

The effect of temperature on the population dynamics of *Aedes aegypti*



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ABSTRACT

The mosquito *Aedes aegypti*, the principal vector of dengue and yellow fever viruses, is an anthropophilic species adapted to urban environments, particularly to housing. A decisive factor in the proliferation of this species is ambient temperature, which has a direct influence on the vital rates of the species.

Here we present a structured matrix population model for analyzing the effect of temperature on the population dynamics of *Aedes aegypti*. The model is structured following the four natural stages of the species: egg, larva, pupa and adult. A set of population projection matrices (one for each temperature between 5 and 30 °C), was constructed and parameterized using published data on the biology of the species. The output of the models showed that pupation does not occur at temperatures below 8 °C. The population's growth rate was calculated for temperatures between 11 and 30 °C, resulting in an increasing function showing that temperatures above 12 °C are sufficient for population growth. For each matrix, a sensitivity and elasticity analysis of the parameters was performed. Together with the results from the population stable distribution analysis, they suggest that policies aimed at reducing the abundance of *Aedes aegypti* should seek to lower the survival probability in the egg and larval stages. The population dynamics was simulated under different seasonal scenarios. This seasonal analysis allows asserting that the egg stage dominates the population dynamics at all seasons.

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1. Introduction

Aedes aegypti is the major urban vector of dengue and yellow fever viruses worldwide. It is an anthropophilic species closely associated to human habitats that readily enters buildings to feed and to rest (Christophers, 1960). Its efficiency is due to its behaviour and its survival ability, including egg laying in a large variety of containers and the eggs' resistance to desiccation. Because of its importance as a vector of deadly diseases, the significance of its distribution in urban areas, and the possibility of breeding in laboratory facilities, *Aedes aegypti* is one of the best-known mosquitoes (Otero et al., 2006).

The northern and southern limits of the distribution of the species seem to be related to temperature. The relationship, however, is not entirely clear. In the United States, the northern limit relates quite well to the January isotherm of 1.7 °C (35 °F) and July isotherm of 23.9 °C (75 °F). In Europe, except in the west, the northern limit of distribution corresponds to the January isotherm of 4.5 °C (40 °F) and July isotherm of 23.9 °C (75 °F). However, this

winter isotherm could include regions of Britain and Ireland, where there are no records of the species. For China, the isotherms would be 10 °C (50 °F) and 26.7 °C (80 °F) in January and July respectively, and in Australia 10 °C (50 °F) and 21.1 °C (70 °F) in July and January respectively. The southern limit in South America would be given by the line joining the city of Tacna in southern Peru (17°36' S, 70°12' W) to the city of Bahía Blanca in Argentina (38°43' S, 62°16' W) (Christophers, 1960).

Christophers (1960) has adopted as limits to the geographical distribution of the species, the winter isotherms of 10 °C, corresponding to the months of July in the southern hemisphere and January in the northern hemisphere. Although the author mentions that this limit is far from being perfect, it has been adopted as reference by many researchers and organizations, including the World Health Organization (WHO).

The incidence of dengue has grown dramatically around the world in recent decades. Over 2.5 billion people – over 40% of the world's population – are now at risk from dengue. WHO currently estimates that there may be some 50–100 million dengue infections worldwide every year. Cases across the Americas, South-East Asia and Western Pacific have exceeded 1.2 million cases in 2008 and over 2.3 million in 2010 (based on official data submitted by Member States of WHO). The number of reported cases has

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continued to increase. In 2013, 2.35 million dengue cases were reported in the Americas alone, of which 37,687 cases were severe dengue (WHO, 2012).

As a result of many previous investigations, it has been determined that a decisive factor for the proliferation of the species is the ambient temperature, which has a direct effect on their vital rates (Christophers, 1960; Fay, 1964; Horsfall, 1955). There are other climatic factors, besides temperature, that affect the *Aedes aegypti* development, such as humidity and rainfall. Humidity has influence over mortality rates, which is relevant in regions with dry seasons (Otero et al., 2008). On the other hand, it is known that the flood of breeding sites is the main stimulus for the egg hatching (Christophers, 1960). Thus, precipitation will be relevant if breeding sites depend on them for water and they are not regularly distributed along the year such as in dry–humid climatic alternations. The contribution of watering and the container filling by humans usually plays a compensating role (Otero et al., 2008). This may need to be taken into account in the population dynamics because the mosquito proliferates in urban environments, but to our knowledge this situation has not been quantified yet. It might be necessary to establish some precipitation threshold below which this contribution becomes significant.

The aim of this work is to understand how the temperature influences the population growth rate, and thus, population dynamics. For this, we construct a set of simple mathematical models. Each one is a matrix population model structured in four stages (egg, larva, pupa and adult), discrete in time (projection interval of one day), based on vital rates dependent on mean daily temperature, and taking into account the female population only. Having determined the population growth rate as a function of temperature, an analysis of elasticity of the models parameters was performed, in order to use the models to set up control policies. We have chosen to develop a set of stage-structured matrix population models because they provide a straightforward link between the individual and the population based on a simple description of the lifecycle (Caswell, 2001) and they are very convenient from the computational viewpoint.

In this first development stage, we chose to consider a set of models dependent only on the temperature because it is the climatic factor that most affects the population dynamics of the species. Moreover, its effect on vital rates has been properly quantified. We have not considered that the flooding of breeding sites may hinder egg hatching, nor that rainfall may be a stimulus for this biological process. That is, once the egg completes its development, we assume that the breeding site will be flooded, either by rain or artificially. On the other hand, the drawback in incorporating the effects of humidity on mortality rates is that we did not find in the literature any clear quantification.

2. Some notes on the ecology of *Aedes aegypti*

Aedes aegypti is an insect which undergoes a complete metamorphosis. During its life cycle, the mosquito goes through four distinct stages: egg, larva, pupa, and adult. The first three stages (egg, larva and pupa) are called immature stages and take place in the water (or very close to water) while air is the medium for the adult stage.

After eggs are laid in the appropriate environment, hatching or eclosion gives rise to the first larval instar. This is followed by three successive moults or ecdyses, leading to the respective stages of second, third and fourth larval instar. A fourth ecdysis, or pupation, gives rise to the pupa, and a final casting of the pupal skin, called emergence, results in the appearance of the imago, commonly called the adult, male or female. To complete the life cycle there is pairing of the sexes, copulation, leading to the fertilization

of the female and then oviposition, if she had a sufficient blood meal (Christophers, 1960).

The eggs are usually laid on the walls of small containers of water whose surface is accessible (cans, buckets, pots, bottles, rainwater containers, etc.) just above the water level. An important feature of *Aedes aegypti* eggs is that they can withstand desiccation and low temperature for a period of up to one year. The eggs have proven to be very resistant to low temperatures. For this reason, several authors have described the species as over-wintering in the egg stage. We have not taken into account the effects of desiccation or hibernation when estimating eggs mortality rate.

The hatching is stimulated when the eggs are immersed in water. This immersion naturally occurs by flooding of the oviposition sites. Therefore, the hatching is most likely to occur after any rainfall. The period of time from oviposition to hatching may take 2–3 days at a temperature between 27 and 29 °C, 4–5 days at 25–26 °C and 100 h at temperatures between 21 and 24 °C according to various works cited by Christophers (1960). Moreover, Horsfall (1955) states that the incubation is completed within 38–50 h at summer temperatures, taking at maximum 4 days. The eggs may suspend their development as a result of external conditions that may be unfavourable for larval development (low temperatures, drought, lack of food, etc).

Larvae feed on suspended organic matter, being live bacteria and yeast essential components of their diet (Fay, 1964). The time interval required to complete the larval development is dependent upon several factors among which are the water temperature and the quantity and quality of food. Here we consider larval vital rates as functions of ambient temperature, without considering intraspecific competition for food resources or any other density-dependent factor.

Pupa is essentially the intermediate stage between two other stages that develop their active life in different environments: larvae in water and adult mosquitoes in air. In this stage a difference between the sexes can be perceived, as females are larger than males. Thus it can be observed that sex ratio is 1:1 (Focks et al., 1993a; Southwood et al., 1972). Pupae, unlike larvae, do not feed nor excrete metabolic waste. The pupal stage lasts from one day to a few weeks depending on temperature. When the development of the last immature stage (pupa) is completed, the adult emerges from the water, leaving behind its pupal skin. Not all the pupae which complete their development survive when emerging from the water, resulting on a success rate of only 83% (Southwood et al., 1972).

Both females and males feed on nectar and sugary liquids. Only the females are hematophagous, since they need a blood meal to complete oogenesis, and they prefer to bite humans rather than other mammals or other vertebrates.

Adult females lay an average of 63 eggs at each oviposition. The number changes according to the weight of the female, but also to other factors (Otero et al., 2006). The gonotrophic cycle (or time elapsed between emergence and first oviposition or between two consecutive ovipositions) and its duration are regulated by the temperature and it is longer for the first oviposition than for the subsequent ones (Otero et al., 2006; Christophers, 1960).

Because temperature can condition their flight capability, low temperatures will be a limiting factor for copulation, and hence for fertilization. According to Christophers (1960), *Aedes aegypti* becomes quite inert and incapable of movement at a temperature of about 10 °C or below, which constitutes a thermal barrier to reproduction.

Hence, the persistence of this species is dependent upon a sequence of events: the female obtaining a blood meal (without which eggs are not formed), the availability of water suitable for larval life, and a temperature that will allow male and female to copulate and lay eggs.

3. Material and methods

3.1. Modelling the population dynamics

The life cycle graph for *Aedes aegypti* considering a population structured in four stages (egg, larva, pupa and adult) and with discrete time step (projection interval of one day) is shown in Fig. 1. In this graph, P_i is the probability of surviving and remaining in stage i , G_i is the probability of surviving and growing from stage i to stage $i+1$ and F_4 is the fertility of adult stage, measured as the number of female eggs per female per day.

The abundance of individuals at each stage at any given discrete time t is represented by the vector $\mathbf{n}(t)$ calculated using the following equation:

$$\mathbf{n}(t+1) = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}_{t+1} = \begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \cdot \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}_t = A \cdot \mathbf{n}(t) \quad (1)$$

Here we consider that vital rates are dependent only on temperature T , which takes integer values. Therefore, the entries of the matrix are functions of T and thus for different integer values of T we will have different population projection matrices.

3.2. Theoretical model parameterization

Parameters P_i and G_i in a stage-structured model can be estimated from information on the duration of the stages. Suppose that the individuals are classified by age within stages, and that the probability of growing to the next stage depends on the time spent in the current stage, but is independent of the time spent in previous stages. With the purpose of estimating P_i and G_i , two low-level parameters that are easier to calculate are introduced:

$$\sigma_i = P(\text{survival of an individual in stage } i)$$

$$\gamma_i = P(\text{growth from } i \text{ to } i+1 | \text{survival})$$

In terms of these parameters, we have

$$G_i = \sigma_i \cdot \gamma_i \quad (2)$$

$$P_i = \sigma_i \cdot (1 - \gamma_i) \quad (3)$$

To estimate γ_i we suppose that every individual spends a fixed time t_i in stage i and then moves to stage $i+1$, and that survival probability (σ_i) is constant for all ages within stage i . Under these assumptions, Caswell (2001) derives the following formulation for γ_i :

$$\gamma_i = \frac{(\sigma_i/\lambda)^{t_i-1}}{1 + \sigma_i/\lambda + (\sigma_i/\lambda)^2 + \dots + (\sigma_i/\lambda)^{t_i-1}}$$

where λ is the dominant eigenvalue of the population projection matrix A . The value of γ_4 determines the proportion of individuals who survive longer than the adult stage duration. They are not taken into account in the population dynamics, since γ_4 is almost zero.

The problem here is that λ is the dominant eigenvalue of the matrix whose entries are being estimated. Caswell (2001) proposes an iterative method to solve this problem which consists in choosing an initial value for λ and calculating the entries in A . Then λ is calculated for the new matrix and the process is iterated until the

coefficients of the matrix are compatible with its own eigenvalue, or when the difference between the values of λ obtained in two consecutive iterations is less than a given tolerance error. To apply this iterative method we first estimate the fertility rates, the stage durations t_i and the daily survival probability σ_i .

The daily fertility F_4 is estimated considering the amount of eggs that a female lays in one oviposition (epo), the number of ovipositions that a female performs along her life (opl) or, in other words, the amount of gonotrophic cycles which a female can complete during her life, and the duration of the adult stage (t_4). Thus, the expression for F_4 is given by:

$$F_4 = \frac{1}{2} \cdot \frac{epo \times opl}{t_4} \quad (4)$$

where the factor $1/2$ is due to a sex ratio 1:1, and the fact that we are counting only eggs that become females. Fertility F_4 is a temperature-dependent parameter because the number of ovipositions that a female performs in her lifetime (opl) is a function of mean daily temperature (Section 3.3.4).

3.3. Biological parameters

For estimating P_i , G_i and F_4 we should know or be able to estimate parameters σ_i , t_i , epo and opl . The vital rates of the species are affected by different factors, temperature being one of the most important. Here the biological parameters are modelled as a function of the mean daily temperature. Due to the wide variety of breeding sites and the impossibility of accurately estimating the temperature of the water in these sites, we assume that the mean daily temperature of water in the breeding sites is equal to the mean daily temperature of the air.

3.3.1. Calculation of daily survival probability σ_i

If we define m_i as the daily mortality probability of stage i , the calculation of the daily survival probability is defined by the expression:

$$\sigma_i = 1 - m_i$$

The daily mortality rates for each stage have been taken from Trpis (1972), Otero et al. (2006) and Focks et al. (1993b) and are as follows.

Egg mortality: Based on laboratory experiments, Trpis (1972) estimated that the daily mortality of eggs is $m_1 = 0.01[\text{day}^{-1}]$ for temperatures in the range $278 \text{ K} \leq T \leq 303 \text{ K}$.

Larval mortality: The natural daily mortality rate of larvae can be approximated by $m_2(T) = 0.01 + 0.9725 \cdot \exp\left(-\frac{T-278}{2.7035}\right)$ and is valid in the range $278 \text{ K} \leq T \leq 303 \text{ K}$ (Otero et al., 2006).

Pupa mortality: The natural daily mortality rate of pupae can be approximated by the same equation developed for the daily mortality rate of larvae. Thus, $m_3(T) = 0.01 + 0.9725 \cdot \exp\left(-\frac{T-278}{2.7035}\right)$, valid in the range $278 \text{ K} \leq T \leq 303 \text{ K}$ (Otero et al., 2006).

Adult mortality: The daily mortality rate for adults was estimated by $m_4 = 0.09[\text{day}^{-1}]$, independent of temperature (Focks et al., 1993b).

3.3.2. Estimate of stage duration t_i

The estimation of stage duration t_i is related to development rates within each stage. To estimate development rates for eggs, larvae, and pupae and the duration of gonotrophic cycle we used a simplified version (Schoolfield et al., 1981) of the model derived by Sharpe and DeMichele (1977), based on enzymes absolute reaction rate kinetics. The enzymatic model derived by Sharpe and DeMichele assumes that the development rate is determined by a single rate-controlling enzyme which is active in a given temperature range. Although the enzyme is deactivated at low T_l and high

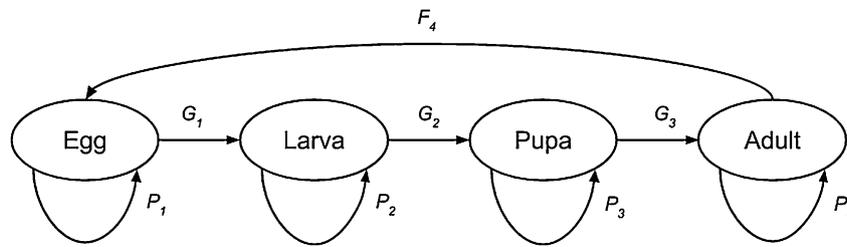


Fig. 1. Life cycle graph of mosquito *Aedes aegypti*.

T_h temperatures, Schoolfield et al. (1981) proposed the following simplification considering only high temperature deactivation:

$$r(T_t) = \frac{r(298\text{ K}) \cdot \left(\frac{T_t}{298}\right) \exp\left(\frac{\Delta H_A^\ddagger}{R} \left(\frac{1}{298} - \frac{1}{T_t}\right)\right)}{1 + \exp\left(\frac{\Delta H_H}{R} \left(\frac{1}{T_{1/2}} - \frac{1}{T_t}\right)\right)} \quad (5)$$

$$CD_n = \sum_{t=0}^n r(T_t) \quad (6)$$

In these expressions, $r(T_t)$ represents the development rate [day^{-1}] at temperature T [K] on day t , T_t is the mean daily temperature [K] on day t , $r(298\text{ K})$ is the development rate [day^{-1}] at 298 K assuming no temperature inactivation of the enzyme, ΔH_A^\ddagger is the enthalpy of activation of the reaction that is catalyzed by the enzyme [cal mol^{-1}], ΔH_H is the enthalpy change associated with high temperature inactivation of the enzyme [cal mol^{-1}], $T_{1/2}$ is the temperature [K] where 50% of the enzyme is inactivated from high temperature, R is universal gas constant [$1.987\text{ cal mol}^{-1}\text{ grad}^{-1}$], and CD_n represents cumulative development from day 0 to day n .

Focks et al. (1993a) give the values for the different coefficients involved in Eq. (5) that allow calculating the hourly development rate for each stage. Table 1 shows this values with a correction in parameter $r_D(298\text{ K})$ that allows us to calculate the daily development rate of each stage using Eq. (5).

Development from a thermal point of view accumulates (CD_n) and, in a discrete model with a daily time step, development is completed on day n when $CD_n > 0.95$ (Focks et al., 1993a). Hence, we can calculate the duration of the stages egg, larva and pupa as a function of mean daily temperature between 5 and 30 °C (Fig. 2), taking account the thermal equivalence used for the enzymatic model ($K = 273 + \text{°C}$) (Focks et al., 1993a; Otero et al., 2006).

The enzymatic model can no longer be used to estimate the duration of adult stage because when an adult mosquito has reached maturity, it remains in the adult stage. Thus, we used the daily mortality rate m_a to estimate the duration of the adult stage.

We suppose that an adult mosquito dies when its survival probability is less or equal to 0.01. Therefore, calculating the duration of adult stage is equivalent to finding the smallest integer n satisfying Eq. (7).

$$(1 - m_a)^n \leq 0.01 \quad (7)$$

Table 1
Coefficients for the enzymatic model of Schoolfield et al. (1981) relating development rates to temperature.

| Stage or process | Parameters | | | |
|--------------------|---------------------|-----------------------|--------------|-----------|
| | $r_D(298\text{ K})$ | ΔH_A^\ddagger | ΔH_H | $T_{1/2}$ |
| Embryogenesis | 0.256 | 10,798.18 | 1,000,000 | 14,184.50 |
| Larval development | 0.2088 | 26,018.51 | 55,990.75 | 304.58 |
| Pupal development | 0.386 | 14,931.94 | -472,379 | 148.45 |
| Gonotrophic cycle | 0.216 | 15,725.23 | 1,756,481.07 | 447.17 |

Taking $m_a = 0.09$, the smallest n satisfying Eq. (7) is $n = 49$. Then, an adult mosquito will live 49 days, independently of temperature.

3.3.3. Estimate of the amount of eggs per oviposition (epo)

Supposing that the amount of eggs that a female lays in one oviposition is roughly proportional to her body weight, Otero et al. (2006) estimated the average value of parameter epo in 63. Thus, a female will lay on the average 63 eggs in each oviposition.

3.3.4. Estimate of the number of ovipositions (opl)

An important assumption when calculating the duration of gonotrophic cycles is that the female has abundant availability of hosts to bite, as is often the case in urban environments. We also assume that at temperatures below 11 °C the mosquitoes do not copulate due to the difficulty in flying (Christophers, 1960). Thus, the value of opl will be zero for temperatures below 11 °C.

Since the duration of the first gonotrophic cycle is equal to the time elapsed between the emergence and the first oviposition and that the duration of subsequent gonotrophic cycles is equal to the time elapsed between two consecutive ovipositions, the number of ovipositions that a female can produce in her lifetime is the same as the amount of gonotrophic cycles that she can complete.

To estimate the duration of each gonotrophic cycle we can use the enzymatic model described above (Eq. (5)), using the parameters corresponding to the fourth row of Table 1. Given that the first gonotrophic cycle is longer than subsequent cycles, Focks et al. (1993a) consider that this cycle is to be completed on the day n such that $CD_n > 1$ (Eq. (6)) and subsequent cycles, from one oviposition to the next, are completed on the day n such that CD_n has increased by an additional 0.58. Following this reasoning, it is possible to estimate the number of days required to complete the first gonotrophic cycle and the subsequent ones for each of the given temperatures (Fig. 3a). Considering that the length of an adult mosquito's life is 49 days and the duration of each gonotrophic cycle can be computed, it is quite simple to calculate the value of opl for each temperature (Fig. 3a).

3.4. Construction of the population projection matrices

Now we are able to calculate the value of parameters P_i , G_i and F_4 for temperatures in the range 5 °C $\leq T \leq 30$ °C ($278\text{ K} \leq T \leq 303\text{ K}$). For estimating the parameters P_i and G_i we will use Eqs. (2) and (3). Hence we need to calculate γ_i using t_i , σ_i and the iterative method. At this point, it is important to remember that there is an additional mortality associated with the unsuccessful emergence of adult individuals (see Section 2). Because on the average 83% of the pupae that reach maturation successfully emerge from water, we have assumed that $\gamma_3 = 0.83$ for all temperatures between 5 and 30 °C. To estimate the parameter F_4 we will use Eq. (4) assuming that $opi = 0$ for temperatures below 11 °C (Fig. 3b). Thus, for each temperature in the range 5 °C $\leq T \leq 30$ °C we can calculate a population projection matrix A which will be analyzed in further sections.

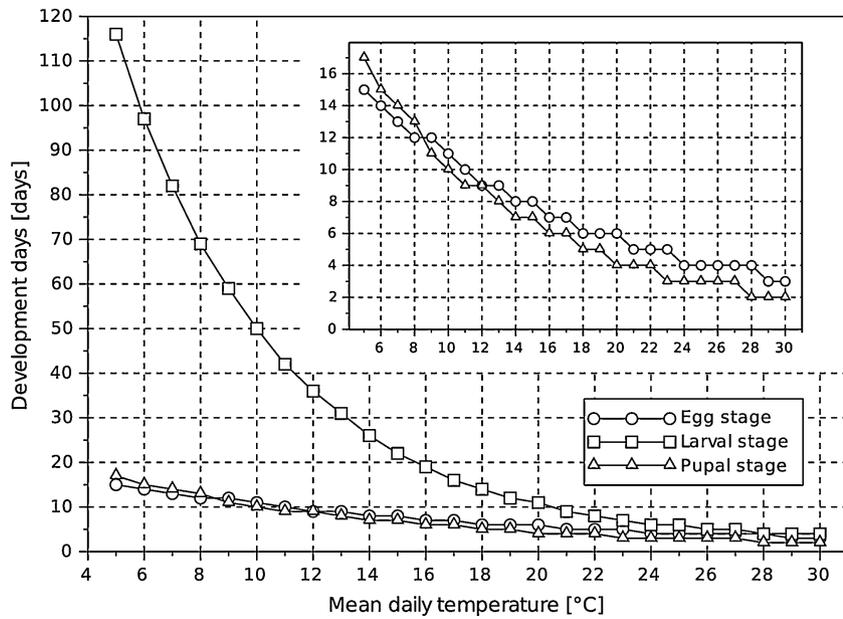


Fig. 2. Stages duration as a function of the mean daily temperature.

4. Results

The first fundamental result of this work is the estimation of the population projection matrices for each integer value of temperature between 5 and 30 °C. From this model, some interesting results were obtained, such as the changes in population growth rates, stable population structure, and reproductive values of each stage as temperature varies. On the other hand, we assess the relative weight of each parameter in the population dynamics through an elasticity analysis. Finally, simulations following different seasonal scenarios were performed for analyzing the seasonal behaviour of the population.

4.1. Structure of the population projection matrices

The population projection matrices computed above can be classified in three groups taking into account when the values of coefficients P_i , G_j and F_4 become null. Since opl is zero for temperatures below 11 °C, it is clear that in population projection matrices

corresponding to these temperatures, coefficient F_4 will be zero. Thus, the matrices A_i with $i = 5, \dots, 10$ will not be primitive matrices (Eqs. (8) and (9)) and hence the Strong Ergodic Theorem cannot be used to analyze the long term population behaviour. From a biological point of view, the case observed in Eq. (8) shows that the probability of a larva growing to the pupa stage is zero for temperatures between 5 and 7 °C. This situation is numerically acceptable, but we are unable to contrast this with biological data on the species. For temperatures between 11 and 30 °C the population projection matrices (Eq. (10)) are primitive and we can apply the Strong Ergodic Theorem to analyze of population dynamics using growth rate λ , the stable population structure \mathbf{w} and the reproductive value vector \mathbf{v} .

$$A_i = \begin{pmatrix} P_1 & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \quad i = 5, 6, 7 \quad (8)$$

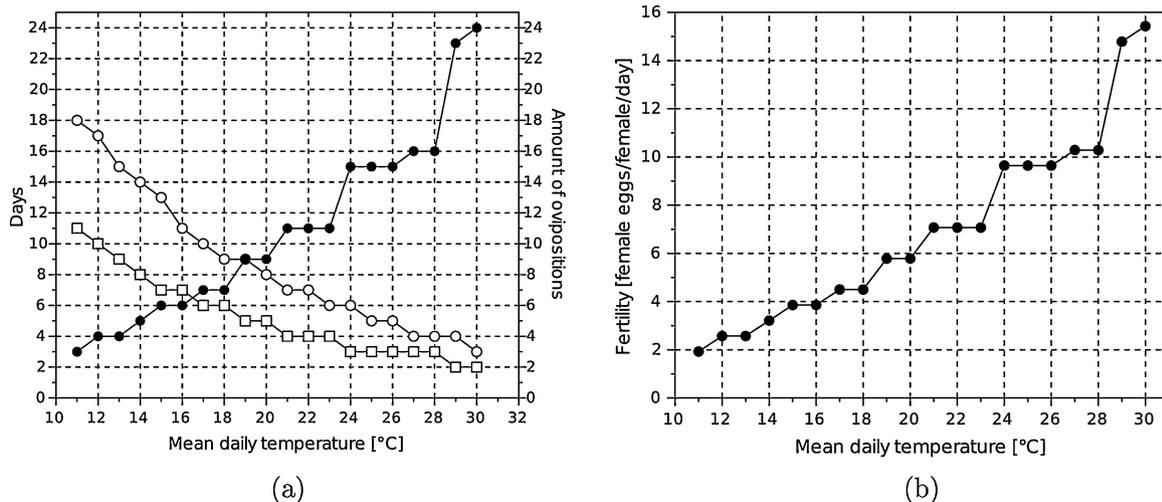


Fig. 3. (a) Days required to complete the first (circle) and subsequent (square) gonotrophic cycles as a function of mean daily temperature, and the amount of ovipositions (black dot) of a female as a function of mean daily temperature; (b) Daily fertility as a function of mean daily temperature.

$$A_i = \begin{pmatrix} P_1 & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \quad i = 8, 9, 10 \quad (9)$$

$$A_i = \begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \quad i = 11, \dots, 30 \quad (10)$$

4.2. Population growth rate λ

Given that the matrices computed for temperatures between 11 and 30 °C are primitive, the population growth rate λ can be calculated for each of these temperatures. Fig. 4a shows growth rate λ as a function of temperature. The function is strictly increasing in the interval where it can be calculated (between 11 and 30 °C). At 12 °C, λ is very close to, but slightly greater than one. This means that the population is close to equilibrium at 12 °C.

At temperatures above 12 °C, the population begins to grow because $\lambda > 1$. It might be assumed that the growth observed in Fig. 4a can be extended to temperatures above 30 °C, and that the population growth rate will continue to increase as temperature increases. This could be a hasty assumption. According to Christophers (1960), at temperatures above 41 °C adult mosquitoes may be kept alive only for a few hours. Therefore the curve in Fig. 4a should begin to decrease at some point as temperature continues to increase. We cannot determine this point because we do not have the information necessary to describe the population dynamics for temperatures above 30 °C.

4.3. Stable population distribution \mathbf{w}

The right eigenvector \mathbf{w} corresponding to the eigenvalue λ gives us the stable population distribution. Fig. 4b shows the normalized right eigenvector \mathbf{w} for each temperature between 11 and 30 °C.

The stages egg and larva exhibit the highest abundance of individuals for all temperatures considered (Fig. 4b). The difference between the proportion in the stable distribution of these two stages and the others is quite noticeable.

At temperatures between 11 and 13 °C the larval stage will have a higher relative abundance within the population, because at these temperatures the fertilities are not high (less than three female individuals per adult female per day), and the number of days required for larval development is high as compared to the egg stage. That is, the new eggs per day will not be many but they will develop faster than larvae.

At 14 °C, the percentage of eggs in the stable distribution starts to be higher than for the rest of the stages, something that will be maintained for all temperatures above this one. This is because fertility is a non-decreasing function, and the larval stage will always need a larger amount of days to develop.

It is interesting to note that at any given temperature the abundance of adult individuals barely reaches 5% of the total population. It might be surprising considering that at high temperatures the number of days that an individual remains in the adult stage is much higher than the days required for the development of the other stages. However, the contribution that the adult stage makes to other stages through egg laying is very large, and generates a greater proportion of individuals in the immature stages.

4.4. Reproductive value of each stage (v_i)

The reproductive values are given by the left eigenvector \mathbf{v} corresponding to the dominant eigenvalue λ . The reproductive value of stage i , v_i , represents the potential contribution of stage i to the egg stage.

The reproductive values for each stage for temperatures between 11 and 30 °C are shown in Fig. 4c. From this graph it can be observed that for neither of the stages the reproductive value is a monotonic function of temperature. The stage that shows higher fluctuations in the reproductive value is the adult stage, without any monotony intervals beyond an amplitude of 4°, while the egg stage is the one exhibiting less variation and fluctuation. The difference between reproductive values of the larva and pupa stages is noticeable. This is due to the low value which parameter G_2 takes causing the probability of a contribution from larval stage to egg stage to be low. This difference decreases as the temperature increases.

4.5. Elasticity analysis

The elasticity coefficient of λ with respect to entry a_{ij} is defined in Eq. (11) where v_i is the reproductive value of stage i , w_i is the proportion of stage i in the stable population distribution and λ is the growth rate.

$$e_{ij} = \frac{a_{ij}}{\lambda} \cdot \frac{v_i \cdot w_j}{\sum w, v} \quad (11)$$

The elasticity coefficients of parameters P_i , G_i and F_4 were calculated for each temperature between 11 and 30 °C (Fig. 4d). The elasticity coefficients with respect to parameters G_i are not visible in the graph because they take the same values as the elasticity with respect to parameter F_4 for all temperatures. We have not been able to find any biological implication from this fact.

The parameter with the highest contribution to λ is P_2 in the interval between 12 and 25 °C, and P_4 for temperatures outside this interval. The high contribution P_2 for temperatures in the interval between 12 and 18 °C is due to the magnitude of the larval stage within the stable distribution (w_2) and the increase in its reproductive value (v_2). Despite the fact that the probabilities of surviving and remaining in the egg, larva and adult stages are relatively higher, as temperature increases these probabilities become less meaningful as compared to fertility and the probabilities of surviving and growing to the next stage. Thus the probabilities of surviving and growing to other stages gain importance as temperature increases. The large proportion of the egg stage in the stable distribution (w_1) is not reflected in an increase in the elasticity coefficient of parameter P_1 , because of the low reproductive value of this stage. Based on the elasticity analysis, more attention should be paid to the estimation of parameters P_2 and P_4 in the above mentioned intervals.

When estimating the contribution of each one of the stages to the population growth rate, we can see that the contribution of the pupa stage increases as the temperature increases. The egg stage is the one with the least variation in its contribution, while the larval stage is the one that most contributes in the interval between 12 and 25 °C. Outside this interval, the stage that most contributes is the adult stage.

Management policies can be applied taking into account the lower level parameters σ_i (growth parameter) and γ_i (survival parameter). To do this, we need to know which of these parameters has a larger weight in the value of λ , i.e. we have to perform an elasticity analysis of λ with respect to σ_i and γ_i .

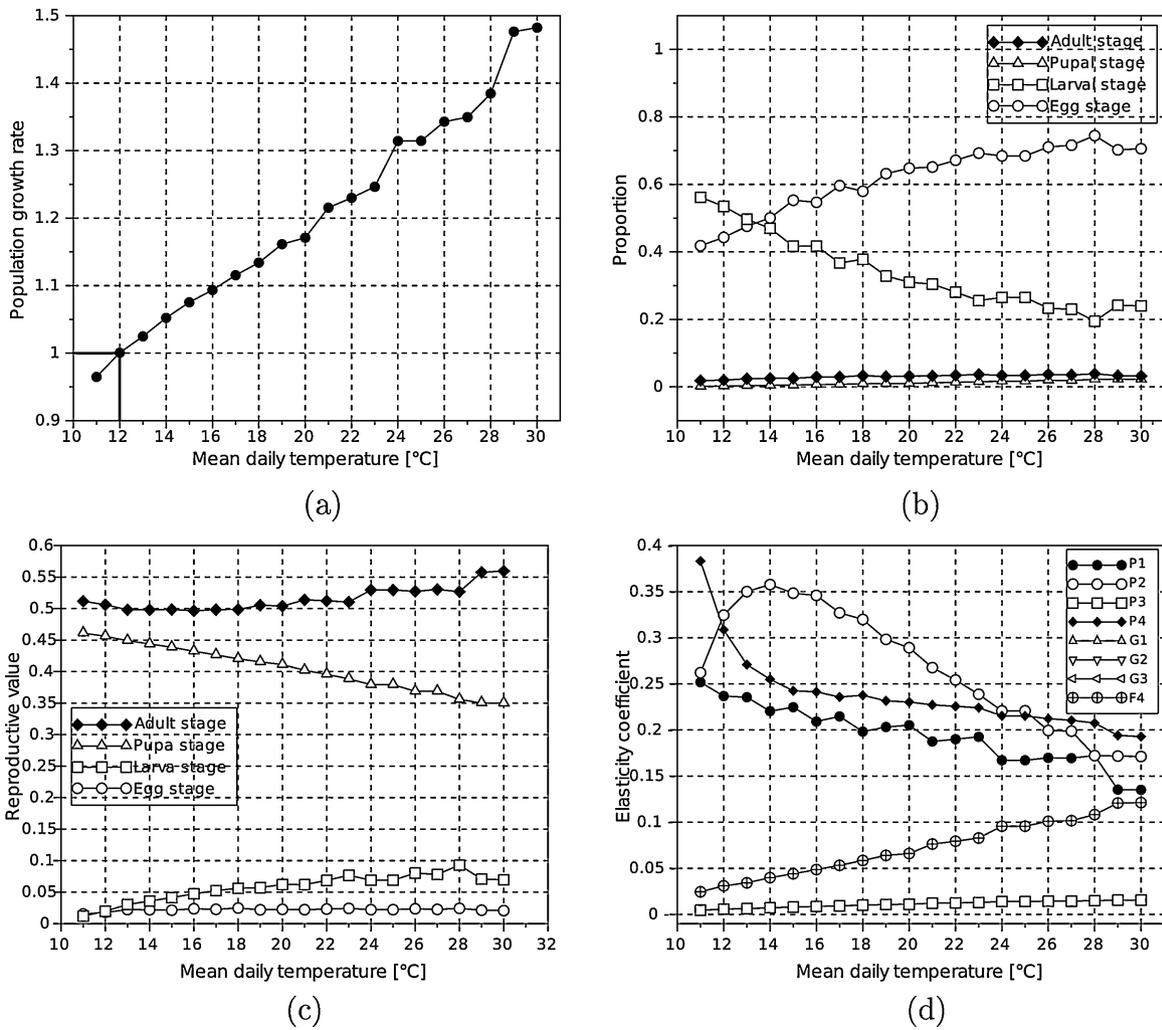


Fig. 4. (a) Population growth rate as a function of temperature; (b) Stable population structure as a function of the mean daily temperature; (c) Reproductive values as a function of the mean daily temperature; (d) Elasticity coefficients of the parameters P_i , G_i and F_4 as function of temperature.

The elasticity coefficient of λ with respect to the parameters γ_i and σ_i (e_{γ_i} and e_{σ_i} respectively) were calculated according to the following equations proposed by Caswell (2001):

$$e_{\gamma_i} = \frac{\sigma_i \gamma_i}{\lambda} \left(\frac{\partial \lambda}{\partial G_i} - \frac{\partial \lambda}{\partial P_i} \right)$$

$$e_{\sigma_i} = \frac{G_i}{\lambda} \frac{\partial \lambda}{\partial G_i} + \frac{P_i}{\lambda} \frac{\partial \lambda}{\partial P_i}$$

As a result of this analysis, we can observe that the elasticities with respect to the γ_i are very small as compared to the elasticities of the σ_i . The highest elasticity coefficient is the one corresponding to σ_2 for each temperature, except for 11 °C where σ_4 has a higher elasticity coefficient. This analysis allows us to state that the policies aimed at reducing the abundance of *Aedes aegypti* should effectively reduce the survival probability in each stage, but most specifically in the larval and egg stages.

4.6. Seasonal dynamics

The temperature-depend set of models was used to simulate a mosquito population along a period of 20 days in each season (using temperatures recorded in 2012) in order to analyze the seasonal behaviour of the species. In this section, it is important to note that the results on population growth rates, stable

distributions of population and reproductive values are not applicable. This happens because when matrices are used to simulate the population dynamic during an interval of time, the results obtained from long-term population behaviour cannot be taken into account. To perform a comparative seasonal analysis, the same initial population n_0 was selected for all the seasons. The initial population n_0 has 1000 individuals distributed according to the stable population structure at 18 °C, (Eq. (12)) central value of the temperature between 5 and 30 °C:

$$n_0 = \begin{pmatrix} 580 \\ 380 \\ 10 \\ 30 \end{pmatrix} \tag{12}$$

The first day of the projection corresponds to the day that marks the middle of the season and the temperature records for these days were obtained from the weather station SAZT 876450 “Tandil Aerodrome” located in the city of Tandil, Argentina (37°23' S; 59°25' W) property of the National Weather Service. Population was observed during the first hours of the day, so to project the population along 20 days, only 19 daily temperature records are needed.

Figs. 5a, b, 6a and b show the seasonal behaviour during summer, autumn, winter and spring respectively. The top graph shows the abundance in each stage, the middle graph the total amount

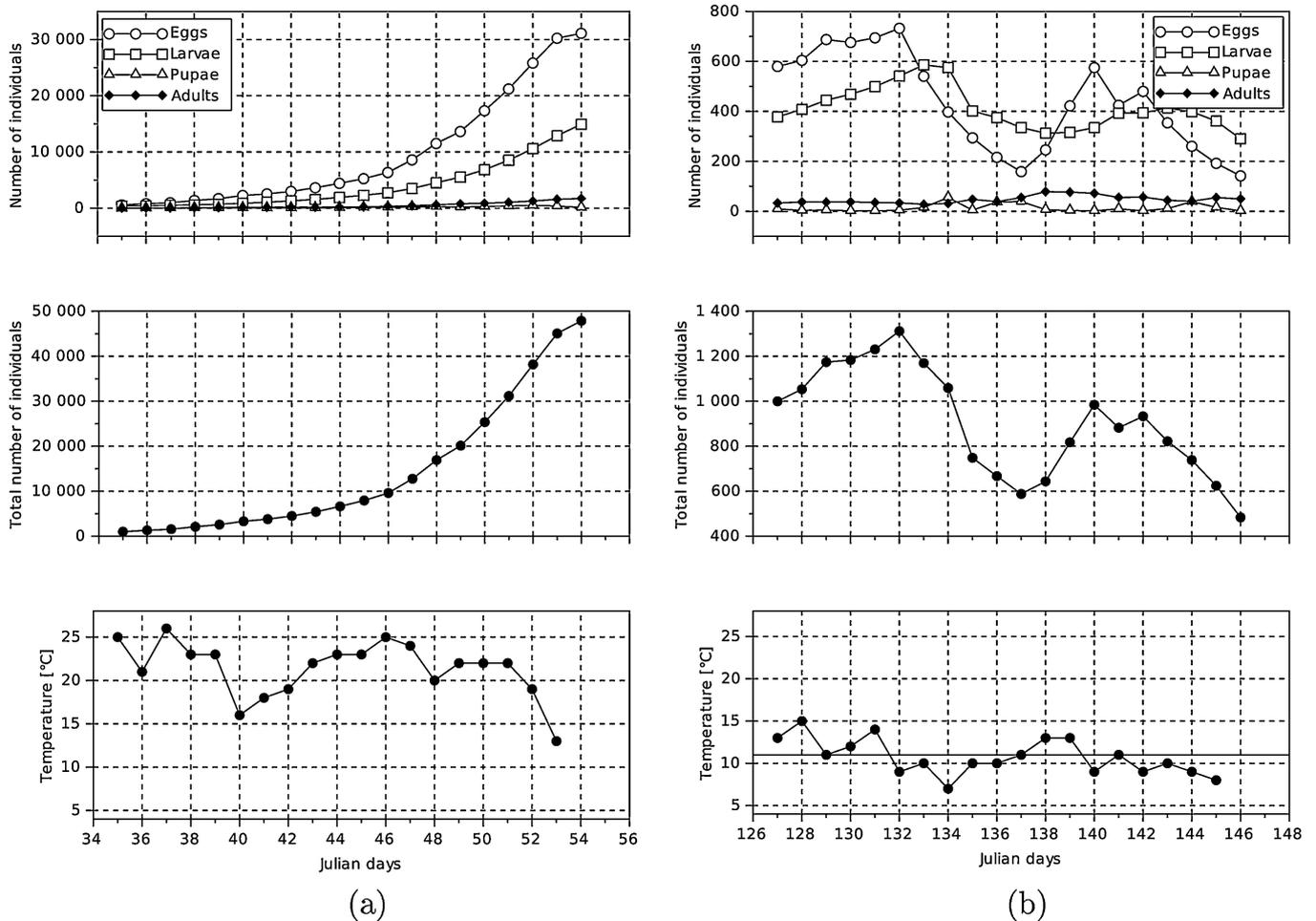


Fig. 5. Population projection (a) in summer from 4 to 23 February 2012 (35–54 Julian days), (b) in autumn from 6 to 25 May 2012 (127–145 Julian days).

of individuals in the population, and the bottom graph the average daily temperature during the interval.

During summer (Fig. 5a), the population is always growing because the temperature remains between 13 and 26 °C. Note that for temperatures above 12 °C, the growth rate is greater than one. The lowest daily growth rate can be observed on Julian day 41 (February 10) in which the population only grew by 14%, due to an abrupt decrease in temperature during day 40.

The season that exhibits more fluctuations is autumn (Fig. 5b). This situation is due to temperature variations during this period. The projection can be divided into four sub-periods depending on the temperatures. The first, from 6 to 10 May (day 127–131), shows temperatures between 15 and 11 °C, so that the population grows. In the second, temperatures are kept for 5 days (132–136) between 7 and 10 °C. This situation causes a reduction in the total abundance of individuals, largely due to the reduction in the number of eggs because of zero fertility. Then, between day 137 and 139 (third sub-period) temperatures grow above 11 °C and thus the population begins to recover due to an important increase in the number of eggs. From day 140 on (fourth sub-period), the temperatures fall below 11 °C. This situation produces a population reduction. As a result of these fluctuations, the number of individuals at the end of the period is approximately 50% of the total initial population.

The largest population decline was recorded during the winter period (Fig. 6a), the final population being only 30.75% of the initial population. This is because during most of the days of the first half of the period the temperatures are below 11 °C, impeding reproduction and making population size recovery impossible.

The population behaviour in spring is similar to that observed during summer (Fig. 6b), because temperatures are above 11 °C during the projection days. The population is always growing, even if in some cases the growth is small. The least growth was recorded on Julian day 316 (November 11) when the population grew by only 3%. A growth of 32% was observed on Julian day 311 (November 6), the highest in this period, resulting in about 500 new individuals.

During all simulations the populations of pupae and adults are those that exhibit less fluctuations and fewer individuals, which is consistent with the proportion that these stages represent in the stable population structure. During spring and summer, the egg stage is the one with the greatest abundance, whereas when the temperatures begin to drop, the larvae begin to have more prominence due to fertility reduction.

5. Discussion

Model outputs show that pupation does not occur at temperatures below 8 °C, i.e., the larvae do not pupate at a temperature 2° below the threshold reported by Christophers (1960). We think that a similar situation may occur in the case of pupae, i.e., there may exist a temperature threshold below which a pupa cannot emerge. This temperature cannot be estimated using our model due to the fact that we assume $\gamma_3 = 0.83$ independently of temperature (Southwood et al., 1972). This value of γ_3 prevents the value of G_3 to become small enough as to forbid the emergence.

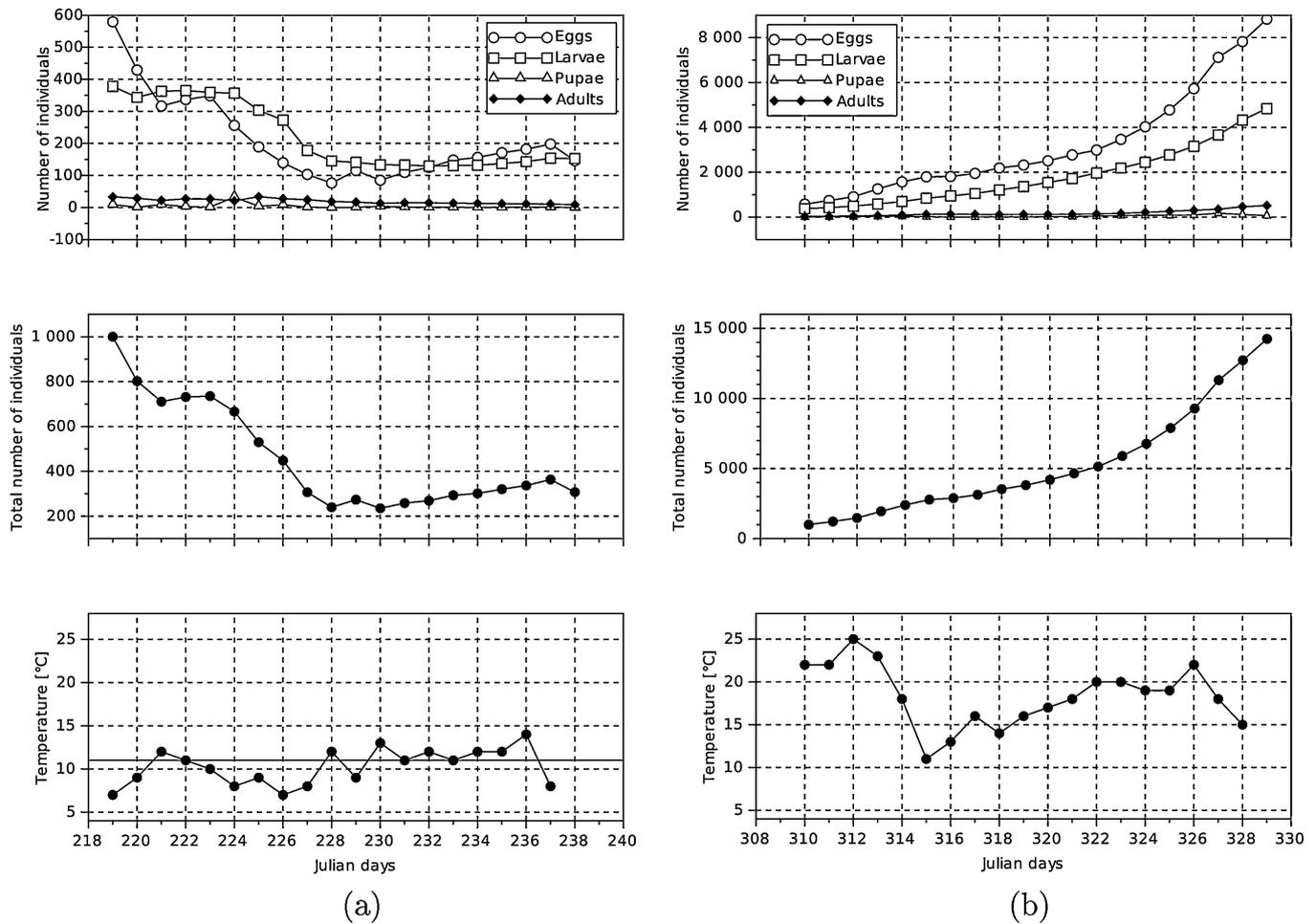


Fig. 6. Population projection (a) in winter from 6 to 25 August 2012 (219–237 Julian days), (b) in spring from 5 to 24 November 2012 (310–328 Julian days).

Table 2 compares between the embryonic development times recorded by Christophers (1960) and the estimation using the enzymatic model. It shows small differences only at high temperatures.

Comparing with the work of Horsfall (1955), who says that between 2 and 3 days (38 and 50 h) are needed for hatching at summer temperatures, we can see that the enzymatic model produces longer development times, and at summer temperatures (above 21 °C) attains a maximum of 5 days. In Cordoba, Argentina (31°24' S, 64°11' W), the average time of embryonic development was estimated to be 4.43 days at a mean temperature of 22.13 °C, 3.18 days at 20.73 °C and 4.17 days at 18.89 °C (Domínguez et al., 2000). Following the enzymatic model, for temperatures within the interval from 19 to 22 °C, the amount of days required for embryonic development was estimated to be between 5 and 6 days. In both cases, there are slight differences between our calculations and the values estimated by these authors, but it should be taken into account that our approach is discrete.

The mean larval development times observed under laboratory conditions by Rueda et al. (1990) and by Bar-Zeev (1958) are presented in Table 2. Generally the times observed are longer than those estimated from the enzymatic model. In the case of pupae development, the estimates produced by the enzymatic model do not present major differences as compared to the observations of Rueda et al. (1990), Christophers (1960) and Bar-Zeev (1958) (see Table 2).

The largest difference relative to the values reported in the above mentioned publications is observed in the duration of the adult stage. Otero et al. (2006) reports a mean longevity of 11 days in urban environments, while Carbajo et al. (2001) chose three

different life expectancy values for adult mosquitoes: 10, 15 and 20 days, in order to cover a broad spectrum of life expectancies. On the other hand, in Posadas, Argentina (27°23' S; 55°53' W), Tejerina et al. (2009) recorded a mean longevity of 57.87 days under semi-natural conditions.

As for the fertilities, Otero et al. (2006) estimated the amount of gonotrophic cycles to be 1 at 20 °C, 4–5 at 25 °C, and 6 at 30 °C. They considered the adult stage to last 11 days and distinguished whether adult females were in their first gonotrophic cycle or in subsequent ones. If we calculate the number of ovipositions following the form proposed in Sec. 3.3.4 considering the adult stage to last 11 days (as proposed in Otero et al. (2006)) the resulting amount of ovipositions performed by a female are 1, 3 and 5 at a temperature of 20, 25 and 30, respectively. These values are below those estimated by Otero et al. (2006).

The survival probabilities from hatching to adult emergence observed by Rueda et al. (1990) and the estimation used on our matrix model are shown in Table 3. To calculate these probabilities, we took into account the values of σ_2 and σ_3 , i.e.

$$\sigma_i = P(\text{survival of an individual in stage } i)$$

for each temperature, and the durations of the larva and pupa stages. Major differences can be seen for the lower temperatures, whereas at higher temperatures the differences are lower. It is important to remark that in the case of Rueda et al. (1990), survival is not a non-decreasing function with respect to temperature, as in our case.

Table 2
Comparison between development times for the immature stages as given by different authors and the enzymatic model output.

| | Development times [days] | | | | | | | | | | | |
|-----------|-------------------------------|-------------|----|-------------|----|------|------|-------------|-------------|------|----|-------------|
| | 15 | 18 | 20 | 21 | 22 | 23 | 24 | 25 | 27 | 28 | 29 | 30 |
| Embryonic | Enzymatic model | 8 | 6 | 6 | 5 | 5 | 4 | 4 | 4 | 4 | 3 | 3 |
| | Christophers (1960) | - | - | - | 5 | 4.16 | 4 | 4 | 4 | 2-3 | 3 | - |
| Larval | Enzymatic model | 22 | 14 | 11 | 9 | 8 | 6 | 6 | 5 | 4 | 4 | 4 |
| | Rueda et al. (1990) mean (SD) | - | - | - | - | - | - | 8.61 (0.29) | 4.47 (0.12) | - | - | 4.99 (1.29) |
| | Bar-Zeev (1958) | - | - | - | - | - | 8.87 | - | - | 6.37 | - | 5.37 |
| Pupal | Enzymatic model | 7 | 5 | 4 | 4 | 3 | 3 | 3 | 3 | 2 | 2 | 2 |
| | Rueda et al. (1990) mean (SD) | 8.49 (1.13) | - | 3.11 (0.07) | - | 4 | - | 3.03 (0.04) | 1.79 (0.03) | - | - | 1.82 (0.04) |
| | Christophers (1960) | - | 5 | - | - | 3-4 | - | - | - | - | - | - |
| | Bar-Zeev (1958) | - | - | 3 | - | - | 2.5 | - | - | 1.75 | - | 1.5 |

Table 3

Comparison of the survival probability from hatching to adult emergence between observed by Rueda et al. (1990) and that calculated through the matrix model.

| Temp. [°C] | Survival probability | |
|------------|-------------------------------|--------------|
| | Rueda et al. (1990) mean (SD) | Matrix model |
| 15 | 0.0311 (0.0133) | 0.3037 |
| 20 | 0.9180 (0.0305) | 0.6739 |
| 25 | 0.6258 (0.0249) | 0.7541 |
| 27 | 0.8976 (0.0375) | 0.7641 |
| 30 | 0.6634 (0.0274) | 0.7809 |

The population grows when the temperature exceeds 12 °C. We are not aware of any previous work analyzing population growth rate as a function of temperature. However Christophers (1960) says that the species could persist in environments with temperatures above 10 °C, in agreement with that estimated by Otero et al. (2006).

This model can be used to project the *Aedes aegypti*'s population during days with temperatures between 5 and 30 °C. It is important to note that the Strong Ergodic Theorem does not allow us to analyze the long term population behaviour when the temperature is not constant during the whole period nor when the temperature falls between 5 and 10 °C, because the theorem does not apply to primitive matrices.

In some areas where the existence of *Aedes aegypti* has been reported, temperatures drop below 5 °C. Thus our model faces a limitation when attempting to project the population during autumn and winter seasons in these areas because of its lower temperature threshold. A similar situation occurs with the upper threshold (30 °C). There is no doubt that the estimation of vital rates at temperatures below 5 °C and above 30 °C is a problem that should be investigated before the model is capable of simulating the population dynamics over long periods using mean temperature time series.

Due to the effects of climate change in temperature, we can assume that the geographic distribution of the species will begin to change. On the one hand, the mosquito would move to areas outside the limits proposed by Christophers (1960), and on the other hand, areas that are now adequate for the species would cease to be because the temperatures would be too high.

6. Conclusions

The matrix model allows analyzing the population dynamics of *Aedes aegypti* depending on ambient temperature. At the same time, this model allows us to determine the population growth rate as a function of the temperature, an important and very interesting result that we have not found in the literature about this species. In spite of being a relatively simple model, with few assumptions, it allows us to understand in which ways climate can affect the population dynamics.

As of the stable population distributions in Sec. 4.3, it can be noted that insecticides use for eradicating the species is a necessary but insufficient measure since the proportion of adults is very small as compared to immature stages, and insecticides have little effect on breeding sites. Therefore, we can conclude that prevention campaigns regarding viruses that have this mosquito as a vector are appropriate if they are focused on the destruction of breeding sites instead of attempting to eliminate adult mosquitoes through the extensive use of insecticides. The elasticity analysis reinforces the fact that the policies aimed at reducing the abundance of *Aedes aegypti* should effectively lower the survival probability in the egg and larval stages. In regions where temperatures remain within the boundaries of this model (5–30 °C) the model can be used for

assessing when these campaigns could be more effective. More importantly, the design of control policies does not necessarily require very sophisticated models that need lots of information on the dynamics of the species to be adequate and effective.

It will be an interesting challenge to incorporate other climatic factors (such as humidity or precipitations) in future stages of model development. Incorporating rainfall as a decisive factor for egg hatching may require, a priori, splitting the egg stage into two stages: one containing mature eggs which will hatch after rainfall and another containing anatomically immature eggs that despite water availability will need more time to develop and hatch. It would also be interesting to incorporate into the model factors associated to microhabitats, such as density dependence, carrying capacity of oviposition sites or distinction of types of containers, since these are variables that could affect population dynamics. Factors associated with the distinction among containers could be incorporated through a metapopulation model, where each population corresponds to a different type of container. A distinction among containers depending on the quantity and quality of food, sun exposure, the way containers fill with water, etc., has been addressed by Focks et al. (1993a) and it can be a good starting point in this regard.

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