



Global stability and oscillations for mosquito population models with diapausing stages

Alfonso Ruiz-Herrera ^{*}, Pablo Pérez, Ana M. San Luis

Received 5 February 2022; revised 6 July 2022; accepted 18 August 2022

Available online 29 August 2022

Abstract

In this paper we analyze the dynamical behavior of a mosquito population with diapausing stages through a mathematical model derived from the classical McKendrick-von Forester equations. The absence of monotonicity properties and the structure of the equations are noticeable features that hinder the use of commonly applied tools in the field. Our main contribution is to provide a novel methodology to derive criteria of global attractivity of a positive solution for periodic and discontinuous delay differential equations. From an applied perspective, we simulate the evolution of *Aedes aegypti* with diapausing stages. Moreover, we discuss the influence of the diapause parameters on the creation/suppression of population oscillations.

© 2022 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Gurney et al. [9] proposed the delay differential equation

$$x'(t) = px(t - \tau)e^{-\alpha x(t-\tau)} - \mu x(t) \quad (1.1)$$

for studying the dynamical behavior of the Australian sheep blowfly *Lucilia cuprina*. From a biological perspective, $x(t)$ denotes the density of mature individuals at time t (days), τ represents the required time from eggs to sexually mature adults, p is the maximum per capita daily egg production rate (corrected for egg to adult survival), $\frac{1}{\alpha}$ is the size at which the population reproduces at its maximum rate, and μ stands for the per capita daily adult death rate. Generally speaking, equation (1.1), or more generally, equation of the form

^{*} Corresponding author.

E-mail address: ruizalfonso@uniovi.es (A. Ruiz-Herrera).

$$x'(t) = px(t - \tau)f(x(t - \tau)) - \mu x(t) \tag{1.2}$$

provides an adequate modeling framework for describing the usual unimodal relationship between future recruitment and current population [2,5,9]. In the ecological literature [3,4], it is broadly documented that the advent of harsh winters or dry seasons leads to a state of low metabolic activity, reduced morphogenesis or limited physical activity in many invertebrate organisms, e.g., ticks, silkworm, ladybirds and dragonflies. This phenomenon, known as diapause, does not fit well in (1.2). The main reason of this limitation is that equation (1.2) assumes implicitly that the growth and mortality rates do not change over time, an oversimplifying condition for populations experiencing strong variations during their life-cycle. In a recent paper [13], Lou et al. proposed a variant of (1.2) to incorporate diapause periods. A key ingredient of this model is that the annual growth period is divided into three intervals, namely, the normal growth period, the diapause period and the post diapause period. Using the classical McKendrick-von Forester equations and integrating along the characteristic lines, they arrived at a scalar delay differential equation with time periodic coefficients. However, despite its apparent simplicity, the mathematical analysis of the model is not an easy task. The absence of monotonicity properties and the structure of the equations hinder the use of commonly applied tools in the field [19,20]. Moreover, as stressed in Section 6, the model displays a broad spectrum of dynamical patterns beyond the simple attraction to a periodic solution.

The main aim of this paper is to derive criteria of global attractivity of a positive solution for mosquito population models with diapausing stages. In brief, the main three contributions of our results in comparison with [1,13] can be outlined as follows: 1.- Our results are not based on the theory of monotone flows and cover the classical unimodal birth rates. 2.- The persistence and global attractivity results are stated in terms of the relevant parameters of the model instead of the spectral radius of an abstract (and unknown) operator. 3.- The introduction of nonmonotone birth rates allows us to reproduce the common oscillations observed in many insect populations [2,5,9]. The method of proof consists of relating the dynamical behavior of the model with a suitable scalar discrete equation. We stress that the approach of this paper can be applied for studying the dynamics of other types of delay differential equations with seasonal succession [10,15,16].

The rest of the paper is organized in six sections. In Section 2 we describe the modeling framework derived in [13] for the reader’s convenience. It worth mentioning that our model is valid for studying the dynamical behavior of any structured population for which there is an additional mortality depending on the age group during an interval of the annual growth period. In Section 3, we deduce some permanence/persistence properties for the solutions of the model. In Section 4 we state the main theorems of this paper. In Section 5 we apply our results in particular situations. We stress that the modeling framework and results are sufficiently versatile and simple to match experimental observations. To illustrate this potential, we simulate the dynamical behavior of a population of *Aedes aegypti* with diapausing stages. Furthermore, we discuss the influence of the diapause parameters on the creation/suppression of oscillations.

Many results of this paper are based on the next variant of the classical fluctuation lemma (the proof is given in the Appendix).

Lemma 1.1 (A variant of the fluctuation lemma). *Let $h : [a, +\infty) \rightarrow \mathbb{R}$ be a bounded and continuous function with*

$$\liminf_{x \rightarrow +\infty} h(x) < \limsup_{x \rightarrow +\infty} h(x).$$

Then, there exist two sequences $\{t_n\}$ and $\{s_n\}$ tending to $+\infty$ with the following properties:

- (P1) $\lim_{n \rightarrow +\infty} h(t_n) = \limsup_{x \rightarrow +\infty} h(x)$ and $h(t_n)$ is a local maximum for all $n \in \mathbb{N}$.
- (P2) $\lim_{n \rightarrow +\infty} h(s_n) = \liminf_{x \rightarrow +\infty} h(x)$ and $h(s_n)$ is a local minimum for all $n \in \mathbb{N}$.

2. Model formulation

The life cycle of the insect is divided into two groups: immature ($I(t)$) and mature ($M(t)$). The development duration from egg to adult is $\tau > 0$. Within each group, all individuals have the same birth and death rates. If $u(a, t)$ represents the population density at time t of age a , then the population sizes for immature and adult individuals are given by

$$I(t) = \int_0^\tau u(a, t) da \quad \text{and} \quad M(t) = \int_\tau^{+\infty} u(a, t) da,$$

respectively. During a regular life cycle, we can use the classical McKendrick-von Forester equations

$$\begin{cases} \frac{\partial u}{\partial a}(a, t) + \frac{\partial u}{\partial t}(a, t) = -\mu(a)u(a, t), \\ u(0, t) = b(M(t)), \\ u(a, 0) = u_0(a), \end{cases} \tag{2.1}$$

to describe the dynamical behavior of $I(t)$ and $M(t)$. In (2.1), $b(M(t))$ is the birth rate function and depends on the adult population size; $u_0(a)$ stands for the initial age distribution. The death rates during the normal growth period are stage-dependent with $\mu(a) = \mu_I$ for $a \leq \tau$ and $\mu(a) = \mu_M$ for $a \geq \tau$.

Using (2.1), we deduce that

$$I'(t) = \int_0^\tau \frac{\partial}{\partial t} u(a, t) da = \int_0^\tau \left(-\frac{\partial}{\partial a} u(a, t) - \mu_I u(a, t) \right) da.$$

Thus,

$$I'(t) = -u(\tau, 0) + u(0, t) - \mu_I I(t) = -u(\tau, 0) + b(M(t)) - \mu_I I(t).$$

Analogously, we can obtain that

$$M'(t) = u(\tau, 0) - u(+\infty, t) - \mu_M M(t).$$

We assume that $u(+\infty, t) = 0$ for all t . This is a realistic assumption because no individual can live forever. Next we determine the expression of $u(\tau, t)$ using the technique of the integration along the characteristic lines [19]. Denote by $\zeta^s(t) = u(t - s, t)$ with $t - s \leq \tau$. Then, by (2.1),

$$\frac{d}{dt}\zeta^s(t) = -\mu_I\zeta^s(t).$$

Notice that $\zeta^s(s) = u(0, s) = b(M(s))$ and $u(\tau, t) = \zeta^{t-\tau}(t)$. Thus, $\zeta^{t-\tau}(t) = b(M(t - \tau))e^{-\mu_I\tau}$ because $\zeta^{t-\tau}(t)$ is the solution of the initial value problem

$$\begin{cases} x' = -\mu_I x, \\ x(t - \tau) = b(M(t - \tau)), \end{cases}$$

evaluated at time t . With this expression we can describe the dynamical behavior of the population through the model

$$\begin{cases} I'(t) = -b(M(t - \tau))e^{-\mu_I\tau} + b(M(t)) - \mu_I I(t) \\ M'(t) = b(M(t - \tau))e^{-\mu_I\tau} - \mu_M M(t). \end{cases} \tag{2.2}$$

Once we know how to model the dynamical behavior of an insect population with a regular cycle, we introduce diapausing stages. We suppose that the annual growth period consists of three intervals, namely, the normal growth period, the diapause period and the post-diapause period with lengths T_1, T_2, T_3 , respectively. We normalize the annual growth period by 1. We assume that $T_3 = \tau$ with τ the maturation threshold. If we fix $T_2 = \tau_d$, then $T_1 = 1 - \tau_d - \tau$.

The dynamical behavior of a seasonal population can be described by the following system (I), consisting of (2.3), (2.4) and (2.5) below.

(A1) During the normal growth period, *i.e.*, $t \in [n, n + 1 - \tau - \tau_d]$,

$$\begin{cases} I'(t) = -b(M(t - \tau))e^{-\mu_I\tau} + b(M(t)) - \mu_I I(t), \\ M'(t) = b(M(t - \tau))e^{-\mu_I\tau} - \mu_M M(t), \end{cases} \tag{2.3}$$

(we are using directly system (2.2)).

(A2) During the diapause period, the development of mature and immature individuals stops and the individuals experience a mortality rate depending on the group, namely d_I and d_M . Thus, when $n + 1 - \tau - \tau_d < t < n + 1 - \tau$,

$$\begin{cases} I'(t) = -d_I I(t), \\ M'(t) = -d_M M(t). \end{cases} \tag{2.4}$$

(A3) For the post-diapause period, *i.e.*, when $n + 1 - \tau \leq t < n + 1$, the individuals have a maturation time $\tau + \tau_d$. The novelty is that during the diapause period, the immature population was reduced by a mortality rate (d_I) according to (2.4). Repeating the analysis to derive model (2.2), we obtain that

$$\begin{cases} I'(t) = -u(\tau + \tau_d, t) + b(M(t)) - \mu_I I(t), \\ M'(t) = u(\tau + \tau_d, t) - \mu_M M(t). \end{cases}$$

Informally speaking, the number of individuals of age $\tau + \tau_d$ at time t is the number of individuals of age τ at time $t - \tau_d$ after a reduction due to the mortality during the diapause period, that is,

$$u(\tau + \tau_d, t) = u(\tau, t - \tau_d) e^{-d_I \tau_d} = b(M(t - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d}.$$

Thus, we arrive at the model

$$\begin{cases} I'(t) = -b(M(t - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d} + b(M(t)) - \mu_I I(t), \\ M'(t) = b(M(t - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t). \end{cases} \tag{2.5}$$

3. Model analysis

3.1. The well-posedness

Since the equations for $M(t)$ can be decoupled in (2.3), (2.4) and (2.5), the dynamical behavior of the model is determined by

$$M'(t) = \begin{cases} b(M(t - \tau)) e^{-\mu_I \tau} - \mu_M M(t), & \text{if } t \in [n, n + 1 - \tau - \tau_d], \\ -d_M M(t), & \text{if } t \in (n + 1 - \tau - \tau_d, n + 1 - \tau), \\ b(M(t - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t), & \text{if } t \in [n + 1 - \tau, n + 1), \end{cases} \tag{3.1}$$

with $n \in \mathbb{N} \cup \{0\}$. We assume the following conditions:

- (H1) The birth rate can be expressed as $b(x) = xf(x)$ with $f : [0, +\infty) \rightarrow (0, +\infty)$ a strictly decreasing function of class C^1 . Moreover, b is a bounded function.
- (H2) $\tau + \tau_d < 1$.

A solution of (3.1) is a continuous and piece-wise C^1 -function $u : [-\tau - \tau_d, +\infty) \rightarrow [0, +\infty)$ that satisfies the equation in the intervals $(n, n + 1 - \tau - \tau_d)$, $(n + 1 - \tau - \tau_d, n + 1 - \tau)$, $(n + 1 - \tau, n + 1)$ for all $n = 0, 1, \dots$ and both one-sided derivatives exist at the break points. We will employ the notation $u'(t_0^+) = \lim_{t \rightarrow t_0^+} u'(t)$ and $u'(t_0^-) = \lim_{t \rightarrow t_0^-} u'(t)$. We observe that, for example, $u'(n^+) = b(u(n - \tau)) e^{-\mu_I \tau} - \mu_M u(n)$.

Let

$$\mathcal{C}([-\tau - \tau_d, 0], I) = \{\phi : [-\tau - \tau_d, 0] \rightarrow I \text{ continuous}\}.$$

For any initial condition $\phi \in \mathcal{C}([-\tau - \tau_d, 0], [0, +\infty))$, we can find a unique solution $u(t, \phi)$ (defined for all $t \geq 0$) so that $u(t, \phi) = \phi(t)$ for all $t \in [-\tau - \tau_d, 0]$ because the solutions of the equations

$$\begin{aligned} M'(t) &= b(M(t - \tau)) e^{-\mu_I \tau} - \mu_M M(t), \\ M'(t) &= -d_M M(t), \\ M'(t) &= b(M(t - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t) \end{aligned}$$

are defined for all $t \geq 0$. Furthermore, if we take an initial function in $\mathcal{C}([-\tau - \tau_d, 0], (0, +\infty))$, $u(t, \phi) > 0$ for all $t \geq 0$. This is a consequence of the variation of the constant formula because (3.1) can be written as

$$M(t) = e^{-\mu_M(t-n)} \left(\int_n^t b(M(s-\tau)) e^{-\mu_I \tau} e^{\mu_M(s-n)} ds + M(n) \right),$$

for $t \in [n, n + 1 - \tau - \tau_d]$;

$$M(t) = e^{-d_M(t-(n+1-\tau-\tau_d))} M(n + 1 - \tau - \tau_d)$$

for $t \in [n + 1 - \tau - \tau_d, n + 1 - \tau]$;

$$M(t) = e^{-\mu_M(t-(n+1-\tau))} \times \left(\int_{n+1-\tau}^t b(M(s-(\tau + \tau_d))) e^{-\mu_I \tau - d_I \tau_d} e^{\mu_M(s-(n+1-\tau))} ds + M(n+1-\tau) \right)$$

for $t \in [n + 1 - \tau, n + 1]$. We will refer to these last solutions as positive solutions.

First we give an useful result.

Lemma 3.1. Assume that (H1) and (H2) hold. If there exists a positive solution $u(t)$ of (3.1) so that $\lim_{t \rightarrow +\infty} u(t) = \xi$ with $\xi \in [0, +\infty)$, then $\xi = 0$.

Proof. Take $u(t)$ a positive solution of (3.1) so that $\lim_{t \rightarrow +\infty} u(t) = \xi$. Assume, by contradiction, that $\xi > 0$. Next we take two constants α, β with the following properties:

- $0 < \alpha < 1 < \beta$,
- $\beta e^{-d_M \tau_d} < \alpha$.

Since $\lim_{t \rightarrow +\infty} u(t) = \xi$ with $\xi > 0$, there is $t_* > 0$ so that

$$u(t) \in (\alpha \xi, \beta \xi)$$

for all $t \geq t_*$. In particular, for $n \in \mathbb{N}$ with $n + 1 - \tau - \tau_d > t_*$, we have that $\alpha \xi < u(n + 1 - \tau)$ and $u(n + 1 - \tau - \tau_d) < \beta \xi$. On the other hand, using the second equation of (3.1),

$$u(n + 1 - \tau) = u(n + 1 - \tau - \tau_d) e^{-d_M \tau_d} < \beta \xi e^{-d_M \tau_d}.$$

This is a contradiction with the choice of α and β . \square

Next we demonstrate that the positive solutions of (3.1) are uniformly bounded.

Proposition 3.1. Assume that **(H1)** and **(H2)** hold. Then, for any positive solution $u(t)$ of (3.1),

$$\limsup_{t \rightarrow +\infty} u(t) \leq \frac{\Delta e^{-\mu_I \tau}}{\mu_M},$$

with Δ an upper bound of $b(x)$.

Proof. Take $u(t)$ a positive solution of (3.1). We observe that if

$$u(t_0) > \frac{\Delta e^{-\mu_I \tau}}{\mu_M}$$

for some $t_0 \in (0, +\infty)$, then $u(t)$ is strictly decreasing in a neighborhood of t_0 . Indeed, from the first and third equation in (3.1), we have that

$$\frac{u'(t)}{\mu_M} \leq \frac{\Delta e^{-\mu_I \tau}}{\mu_M} - u(t),$$

if $t \in (n, n + 1 - \tau - \tau_d)$ and

$$\frac{u'(t)}{\mu_M} \leq \frac{\Delta e^{-\mu_I \tau} e^{-d_M \tau_d}}{\mu_M} - u(t) \leq \frac{\Delta e^{-\mu_I \tau}}{\mu_M} - u(t),$$

if $t \in (n + 1 - \tau, n + 1)$. Notice that in the intervals $(n + 1 - \tau - \tau_d, n + 1 - \tau)$, $u(t)$ is always strictly decreasing by the expression of the second equation of (3.1). From these inequalities, the conclusion of the proposition is clear. \square

3.2. Global extinction vs. permanence

A strength of the following results is that they are stated in terms of the biological parameters of the model instead of the spectral radius of an abstract operator. First, we provide a criterion for the global extinction of the population in model (3.1).

Proposition 3.2. Assume that **(H1)** and **(H2)** hold. If

$$\frac{e^{-\mu_I \tau} f(0)}{\mu_M} < 1, \tag{3.2}$$

0 is a global attractor, that is, $\lim_{t \rightarrow +\infty} u(t) = 0$ for any positive solution $u(t)$ of (3.1).

Proof. First we observe that by **(H1)**,

$$u'(t) \leq u(t - \tau) f(0) e^{-\mu_I \tau} - \mu_M u(t), \tag{3.3}$$

if $t \in (n, n + 1 - \tau - \tau_d)$ and

$$u'(t) \leq u(t - \tau - \tau_d) f(0) e^{-\mu_I \tau} - \mu_M u(t), \tag{3.4}$$

if $t \in (n + 1 - \tau, n + 1)$. Notice that in the intervals $(n + 1 - \tau - \tau_d, n + 1 - \tau)$, $u(t)$ is always strictly decreasing by the expression of the second equation of (3.1). Next we take a positive solution $u(t)$ of (3.1). Assume, by contradiction, that $u(t) \not\rightarrow 0$ as $t \rightarrow +\infty$. Then, $\limsup_{t \rightarrow +\infty} u(t) = \xi > 0$, (recall that $u(t)$ is bounded by Proposition 3.1). By Lemma 3.1, we can assume that $u(t) \not\rightarrow \xi$ as $t \rightarrow +\infty$, otherwise, we have already found a contradiction. Then, $\liminf_{t \rightarrow +\infty} u(t) < \limsup_{t \rightarrow +\infty} u(t)$. Applying Lemma 1.1, we can take a sequence $\{t_n\} \rightarrow +\infty$ with $\xi = \limsup_{t \rightarrow +\infty} u(t) = \lim_{n \rightarrow +\infty} u(t_n)$, so that $u(t_n)$ is a local maximum for all $n \in \mathbb{N}$. Then, $u'(t_n^-) \geq 0$ for all $n \in \mathbb{N}$. Since $u(t)$ is strictly decreasing in the intervals $(m + 1 - \tau - \tau_d, m + 1 - \tau)$ with $m \in \mathbb{N}$, we conclude that t_n does not belong to these intervals. From inequalities (3.3) and (3.4), we deduce that

$$u(t_n) \leq \frac{f(0)e^{-\mu_I \tau}}{\mu_M} u(s_n) \tag{3.5}$$

with $s_n \in \{t_n - \tau - \tau_d, t_n - \tau\}$. Since $u(t_n)$ is bounded, it is not restrictive to assume $\rho = \lim_{n \rightarrow +\infty} u(s_n) \leq \limsup_{t \rightarrow +\infty} u(t) = \lim_{n \rightarrow +\infty} u(t_n) = \xi$. On the other hand, making $n \rightarrow +\infty$ in (3.5) and using (3.2), we conclude that $\xi < \rho$, a contradiction. \square

To guarantee that the positive solutions of (3.1) are bounded apart from zero, we impose two additional conditions:

- (H3) $\frac{f(0)e^{-\mu_I \tau - d_* \tau_d}}{\mu_M} > 1$ with $d_* = \max\{d_I, d_M\}$.
- (H4) $e^{d_M \tau_d} < e^{-\mu_M(1-\tau-\tau_d)} + (1 - e^{-\mu_M(1-\tau-\tau_d)}) f(0) \frac{e^{-\mu_I \tau}}{\mu_M}$.

From a biological point of view, (H3) is a sufficient condition to guarantee the survival of the species for the normal-growth and post diapause periods in the absence of diapause. Condition (H4) indicates when the decrease of the population for the diapause period does not prevent the survival during the other periods. Notice that condition (H4) holds when d_M and τ_d are small because it involves a convex combination and $f(0) \frac{e^{-\mu_I \tau}}{\mu_M} > 1$ by (H3).

Next we give a preliminary result to prove that the positive solutions are bounded apart from zero.

Lemma 3.2. *Assume that (H1), (H2), (H3) and (H4) hold. If $u(t)$ is a positive solution of (3.1), then there does not exist a sequence $\{t_n\} \subset \bigcup_{m \in \mathbb{N} \cup \{0\}} [m + 1 - \tau - \tau_d, m + 1 - \tau]$ tending to $+\infty$ with the following properties:*

- (P1) $u(t_n) = \min\{u(t) : t \in [0, t_n]\}$.
- (P2) $\lim_{n \rightarrow +\infty} u(t_n) = 0$.

Proof. Assume, by contradiction, that such a sequence $\{t_n\}$ exists. Since $u(t)$ is strictly decreasing in the intervals $(m + 1 - \tau - \tau_d, m + 1 - \tau)$ for all $m \in \mathbb{N} \cup \{0\}$, it is not restrictive to assume that $\{t_n\} \subset \{m + 1 - \tau : m \in \mathbb{N}\}$. On the other hand, we notice that

$$u'(t) \geq -\mu_* u(t) \tag{3.6}$$

for all $t \in [t_n - 1, t_n]$ except for the break points $t_n - \tau_d$ and $t_n + \tau - 1$ with $\mu_* = \max\{d_M, \mu_M\}$. Using that $x(t)$ is continuous and (3.6), we obtain that

$$u(t_n) \geq e^{-\mu_* s} u(t_n - s)$$

for all $s \in [0, 1]$, or equivalently,

$$u(t_n) e^{\mu_* s} \geq u(t_n - s)$$

for all $s \in [0, 1]$. Thus,

$$u(t_n - s) \leq u(t_n) e^{\mu_* s} \tag{3.7}$$

for all $s \in [0, 1]$ and $n \in \mathbb{N}$. Now, by **(H3)** and **(H4)**, we can pick $\delta > 0$ so that

$$\frac{f(\delta) e^{-\mu_I \tau - d_* \tau_d}}{\mu_M} > 1 \tag{3.8}$$

and

$$e^{d_M \tau_d} < e^{-\mu_M(1-\tau-\tau_d)} + f(\delta) \frac{e^{-\mu_I \tau} (1 - e^{-\mu_M(1-\tau-\tau_d)})}{\mu_M}. \tag{3.9}$$

In addition, by **(P2)** and **(3.7)**, we can take $n_0 > 0$ large enough so that

$$u(t_{n_0} - s) < \delta \text{ for all } s \in [0, 1]. \tag{3.10}$$

We divide the rest of the proof into three steps:

Step 1: We prove that $u'((t_{n_0} - \tau_d)^-) > 0$.

We know by the second equation of **(3.1)** that

$$u(t_{n_0}) e^{d_M \tau_d} = u(t_{n_0} - \tau_d).$$

Using the first equation of **(3.1)**, we deduce that

$$\begin{aligned} u'((t_{n_0} - \tau_d)^-) &= u(t_{n_0} - \tau_d - \tau) f(u(t_{n_0} - \tau_d - \tau)) e^{-\mu_I \tau} - \mu_M u(t_{n_0} - \tau_d) \\ &\geq u(t_{n_0}) f(\delta) e^{-\mu_I \tau} - \mu_M e^{d_M \tau_d} u(t_{n_0}). \end{aligned}$$

In this inequality, we have used that $u(t_{n_0} - \tau_d - \tau) \geq u(t_{n_0})$ by **(P1)**, $u(t_{n_0} - \tau_d - \tau) \leq \delta$ by **(3.10)** and **(H1)**. Finally, notice that, using **(3.8)**,

$$u(t_{n_0}) (f(\delta) e^{-\mu_I \tau} - \mu_M e^{d_M \tau_d}) > 0.$$

Step 2: We prove that $u'(t_{n_0} - \tau_d - s) > 0$ for all $s \in (0, 1 - \tau_d - \tau)$.

Assume, by contradiction, that there is a first $s_* \in (0, 1 - \tau_d - \tau)$ so that $u'(t_{n_0} - \tau_d - s_*) = 0$. We stress that by the previous step, the definition of s_* is meaningful. Recall that $u'(t)$ is continuous in $(t_{n_0} - 1 + \tau, t_{n_0} - \tau_d)$ and $\lim_{t \rightarrow (t_{n_0} - \tau_d)^-} u'(t) = u'((t_{n_0} - \tau_d)^-)$. Therefore, $u(t)$ is strictly increasing in $(t_{n_0} - \tau_d - s_*, t_{n_0} - \tau_d)$. This implies that

$$u(t_{n_0} - \tau_d - s_*) \leq u(t_{n_0} - \tau_d) = e^{d_M \tau_d} u(t_{n_0}). \tag{3.11}$$

On the other hand, using the first equation of (3.1), (3.10) and (H1), we obtain that

$$\begin{aligned} \mu_M u(t_{n_0} - \tau_d - s_*) &= u(t_{n_0} - \tau_d - s_* - \tau) f(u(t_{n_0} - \tau_d - s_* - \tau)) e^{-\mu_M \tau} \\ &\geq u(t_{n_0} - \tau_d - s_* - \tau) f(\delta) e^{-\mu_M \tau}. \end{aligned} \tag{3.12}$$

Notice that by (P1), we have that

$$u(t_{n_0} - \tau_d - s_* - \tau) \geq u(t_{n_0}).$$

Using (3.11), (3.12) and this last inequality, we arrive at

$$e^{d_M \tau_d} \mu_M u(t_{n_0}) \geq u(t_{n_0}) f(\delta) e^{-\mu_M \tau}.$$

This is a contradiction with (3.8).

Step 3: Conclusion.

Using the previous step, $u(t)$ is strictly increasing in the interval $(t_{n_0} - 1 + \tau, t_{n_0} - \tau_d)$. Thus, $u(t_{n_0} - 1 + \tau) \leq u(t_{n_0} - \tau_d)$. Furthermore, for all $t \in (t_{n_0} - 1 + \tau, t_{n_0} - \tau_d)$, we have that

$$u'(t) \geq u(t_{n_0}) f(\delta) e^{-\mu_M \tau} - \mu_M u(t).$$

From this expression we deduce that

$$u(t_{n_0} - \tau_d) \geq u(t_{n_0} - 1 + \tau) e^{-\mu_M(1-\tau-\tau_d)} + u(t_{n_0}) \frac{f(\delta) e^{-\mu_M \tau}}{\mu_M} \left(1 - e^{-\mu_M(1-\tau-\tau_d)}\right).$$

Since $u(t_{n_0} - \tau_d) = u(t_{n_0}) e^{d_M \tau_d}$, we arrive at

$$u(t_{n_0}) e^{d_M \tau_d} \geq u(t_{n_0} - 1 + \tau) e^{-\mu_M(1-\tau-\tau_d)} + u(t_{n_0}) \frac{f(\delta) e^{-\mu_M \tau}}{\mu_M} \left(1 - e^{-\mu_M(1-\tau-\tau_d)}\right). \tag{3.13}$$

If $e^{d_M \tau_d} \leq \frac{f(\delta) e^{-\mu_M \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)})$, we have already found a contradiction in (3.13). If $e^{d_M \tau_d} > \frac{f(\delta) e^{-\mu_M \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)})$, then

$$u(t_{n_0}) \left(e^{d_M \tau_d} - f(\delta) \frac{e^{-\mu_M \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)}) \right) \frac{1}{e^{-\mu_M(1-\tau-\tau_d)}} \geq u(t_{n_0} - 1 + \tau).$$

Using (P1), we have that $u(t_{n_0} - 1 + \tau) \geq u(t_{n_0})$. Hence,

$$\left(e^{d_M \tau_d} - f(\delta) \frac{e^{-\mu_M \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)}) \right) \frac{1}{e^{-\mu_M(1-\tau-\tau_d)}} \geq 1.$$

This is a contradiction with (3.9). The proof is completed. \square

Theorem 3.1. Assume that **(H1)**, **(H2)**, **(H3)** and **(H4)**. Then, given $u(t)$ a positive solution of (3.1),

$$\liminf_{t \rightarrow +\infty} u(t) > 0.$$

Proof. Assume, by contradiction, that $\liminf_{t \rightarrow +\infty} u(t) = 0$. Then, we can take a sequence $\{t_n\} \rightarrow +\infty$ with the following properties:

(P1) $u(t_n) = \min\{u(t) : t \in [0, t_n]\}$ for all $n \in \mathbb{N}$.

(P2) $\lim_{n \rightarrow +\infty} u(t_n) = 0$.

The construction of this sequence is as follows. Define $q = \min\{u(t) : t \in [-\tau - \tau_d, 0]\}$. Take $t_n = \min\{t \in [0, +\infty) : u(t) = \frac{q}{n}\}$.

Consider

$$\begin{aligned} \mathcal{F}_1 &= \bigcup_{m \in \mathbb{N} \cup \{0\}} (m, m + 1 - \tau - \tau_d), \\ \mathcal{F}_2 &= \bigcup_{m \in \mathbb{N} \cup \{0\}} [m + 1 - \tau - \tau_d, m + 1 - \tau], \\ \mathcal{F}_3 &= \bigcup_{m \in \mathbb{N} \cup \{0\}} (m + 1 - \tau, m + 1]. \end{aligned}$$

By Lemma 3.2, there is $n_0 \in \mathbb{N}$ so that $t_n \notin \mathcal{F}_2$ for all $n \geq n_0$. Otherwise, we have already found the contradiction.

Next we distinguish between two cases:

Case 1: $t_n \in \mathcal{F}_1$ for some $n \in \mathbb{N}$.

Suppose that $t_n \in (m, m + 1 - \tau - \tau_d)$ with $m \in \mathbb{N}$. The function $u(t)$ is of class C^1 in $(m, m + 1 - \tau - \tau_d)$. Notice that **(P1)** implies that $u'(t_n) \leq 0$. Using the first equation of (3.1), we conclude that

$$u(t_n - \tau) f(u(t_n - \tau)) e^{-\mu_I \tau} - \mu_M u(t_n) \leq 0$$

or equivalently,

$$u(t_n - \tau) f(u(t_n - \tau)) e^{-\mu_I \tau} \leq \mu_M u(t_n). \tag{3.14}$$

By **(P1)**, we know that $u(t_n - \tau) \geq u(t_n)$ and so,

$$\frac{f(u(t_n - \tau)) e^{-\mu_I \tau}}{\mu_M} \leq 1. \tag{3.15}$$

The function

$$h(x) = \frac{f(x) e^{-\mu_I \tau}}{\mu_M}$$

is strictly decreasing, $h(0) > 1$ and $\lim_{x \rightarrow +\infty} h(x) = 0$ (see **(H1)** and **(H3)**). Let $\xi \in (0, +\infty)$ be the constant satisfying $h(\xi) = 1$. Then, inequality (3.15) implies that $u(t_n - \tau) \geq \xi$. Finally, as a direct consequence of (3.14), we arrive at

$$u(t_n) \geq \min\{x h(x) : x \in [\xi, \rho]\} \tag{3.16}$$

with $\rho > 0$ an upper bound of $u(t)$, see Proposition 3.1.

Case 2: $t_n \in \mathcal{F}_3$ for some $n \in \mathbb{N}$.

Suppose that $t_n \in (m + 1 - \tau, m + 1]$. The function $u(t)$ is of class \mathcal{C}^1 in $(m + 1 - \tau, m + 1)$ and the left-side derivative exists at $m + 1$. Thus, by **(P1)**,

$$u'(t_n) \leq 0 \quad \text{if } t_n \in (m + 1 - \tau, m + 1)$$

and

$$u'(t_n^-) \leq 0 \quad \text{if } t_n = m + 1.$$

In both cases, using the third equation of (3.1), we obtain that

$$u(t_n - \tau - \tau_d) f(u(t_n - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d} \leq \mu_M u(t_n). \tag{3.17}$$

By **(P1)**, we know that $u(t_n - \tau - \tau_d) \geq u(t_n)$. Thus,

$$\frac{f(u(t_n - \tau - \tau_d)) e^{-\mu_I \tau - d_I \tau_d}}{\mu_M} \leq 1. \tag{3.18}$$

As above, the function

$$\tilde{h}(x) = \frac{f(x) e^{-\mu_I \tau - d_I \tau_d}}{\mu_M}$$

is strictly decreasing, $\tilde{h}(0) > 1$ and $\lim_{x \rightarrow +\infty} \tilde{h}(x) = 0$ (see **(H1)** and **(H3)**). Let $\tilde{\xi} \in (0, +\infty)$ be the constant with $\tilde{h}(\tilde{\xi}) = 1$. Then, inequality (3.18) implies that $x(t_n - \tau - \tau_d) \geq \tilde{\xi}$. Finally, by (3.17), we deduce that

$$u(t_n) \geq \min\{x \tilde{h}(x) : x \in [\tilde{\xi}, \rho]\} \tag{3.19}$$

with $\rho > 0$ an upper bound of $u(t)$, see Proposition 3.1.

To conclude the proof, we realize that by (3.16) and (3.19), $u(t_n)$ cannot converge to 0. This is a contradiction with **(P2)**. \square

4. Global attractivity in model (3.1)

4.1. Some useful results on discrete dynamics

The main result of this paper is based on the global attraction of a scalar discrete equation of the form

$$x_{n+1} = \varphi(x_n), \tag{4.1}$$

with $\varphi : [0, +\infty) \rightarrow [0, +\infty)$ a function of class C^1 satisfying that $\varphi((0, +\infty)) \subset (0, +\infty)$. Next we recall two basic results on discrete dynamics:

Proposition 4.1 (Lemma 2.5 in [6]). *Assume that $\bar{x} \in (0, +\infty)$ with $\varphi(\bar{x}) = \bar{x}$ is globally attracting for equation (4.1) in $(0, +\infty)$, that is, for all $x_0 \in (0, +\infty)$,*

$$\lim_{n \rightarrow +\infty} \varphi^n(x_0) = \bar{x}$$

with $\varphi^n = \varphi \circ \dots \circ \varphi$. Then, there is no interval $[L, S] \subset (0, +\infty)$ with $L < S$ so that $[L, S] \subset \varphi([L, S])$.

Proposition 4.2. *Assume that φ is a decreasing or unimodal function of class C^3 with negative Schwarzian derivative, that is,*

$$(S\varphi)(x) = \frac{\varphi'''(x)}{\varphi'(x)} - \frac{3}{2} \left(\frac{\varphi''(x)}{\varphi'(x)} \right)^2 < 0 \quad \text{for all } x > 0,$$

provided $\varphi'(x) \neq 0$. If (4.1) has a unique positive equilibrium $\bar{x} > 0$ and $|\varphi'(\bar{x})| < 1$, then \bar{x} is globally attracting for equation (4.1) in $(0, +\infty)$.

The previous result is Corollary 2.10 in [6] for unimodal functions. For decreasing maps, we can deduce the result by a simple adaptation of the arguments in [18]. It is worth mentioning that $\varphi(x) = x e^{\rho(1-x)}$ with $\rho > 0$ and $\varphi(x) = \frac{1+\rho^\gamma}{1+(\rho x)^\gamma} x$ with $\rho > 0$ and $\gamma > 1$ are unimodal functions with negative Schwarzian derivative.

4.2. Main results

Fix $u_*(t)$ a positive solution of (3.1). We employ the change of variable

$$y(t) = \frac{u(t)}{u_*(t)},$$

with $u(t)$ a positive solution of (3.1). After simple computations, we obtain:

- if $t \in [n, n + 1 - \tau - \tau_d]$, then

$$y'(t) = \frac{u_*(t - \tau) e^{-\mu_1 \tau}}{u_*(t)} \left(y(t - \tau) f(u_*(t - \tau)y(t - \tau)) - y(t) f(u_*(t - \tau)) \right), \tag{4.2}$$

- if $t \in (n + 1 - \tau - \tau_d, n + 1 - \tau)$, then

$$y'(t) = 0, \tag{4.3}$$

- and if $t \in [n + 1 - \tau, n + 1)$, then

$$y'(t) = \frac{u_*(t - \tau - \tau_d)e^{-\mu_1\tau - d_1\tau_d}}{u_*(t)} \times \left(y(t - \tau - \tau_d)f(u_*(t - \tau - \tau_d)y(t - \tau - \tau_d)) - y(t)f(u_*(t - \tau - \tau_d)) \right). \tag{4.4}$$

Since f is strictly decreasing, it is clear that $y = 1$ is the unique positive constant solution of the equation made of (4.2)-(4.3)-(4.4). Next we define the map

$$H : (0, +\infty)^2 \longrightarrow (0, +\infty)$$

$$H(t, x) = \frac{f(tx)}{f(t)}.$$

We will work with the following conditions:

- (H5) $\frac{\partial H}{\partial t}(t, x) \geq 0$ for all $t > 0$ and $x \in (0, 1)$.
- (H6) $\frac{\partial H}{\partial t}(t, x) \leq 0$ for all $t > 0$ and $x \in (1, +\infty)$.

Although these conditions seem strong, most growth rates in mathematical biology satisfy (H5) and (H6). For example, for $f(x) = \alpha e^{-x}$ with $\alpha > 0$, the birth rate associated with the classical Nicholson’s blowfly equation, we have that $H(t, x) = e^{t(1-x)}$. Analogously, for $f(x) = \frac{\theta}{1+x^\gamma}$ with $\theta > 0$ and $\gamma \geq 1$, the birth rate associated with the Mackey-Glass model, $H(t, x) = \frac{1+t^\gamma}{1+(tx)^\gamma}$. In both case, (H5) and (H6) clearly hold.

Now we are ready to prove that main result of this paper:

Theorem 4.1. Assume that (H1)-(H6) hold. Take a positive constant θ_{\max} so that

$$\limsup_{t \rightarrow +\infty} u(t) \leq \theta_{\max}$$

for any $u(t)$ positive solution of (3.1). If 1 is globally attracting in $(0, +\infty)$ for the difference equation

$$x_{n+1} = x_n G(x_n) \tag{4.5}$$

with $G(x) = H(\theta_{\max}, x)$, then, for any pair of positive solutions $u_*(t), u(t)$ of (3.1),

$$\lim_{t \rightarrow +\infty} (u(t) - u_*(t)) = 0.$$

Proof. Fix $u(t)$ and $u_*(t)$ two positive solutions of (3.1). Then, by Theorem 3.1 and Proposition 3.1, $u(t)$ and $u_*(t)$ are bounded and there is $\omega > 0$ so that

$$\omega \leq u(t), u_*(t) \quad \text{for all } t \in [-\tau - \tau_d, +\infty).$$

Assume, by contradiction, that $(u(t) - u_*(t)) \rightarrow 0$ as $t \rightarrow +\infty$. Since

$$u_*(t) (y(t) - 1) = (u(t) - u_*(t))$$

with

$$y(t) = \frac{u(t)}{u_*(t)},$$

we conclude that $y(t) - 1 \rightarrow 0$ as $t \rightarrow +\infty$. We know that $y(t)$ satisfies the equation made of (4.2)-(4.3)-(4.4). Using that $y = 1$ is the unique positive constant solution of this equation, we deduce that

$$\liminf_{t \rightarrow +\infty} y(t) < \limsup_{t \rightarrow +\infty} y(t).$$

Then, by Lemma 1.1, there are two sequences $\{t_n\}$ and $\{s_n\}$ tending to $+\infty$ with the following properties:

- (R1) $\lim_{n \rightarrow +\infty} y(t_n) = \limsup_{t \rightarrow +\infty} y(t)$ and $y(t_n)$ is a local maximum for all $n \in \mathbb{N}$.
- (R2) $\lim_{n \rightarrow +\infty} y(s_n) = \liminf_{t \rightarrow +\infty} y(t)$ and $y(s_n)$ is a local minimum for all $n \in \mathbb{N}$.

Set $L = \liminf_{t \rightarrow +\infty} y(t)$ and $S = \limsup_{t \rightarrow +\infty} y(t)$. Notice that $L > 0$. Since $y(t)$ is constant in the intervals of the form $(m + 1 - \tau - \tau_d, m + 1 - \tau)$ with $m \in \mathbb{N} \cup \{0\}$, it is not restrictive to assume that $t_n > 1$ and

$$t_n \in \mathcal{A} \cup \mathcal{A}_b \cup \mathcal{A}_e \cup \mathcal{B} \cup \mathcal{B}_b$$

with

$$\begin{aligned} \mathcal{A} &= \cup_{m \in \mathbb{N}} (m, m + 1 - \tau - \tau_d), & \mathcal{A}_b &= \{m : m \in \mathbb{N}\}, & \mathcal{A}_e &= \{m + 1 - \tau - \tau_d : m \in \mathbb{N}\}, \\ \mathcal{B} &= \cup_{m \in \mathbb{N}} (m + 1 - \tau, m + 1), & \mathcal{B}_b &= \{m + 1 - \tau : m \in \mathbb{N}\}. \end{aligned}$$

Our first aim is to find a constant $\tilde{S} \in [L, S]$ from the sequence $\{t_n\}$ given in (R1) so that

$$S \leq \tilde{S} G(\tilde{S}). \tag{4.6}$$

We distinguish among five cases:

Case 1: There is a subsequence $\{t_{\sigma(n)}\} \subset \mathcal{A}$.

The function $y(t)$ is of class \mathcal{C}^1 in \mathcal{A} . Using that $y(t_{\sigma(n)})$ is a local maximum, we have that $y'(t_{\sigma(n)}) = 0$. Now, by the expression of (4.2), we deduce that

$$y(t_{\sigma(n)} - \tau) f(u_*(t_{\sigma(n)} - \tau)y(t_{\sigma(n)} - \tau)) - y(t_{\sigma(n)}) f(u_*(t_{\sigma(n)} - \tau)) = 0. \tag{4.7}$$

The sequences $\{y(t_{\sigma(n)} - \tau)\}$ and $\{u_*(t_{\sigma(n)} - \tau)\}$ are bounded. Hence, it is not restrictive (after passing to subsequences if necessary) to suppose that $y(t_{\sigma(n)} - \tau) \rightarrow \tilde{S}$ with $\tilde{S} \in [L, S]$ and $u_*(t_{\sigma(n)} - \tau) \rightarrow \kappa_1$ with $0 < \kappa_1 \leq \theta_{\max}$. Making $n \rightarrow +\infty$ in (4.7), we conclude that

$$\tilde{S} f(\kappa_1 \tilde{S}) = S f(\kappa_1). \tag{4.8}$$

Using that $\tilde{S} \leq S$, we obtain that

$$f(\kappa_1 \tilde{S}) \geq f(\kappa_1).$$

Thus, $\tilde{S} \leq 1$ because f is strictly decreasing. Finally, we re-write (4.8) as

$$\tilde{S} H(\kappa_1, \tilde{S}) = S.$$

Using that $\tilde{S} \leq 1$ together with **(H5)**, $H(\kappa_1, \tilde{S}) \leq H(\theta_{\max}, \tilde{S}) = G(\tilde{S})$. Therefore, we arrive at

$$\tilde{S} G(\tilde{S}) \geq S.$$

Case 2: There is a subsequence $\{t_{\sigma(n)}\} \subset \mathcal{A}_b$.

In this case, $y'(t_{\sigma(n)}^-) \geq 0$ for all $n \in \mathbb{N}$. Using the expression of (4.4), we deduce that

$$y(t_{\sigma(n)} - \tau - \tau_d) f(u_*(t_{\sigma(n)} - \tau - \tau_d)y(t_{\sigma(n)} - \tau - \tau_d)) - y(t_{\sigma(n)}) f(u_*(t_{\sigma(n)} - \tau - \tau_d)) \geq 0.$$

Arguing as in the previous case, we conclude that there is $\tilde{S} \in [L, S]$ so that

$$\tilde{S} G(\tilde{S}) \geq S.$$

Case 3: There is a subsequence $\{t_{\sigma(n)}\} \subset \mathcal{A}_e$.

In this case, we have that $y'(t_{\sigma(n)}^-) \geq 0$ for all $n \in \mathbb{N}$. Repeating the same argument as in **Case 2**, we find a constant $\tilde{S} \in [L, S]$ so that

$$\tilde{S} G(\tilde{S}) \geq S.$$

The unique difference is that we employ equation (4.2) instead of equation (4.4).

Case 4: There is a subsequence $\{t_{\sigma(n)}\} \subset \mathcal{B}$.

This case is analogous to **Case 1** considering equation (4.4) instead of equation (4.2).

Case 5: There is a sequence $\{t_{\sigma(n)}\} \subset \mathcal{B}_b$.

The function $y(t)$ is constant in the interval $(m + 1 - \tau - \tau_d, m + 1 - \tau)$. Thus, $y(t_{\sigma(n)}) = y(t_{\sigma(n)} - \tau_d)$. Since $y(t_{\sigma(n)})$ is a local maximum we have that $y'((t_{\sigma(n)} - \tau_d)^-) \geq 0$. Now we repeat the same argument as **Case 2** with the sequence $\{t_{\sigma(n)} - \tau_d\}$.

We can reason analogously with the sequence $\{s_n\}$ to obtain a constant $\tilde{L} \in [L, S]$ so that

$$L \geq \tilde{L} G(\tilde{L}). \tag{4.9}$$

Finally, we observe that by (4.6) and (4.9), $[L, S] \subset \varphi([L, S])$ with $\varphi(x) = xG(x)$. This is a contradiction because we know in advance that such an interval cannot exist by Lemma 4.1. \square

Remark 4.1. As stressed in the next section, the condition that 1 is globally attracting for equation (4.5) is easy to verify in most applications. In fact, by the results of Section 4.1, we have this condition when $|\varphi'(1)| < 1$ with $\varphi(x) = xG(x)$.

5. Examples

In this subsection we apply Theorem 4.1 to model (3.1) for the classical birth rates $b(x) = rx e^{-x}$ and $b(x) = \frac{rx}{1+x^2}$ with $r > 1$ in both cases. As we will see, the conditions are easily checked for these choices of the birth rates.

5.1. Example 1: exponential birth rate

Consider

$$u'(t) = \begin{cases} ru(t - \tau)e^{-u(t-\tau)}e^{-\mu_I \tau} - \mu_M u(t), & \text{if } t \in [n, n + 1 - \tau - \tau_d], \\ -d_M u(t), & \text{if } t \in (n + 1 - \tau - \tau_d, n + 1 - \tau), \\ ru(t - \tau - \tau_d)e^{-u(t-\tau-\tau_d)}e^{-\mu_I \tau - d_I \tau_d} - \mu_M u(t), & \text{if } t \in [n + 1 - \tau, n + 1], \end{cases} \tag{5.1}$$

where $r > 0$ and the rest of the parameters involved in (5.1) are strictly positive. Let us re-write the conditions of Theorem 4.1 for this model.

- (B1) $\tau + \tau_d < 1$.
- (B2) $\frac{r e^{-\mu_I \tau - d_* \tau_d}}{\mu_M} > 1$ with $d_* = \max\{d_I, d_M\}$.
- (B3) $e^{d_M \tau_d} < e^{-\mu_M(1-\tau-\tau_d)} + r \frac{e^{-\mu_I \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)})$.

Since

$$H(t, x) = e^{t(1-x)},$$

it is clear that this map satisfies (H5) and (H6). In order to apply Theorem 4.1, we need that 1 is globally attracting in $(0, +\infty)$ for the difference equation

$$x_{n+1} = x_n G(x_n), \tag{5.2}$$

with $G(x) = e^{\theta_{\max}(1-x)}$ and θ_{\max} an uniform bound of the positive solutions of (3.1). By Proposition 3.1, this bound can be taken as

$$\theta_{\max} = \frac{r e^{-\mu_I \tau - 1}}{\mu_M}.$$

We notice that $\varphi(x) = xG(x)$ is an unimodal function with negative Schwarzian derivative. By Proposition 4.2, we can guarantee that 1 is globally attracting in $(0, +\infty)$ if $|\varphi'(1)| < 1$. This last condition is satisfied when $\theta_{\max} < 2$. Collecting the above information, we deduce the following result:

Theorem 5.1. Assume (B1), (B2) and (B3). If

$$\frac{r e^{-\mu_I \tau - 1}}{\mu_M} < 2, \tag{5.3}$$

then, for any pair of positive solutions $u_1(t)$ and $u_2(t)$ of (5.1),

$$\lim_{t \rightarrow +\infty} (u_1(t) - u_2(t)) = 0.$$

As mentioned above, condition (5.3) implies the global attractivity required in Theorem 4.1, a critical condition for the validity of the theorem. Notice that for $\tau_d = 0$, that is, in the absence of diapause periods, we recover the classical Nicholson’s blowfly equation

$$u'(t) = ru(t - \tau)e^{-u(t-\tau)}e^{-\mu_I \tau} - \mu_M u(t). \tag{5.4}$$

It is well known that for large values of r , (5.4) exhibits a broad range of dynamical patterns beyond the simple behavior predicted by Theorem 5.1. On the other hand, $0 < \tau < 1$ and $\frac{r e^{-\mu_I \tau}}{\mu_M} > 1$ imply (B1)-(B3) provided $\tau_d = 0$. We observe that $\frac{r e^{-\mu_I \tau}}{\mu_M} > 1$ is the optimal condition that guarantees that the origin is unstable for equation (5.4).

5.2. Bifurcation vs. diapause

In this paper we illustrate how Proposition 3.2 and Theorem 3.1 provide bifurcation insights in model (5.1). Arguing as in [13], we can deduce the following result when (5.1) additionally satisfies that $2\tau + \tau_d < 1$. Notice that in a neighborhood of the origin, equation (5.1) satisfies the monotonicity assumptions required in [13].

Theorem 5.2. The following statements hold for system (5.1):

- (i) If $\mathcal{R} \leq 1$, then the origin is globally asymptotically stable for the positive solutions.
- (ii) If $\mathcal{R} > 1$, then $\liminf_{t \rightarrow +\infty} u(t) > 0$ for any positive solution.

In the previous result, \mathcal{R} denotes the spectral radius of $P(1)$ where $P(t)$ is the solution map of the linear system

$$u'(t) = \begin{cases} ru(t - \tau)e^{-\mu_I \tau} - \mu_M u(t), & \text{if } t \in [n, n + 1 - \tau - \tau_d], \\ -d_M u(t), & \text{if } t \in (n + 1 - \tau - \tau_d, n + 1 - \tau), \\ ru(t - \tau - \tau_d)e^{-\mu_I \tau - d_I \tau_d} - \mu_M u(t), & \text{if } t \in [n + 1 - \tau, n + 1), \end{cases} \tag{5.5}$$

for $n = 1, 2, \dots$. Theorem 5.2 establishes the transcritical bifurcation of the origin in terms of the spectral radius of the operator $P(1)$. This operator is hard to handle but Proposition 3.2 and Theorem 3.1 are able to simplify the task.

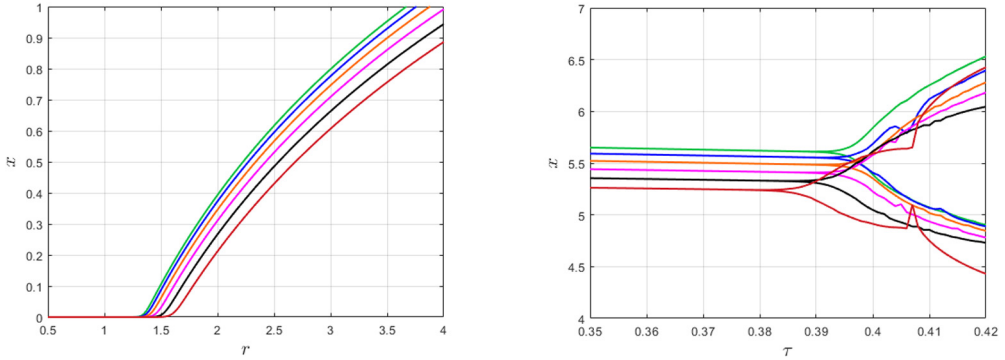


Fig. 1. Bifurcation diagrams in model (5.1). Fixed parameters $d_I = 1, \mu_I = 1, \mu_M = 1$. We compute a solution of (5.1) with a random initial condition during 200 years. Then, we plot $\max\{x(180), x(181), \dots, x(200)\}$ and $\min\{x(180), x(181), \dots, x(200)\}$. (Left) We consider r as a bifurcation parameter. Fixed parameter $\tau = 0.3$. (Right) We consider τ as a bifurcation parameter. Fixed parameter $r = e^6$. Green ($\tau_d = d_M = 0$) (Model (5.4)), Blue ($\tau_d = d_M = 0.05$), Orange ($\tau_d = d_M = 0.1$), Magenta ($\tau_d = d_M = 0.15$), Black ($\tau_d = d_M = 0.2$), Red ($\tau_d = d_M = 0.25$). (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

Corollary 5.1. Assume that (H1) and (H2) hold. If

$$\frac{r e^{-\mu_I \tau}}{\mu_M} < 1, \tag{5.6}$$

then $\mathcal{R} \leq 1$.

Corollary 5.2. If (B2) and (B3) hold, then $\mathcal{R} > 1$.

To understand in depth these corollaries, it is convenient to compare models (5.4) and (5.1). Since $r \frac{e^{-\mu_I \tau}}{\mu_M} = 1$ is the threshold condition of the transcritical bifurcation in (5.4), Corollary 5.1 implies that the introduction of diapause promotes the extinction of the population. Translating this claim in a bifurcation scenario, the threshold in which the transcritical bifurcation takes place is greater in (5.1) than in (5.4). In Fig. 1 Left, we illustrate this fact when we move r and the rest of parameters remain fixed. On the other hand, it is well-known that model (5.4) exhibits a Hopf bifurcation when we move τ , (see Theorem 2.3 in [21]). In contrast with the transcritical bifurcation of the origin, the introduction of diapause can promote this Hopf bifurcation, (see Fig. 1 Right).

5.3. Example 2: rational birth rate

Arguing in a similar manner as above with the model

$$u'(t) = \begin{cases} \frac{r u(t-\tau)}{1+u(t-\tau)^2} e^{-\mu_I \tau} - \mu_M u(t), & \text{if } t \in [n, n+1-\tau-\tau_d], \\ -d_M u(t), & \text{if } t \in (n+1-\tau-\tau_d, n+1-\tau), \\ \frac{r u(t-\tau-\tau_d)}{1+u(t-\tau-\tau_d)^2} e^{-\mu_I \tau-d_I \tau_d} - \mu_M u(t), & \text{if } t \in [n+1-\tau, n+1), \end{cases} \tag{5.7}$$

we have the next result:

Theorem 5.3. Assume the following conditions:

- (B1) $\tau + \tau_d < 1$.
- (B2) $\frac{r e^{-\mu_I \tau - d_* \tau_d}}{\mu_M} > 1$ with $d_* = \max\{d_I, d_M\}$.
- (B3) $e^{d_M \tau_d} < e^{\mu_M(1-\tau-\tau_d)} + r \frac{e^{-\mu_I \tau}}{\mu_M} (1 - e^{-\mu_M(1-\tau-\tau_d)})$.

Then, for any pair of positive solutions $u_1(t)$ and $u_2(t)$ of (5.7)

$$\lim_{t \rightarrow +\infty} (u_1(t) - u_2(t)) = 0.$$

Proof. Notice that $G(x) = \frac{1+\theta_{\max}^2}{1+(\theta_{\max}x)^2}$ and by Proposition 3.1, we can take

$$\theta_{\max} = \frac{r e^{-\mu_I \tau}}{2\mu_M}.$$

We observe that $\varphi(x) = x G(x)$ is an unimodal function with negative Schwrtzian derivative. Moreover, $|\varphi'(1)| < 1$ is always satisfied.

6. Oscillations in mosquito populations with diapause

In this section we provide some biological patterns expected for populations with diapause. To this task, we carry out several numerical simulations with (3.1) using the classical Nicholson’s blowfly birth rate [2,5,9]. Now, we consider the annual growth period as 365 days. Regarding the biological parameters, the diapause period comes from the winter season, typically three months. The values of the mortality rates related to the diapause are expressed in terms of the proportion of individuals surviving. For the rest of parameters, we use the estimates given in [5] for the *Aedes aegypti*. This species is the primary vector of yellow fever, a disease that is predominant in tropical South America and Africa, and sometimes appears in temperate regions during summer months. *Aedes aegypti* normally experiences a diapause during the harsh winters. Specifically, the immature individuals survive and the adults essentially become extinct during the diapause. In the language of model (3.1), this is translated via $P_I \gg P_M$, see Table 1. Fig. 2 indicates that the data collected in Table 1 typically produces a periodic pattern in which there is a pronounced decline of the adult population during the diapause. We stress the oscillatory behavior of these solutions during the normal growth period. Notice that the solutions of (3.1) when the growth rate is increasing normally tend to a periodic pattern with three monotone intervals during the year, see Fig. 4 in [13].

In nature, there are mainly two types of diapause, namely, adult diapause and immature diapause. In the first (resp. second) type, the adult (resp. immature) individuals can survive whereas the immature (resp. adult) individuals become extinct. Following this classification, *Aedes aegypti* is a species with immature diapause. The home mosquito *Culex pipiens* is an example of species with mature diapause, see [13]. In Fig. 3, we analyze the influence of the type of diapause on the creation/suppression of oscillations. In other words, the stabilizing role of the parameters P_I and P_M . The key conclusion is that an increment of P_I or P_M can buffer or magnify the dynamical behavior. Apart from Hopf bifurcations, we have found bubbles ((a)) and the usual periodic-doubling route to chaos ((b), (c), (d)). We remark that these phenomena are rather frequent in population dynamics, epidemiology or physiology, see [8].

Table 1
 Model parameters. We employ $b(x) = rx e^{-\alpha x}$ with $r > 0$ in (3.1). The values are taken from [13] and [5]. Let $P_M, P_I \in [0, 1]$ be the proportion of mature and immature individuals that survive during the diapause period. Then, $d_M = \frac{-\ln P_M}{\tau_d}$ and $P_I = e^{-d_I \tau_d}$.

Symbol	Value	Units
t		days
$M(t)$		individuals
α	$(5.128 \cdot 10^{-4}, 1.031 \cdot 10^{-3})$	individuals ⁻¹
μ_M	0.12	days ⁻¹
$A = r e^{-\mu_I \tau}$	(0.367, 1.31)	days ⁻¹
τ	(12, 30)	days
τ_d	(60, 240)	days

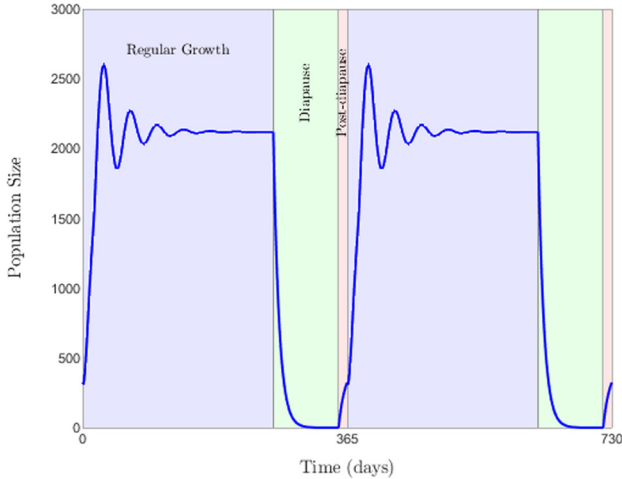


Fig. 2. Simulated mosquito population abundance for *Aedes aegypti* through model (3.1) using the parameters in Table 1 ($\tau = 12, \tau_d = 90, \alpha = 0.001, \mu_M = 0.12, A = 1, P_I = 0.2, P_M = 10^{-5}$). The positive solutions tend to a periodic pattern with an oscillatory behavior during the regular growth period and monotone behaviors in the rest of the annual growth period.

7. Discussion

Seasonal fluctuations of environmental conditions are of critical importance for the growth and survival of species, especially when there are strong variations during the year. In this paper we have analyzed the dynamical behavior of a general class of non-autonomous single population models. Generally speaking, we have studied a scalar equation where we employ a nonlinearity of Nicholson’s type in good seasons and a linear equation with negative constants in bad seasons. Mathematically, the model is discontinuous and periodic in time, but the associated solutions are continuous. Our main goal was to derive a criterion of global attractivity of a positive solution for this class of models. The method of proof can be viewed as the extension for nonautonomous

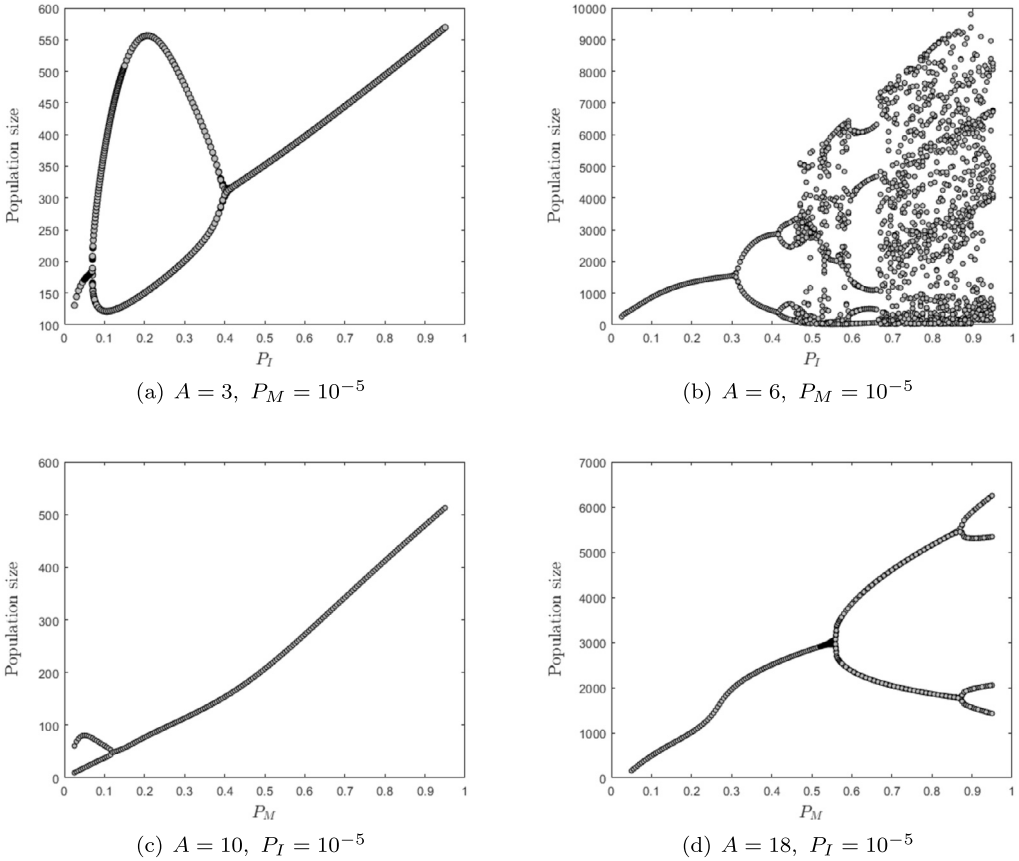


Fig. 3. Bifurcation diagrams of (3.1) with P_I ((a) and (b)) and P_M ((c) and (d)) as bifurcation parameters. Fixed parameters: $\tau = 12, \tau_d = 90, \alpha = 0.001, \mu_M = 0.12$. We compute a solution of (3.1) with a random initial condition during 200 years. Then, we plot it at the end of the year during the last 20 years. (a) An annual periodic solution loses its stability through a periodic doubling bifurcation and the annual periodic solution regains its stability for large values of P_I . (b), (c) and (d) There is the usual periodic-doubling route to chaos. We stress that in (a) and (c) (resp. (b) and (d)) increasing (resp. decreasing) the survival during the diapause stabilize (resp. destabilize) the dynamical behavior of the model.

and discontinuous equations of the folkloric connection between scalar delay differential equations and discrete equations developed by Mallet-Paret and Nussbaum in [14] and Ivanov and Sharkovskii in [11], (see also [12,17,7,8]). As Lemma 3.2 and Theorem 3.1 shown, the discontinuous reduction during the diapause period considerably obstructs the mathematical analysis.

Based on the theory of monotone systems [19,20], Lou et al. in [13] have described the dynamical behavior of (3.1) when the birth rate is monotone. Specifically, they proved that the global attractivity of a periodic solution is determined by the spectral radius of the linearized equation at 0. In comparison with [13], Theorem 4.1 drops the condition of monotone birth rate function. The main conclusion of this framework is that time delays are critical on the dynamical behavior of the model.

The use of nonmonotone birth rates in mosquito population models with diapause leads to the presence of population oscillations. This fact opens the door for the analysis of the influence of the diapause parameters on the creation/suppression of oscillations. However, the bifurcation

diagrams discussed in Section 5 indicate that none biological parameter associated with the diapause plays a stabilizing or destabilizing role.

Data availability

No data was used for the research described in the article.

Acknowledgments

We are grateful to the referee for careful reading and suggestions, which greatly improve the original version. The first author is supported by the Spanish project PID2021-128418NA-I00.

Appendix A

Proof of Lemma 1.1. Take a constant c and a sequence $\{\tilde{t}_n\}$ tending to $+\infty$ with

- $\liminf_{x \rightarrow +\infty} h(x) < c < \limsup_{x \rightarrow +\infty} h(x)$,
- $\lim_{n \rightarrow +\infty} h(\tilde{t}_n) = \limsup_{x \rightarrow +\infty} h(x)$ with $h(\tilde{t}_n) > c$ for all $n \in \mathbb{N}$.

Since $\liminf_{x \rightarrow +\infty} h(x) < c$, it is not restrictive (after passing to subsequences if necessary) to suppose the existence of two sequences $\{a_n\}$ and $\{b_n\}$ tending to $+\infty$ so that

- $a_n < \tilde{t}_n < b_n$ for all $n \in \mathbb{N}$,
- $h(a_n) = h(b_n) = c$ for all $n \in \mathbb{N}$.

Finally, we choose $\{t_n\}$ as

$$h(t_n) = \max\{h(x) : x \in [a_n, b_n]\}.$$

The proof for the existence of $\{s_n\}$ is analogous and we omit the details. \square

References

[1] Z. Bai, Y. Lou, X.Q. Zhao, A delayed succession model with diffusion for the impact of diapause on population growth, *SIAM J. Appl. Math.* 80 (2020) 1493–1519.
 [2] S.P. Blythe, R.M. Nisbet, W.S.C. Gurney, The dynamics of population models with distributed maturation periods, *Theor. Popul. Biol.* 25 (1984) 289–311.
 [3] D.L. Denlinger, Why study diapause?, *Entomol. Res.* 38 (2008) 1–9.
 [4] D.L. Denlinger, Regulation of diapause, *Annu. Rev. Entomol.* 47 (2002) 93–122.
 [5] C. Dye, Models for the population dynamics of the yellow fever mosquito, *Aedes aegypti*, *J. Anim. Ecol.* (1984) 247–268.
 [6] H.A. El-Morshedy, V.J. López, Global attractors for difference equations dominated by one-dimensional maps, *J. Differ. Equ. Appl.* 14 (2008) 391–410.
 [7] H.A. El-Morshedy, A. Ruiz-Herrera, Geometric methods of global attraction in systems of delay differential equations, *J. Differ. Equ.* 263 (2017) 5968–5986.
 [8] H.A. El-Morshedy, A. Ruiz-Herrera, Asymptotic convergence in delay differential equations arising in epidemiology and physiology, *SIAM J. Appl. Math.* 81 (2021) 1781–1798.
 [9] W.S.C. Gurney, S.P. Blythe, R.M. Nisbet, Nicholson’s blowflies revisited, *Nature* 287 (1980) 17–21.
 [10] S.B. Hsu, X.Q. Zhao, A Lotka–Volterra competition model with seasonal succession, *J. Math. Biol.* 64 (2012) 109–130.

- [11] A.F. Ivanov, A.N. Sharkovsky, Oscillations in singularly perturbed delay equations, in: *Dynamics Reported*, Springer, Berlin, Heidelberg, 1992, pp. 164–224.
- [12] E. Liz, A. Ruiz-Herrera, Attractivity, multistability, and bifurcation in delayed Hopfield's model with non-monotonic feedback, *J. Differ. Equ.* 255 (2013) 4244–4266.
- [13] Y. Lou, K. Liu, D. He, D. Gao, S. Ruan, Modelling diapause in mosquito population growth, *J. Math. Biol.* 78 (2019) 2259–2288.
- [14] J. Mallet-Paret, R.D. Nussbaum, Global continuation and asymptotic behaviour for periodic solutions of a differential-delay equation, *Ann. Mat. Pura Appl.* 145 (1986) 33–128.
- [15] R. Peng, X.Q. Zhao, The diffusive logistic model with a free boundary and seasonal succession, *Discrete Contin. Dyn. Syst.* 33 (2013) 2007.
- [16] A. Ruiz-Herrera, F. Zanolin, Horseshoes in 3D equations with applications to Lotka–Volterra systems, *NoDEA Nonlinear Differ. Equ. Appl.* 22 (2015) 877–897.
- [17] A. Ruiz-Herrera, Delay reaction-diffusion systems via discrete dynamics, *SIAM J. Math. Anal.* 52 (2020) 6297–6312.
- [18] D. Singer, Stable orbits and bifurcation of maps of the interval, *SIAM J. Appl. Math.* 35 (1978) 260–267.
- [19] H.L. Smith, *An Introduction to Delay Differential Equations with Applications to the Life Sciences*, vol. 57, Springer, New York, 2011.
- [20] H.L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, American Mathematical Soc., 2008.
- [21] J. Wei, M.Y. Li, Hopf bifurcation analysis in a delayed Nicholson blowflies equation, *Nonlinear Anal.* 60 (2005) 1351–1367.