threshold that is clearly lower than the temperature at which development can be completed according to our estimates.

A variety of control measures have been employed or tested against invasive *Pomacea* species in rice, taro and other paddy field crops but the results are far from satisfactory (e.g., Wada, 2004; Ranamukhaarachchi & Wickramasinghe, 2006). Among the control measures,

spraying of egg masses with water (Wang et al., 2012) or low toxicity hatching inhibitors (Wu et al., 2005) and collection or destruction of eggs *in situ* (e.g., Adalla & Magsino, 2006; Yang et al., 2006) have been proposed as environmentally friendly options. The extended reproductive season and the short development duration in tropical and subtropical areas implicates that the application of these treatments needs to be numerous and frequent. Moreover, these procedures would be ineffective if a certain number of eggs hatch between consecutive treatments or inefficient if, to avoid this possibility, the treatments are applied more often than actually required. The use of degree-day models for egg development in *Pomacea* will serve to increase the effectiveness and efficacy of these control measures through a better timing in their application, especially in localities with highly variable temperatures. According to our results, a simple and economic min-max thermometer located in the field would be sufficient to achieve a reduction in costs of spraying or egg mass harvesting and thence its application would be suitable even with low levels of technology and in low profit areas.

The estimation of lower thresholds and cumulative degree-days for embryonic development on the basis of hourly or daily records of fluctuating temperatures provided results comparable to those already available for *Pomacea* spp. and computed on the basis of development duration at different constant temperatures (e.g., Liu et al., 1991; Zhou et al., 2003). Additionally, our general approach is more economical as it does not involve special equipment (temperature controlled rearing chambers), instead it only requires a max-min thermometer (or a thermograph or data-logger if available) and it can also be applied in the field. This would permit the development of specific degree-day models at a local scale even if apple snails are not correctly identified.

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