

Z. Angew. Math. Phys.
 © 2016 Springer International Publishing
 DOI 10.1007/s00033-016-0644-0

Zeitschrift für angewandte
 Mathematik und Physik ZAMP



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Global dynamics of delay recruitment models with maximized lifespan

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Abstract. We study the dynamics of the differential equation

$$u'(t) = -\gamma u(t) + bf(u(t - \tau)) - cf(u(t - \sigma))$$

with two delayed terms, representing a positive and a negative feedback. We prove delay-dependent and absolute global stability results for the trivial and for the positive equilibrium. Our theorems provide new mathematical results as well as novel insights for several biological systems, including three-stage populations, neural models with inhibitory and excitatory loops, and the blood platelet model of Bélair and Mackey. We show that, somewhat surprisingly, the introduction of a removal term with fixed delay in population models simplifies the dynamics of the equation.

Mathematics Subject Classification. 39A30 · 39A33 · 37D45 · 92B20.

Keywords. Global attraction · Positive and negative feedbacks · Removal terms · Delay differential equation · Bélair–Mackey's model.

1. Introduction

Time delays are naturally present in many physical and biological systems. For example, the length of the juvenile period can play an important role in the time evolution of the population of a species. Delays are involved in most physiological processes as well, such as the time it takes for a nerve impulse to travel along the axons and across the synapses or the required time for producing new cells in an organism and for the cells to mature. In those processes, time delays play a paramount role from both biological and dynamical perspectives.

There is a vast literature of comprehensive results for equations of the form

$$u'(t) = -\gamma u(t) + f(u(t - \tau)), \quad (1.1)$$

where $f(u)$ is a monotone function representing delayed negative [10, 13] or delayed positive feedback [11], or when $f(u)$ is a unimodal function [1, 6, 14, 18, 24]. In contrast, much less is known about the global dynamics of

$$u'(t) = -\gamma u(t) + bf(u(t - \tau)) - cf(u(t - \sigma)), \quad (1.2)$$

where all parameters are positive and $f : \mathbb{R} \rightarrow \mathbb{R}$ is a smooth real function with $f(0) = 0$ and $xf(x) > 0$ for $x \neq 0$.

Equation (1.2) can describe the dynamics of a single neuron (or the mean field equation for a population of neurons in a network) with an excitatory and an inhibitory loop, having different delays. The pair of a positive and a negative delayed feedback occurs on the processing of sensory information and other processes in neuroscience (see [5, 12, 17, 19] and references therein).

From a population dynamics perspective, with the choice $b = 1$, $c = e^{-\gamma(\sigma - \tau)}$ and $\sigma > \tau$, (1.2) models the time evolution of a population when there is a natural mortality rate (γ) independent of the age of

individuals, a recruitment term given by the function $f : [0, \infty) \rightarrow [0, \infty)$ with maturation delay τ , and a removal from the population at the “old” adult age $\sigma - \tau > 0$. Then (1.2) becomes

$$u'(t) = -\gamma u(t) + f(u(t - \tau)) - e^{-\gamma(\sigma - \tau)} f(u(t - \sigma)). \quad (1.3)$$

Originally, Bélair and Mackey [2] proposed this equation to study the mammalian platelet production. Here $u(t)$ is the total number of platelets, τ denotes the maturation time of megakaryocyte, $\sigma - \tau$ stands for the age of death of a platelet due to senescence, and γ refers to the random destruction of platelets. Typically the real values of τ and $\sigma - \tau$ are 9 and 10 days, respectively. The function f reflects the thrombopoietin feedback influencing the influx of cells into the recognizable megakaryocyte compartment, and was chosen in [2] as $f(u) = \frac{\beta_0 \theta^n u}{\theta^n + u^n}$. We mention that Eq. (1.3) also appears in the regulation of mammalian erythropoiesis [3].

A similar situation occurs in a population of a species with three life stages, namely juvenile, adult, and elder. If we assume that both the juvenile and the adult stages have fixed length, τ and $\sigma - \tau$, respectively, and that only the adults contribute to reproduction, then again we arrive at (1.3), where $u(t)$ denotes the total reproductive (adult) population. Recently, in the context of vector borne diseases, and in particular malaria control, Gourley, Liu and Wu [8] used three stage populations as a subsystem to model late-life acting insecticides for mosquitoes. In their model, τ represented the duration of the larval stage, while $\sigma - \tau$ was the length of adult stage, and the insecticide had effect only on old mosquitoes whose age exceeding σ . See [28] for additional biological models involving equations like (1.3).

Despite its relevance for applications, the literature for (1.2) is relatively scarce, given the mathematical challenges posed by the two (positive and negative) delayed feedback terms. Note that for Eq. (1.2), even the local stability analysis is very difficult (partial analysis was given in [9, 20, 21, 23]), and the complete picture of the stability chart is still unknown in the general case, nonetheless this information is fully encoded into the characteristic equation $\lambda = -\gamma + bf'(0)e^{-\tau\lambda} - cf'(0)e^{-\sigma\lambda}$.

Our aim here is to initiate a systematic study for proving global attractivity results in (1.2). The paper is structured as follows. In the next section, we present delay-dependent conditions of global attraction of the trivial solution of (1.2) in $\mathcal{C}([\varrho, 0], \mathbb{R})$ with f defined on \mathbb{R} and $\varrho = -\max\{\tau, \sigma\}$. Then in Sect. 3 we give sufficient criteria for the global attraction of positive equilibria for initial conditions producing positive solutions. Section 4 is devoted to the applications of the abstract results. In Sect. 4.1, we derive the model of Bélair and Mackey from an age-structured model and provide a precise description of the set of biologically meaningful initial conditions. In this scenario, we give the following biological insight: the introduction of the removal term in (1.3) does not alter the global attraction, only produces a reduction of the population size. In fact, the removal term typically simplifies the dynamical behavior of (1.1). Finally, in Sects. 4.3 and 4.4 we show the implications of our theorems for a three-stage population model of Beverton–Holt and Ricker type, and for a neuron model with excitatory and inhibitory loops.

2. Delay-dependent conditions of global attraction in (1.2)

Throughout the paper, $\mathcal{C}([a, b], I)$ refers to the Banach space of continuous functions defined on $[a, b]$ taking values from I , and equipped with the supremum norm. Given an initial condition $\phi \in \mathcal{C}([\varrho, 0], \mathbb{R})$, we employ the notation $u(t, \phi)$ to the solution of (1.2) with initial condition at ϕ . A solution of Eq. (1.2), say $u(t) \equiv u(t, \phi)$, can be written as

$$u(t) = e^{-\gamma t} \left(u(0) + b \int_0^t e^{\gamma s} f(u(s - \tau)) ds - c \int_0^t e^{\gamma s} f(u(s - \sigma)) ds \right).$$

After doing some simple manipulations when $\sigma > \tau \geq 0$, we obtain

$$\begin{aligned}
 u(t) = & e^{-\gamma t} \Theta + e^{-\gamma t} (be^{\gamma\tau} - ce^{\gamma\sigma}) \int_{-\tau}^{t-\sigma} e^{\gamma s} f(u(s)) ds \\
 & + be^{-\gamma t} e^{\gamma\tau} \int_{t-\sigma}^{t-\tau} e^{\gamma s} f(u(s)) ds,
 \end{aligned}
 \tag{2.1}$$

where $\Theta = u(0) - ce^{\gamma\sigma} \int_{-\sigma}^{-\tau} e^{\gamma s} f(u(s)) ds$. By (2.1), whenever f is exponentially bounded, solutions are defined on $[-\sigma, \infty)$.

For convenience in the next arguments, given any $t_* > 0$, we write

$$u(t) = e^{-\gamma t} (B_* + C(t))
 \tag{2.2}$$

with $t_* + \sigma < t$, where

$$B_* = \Theta + (be^{\gamma\tau} - ce^{\gamma\sigma}) \int_{-\tau}^{t_*} e^{\gamma s} f(u(s)) ds,$$

and

$$C(t) = (be^{\gamma\tau} - ce^{\gamma\sigma}) \int_{t_*}^{t-\sigma} e^{\gamma s} f(u(s)) ds + be^{\gamma\tau} \int_{t-\sigma}^{t-\tau} e^{\gamma s} f(u(s)) ds.$$

Now we are in a position to state the main result of this section.

Theorem 2.1. *Assume that there exists $k > 0$ so that*

$$|f(x)| \leq k|x| \text{ for all } x \in \mathbb{R}.
 \tag{2.3}$$

If

$$\tau < \sigma \text{ and } \left(|be^{\gamma(\tau-\sigma)} - c| + |b|(1 - e^{\gamma(\tau-\sigma)}) \right) k < \gamma
 \tag{2.4}$$

then $\lim_{t \rightarrow \infty} u(t) = 0$ *for any solution of (1.2).*

Proof. Consider a solution $u(t)$ of (1.2). We split the proof into two steps.

Step 1: $u(t)$ is bounded. Assume by contradiction that

$$\limsup_{t \rightarrow \infty} |u(t)| = \infty.$$

In such a case, there is an increasing sequence $\{t_n\}_{n \in \mathbb{N}}$ with $t_n \rightarrow +\infty$ satisfying

$$\lim_{n \rightarrow \infty} |u(t_n)| = \infty$$

and

$$|u(t_n)| = \max\{|u(t)| : t \leq t_n\}$$

for all n . This property and condition (2.3) enable us to estimate the integral terms in (2.1) in a simple way. For instance,

$$\left| \int_{-\tau}^{t_n-\sigma} e^{\gamma s} f(u(s)) ds \right| \leq k|u(t_n)| \frac{e^{\gamma(t_n-\sigma)} - e^{-\gamma\tau}}{\gamma}.$$

Now, by expression (2.1) together with the previous type of estimates, we get

$$|u(t_n)| \leq e^{-\gamma t_n} |\Theta| + e^{-\gamma t_n} |be^{\gamma\tau} - ce^{\gamma\sigma}| \left(\frac{e^{\gamma(t_n-\sigma)} - e^{-\gamma\tau}}{\gamma} \right) k |u(t_n)| \\ + |b| e^{-\gamma t_n} e^{\gamma\tau} \left(\frac{e^{\gamma(t_n-\tau)} - e^{\gamma(t_n-\sigma)}}{\gamma} \right) k |u(t_n)|.$$

Then,

$$|u(t_n)|(1 - B_n) \leq e^{-\gamma t_n} |\Theta| \tag{2.5}$$

with

$$B_n = e^{-\gamma t_n} |be^{\gamma\tau} - ce^{\gamma\sigma}| \left(\frac{e^{\gamma(t_n-\sigma)} - e^{-\gamma\tau}}{\gamma} \right) k + |b| e^{-\gamma t_n} e^{\gamma\tau} \left(\frac{e^{\gamma(t_n-\tau)} - e^{\gamma(t_n-\sigma)}}{\gamma} \right) k.$$

On the other hand, (2.4) yields

$$\lim_{n \rightarrow \infty} B_n = \left(|be^{\gamma(\tau-\sigma)} - c| + |b|(1 - e^{\gamma(\tau-\sigma)}) \right) \frac{k}{\gamma} < 1.$$

Therefore, by (2.5), $\lim_{n \rightarrow \infty} |u(t_n)| = 0$. This is a contradiction because we were assuming that $\lim_{n \rightarrow \infty} |u(t_n)| = \infty$.

Step 2: $\lim_{t \rightarrow \infty} |u(t)| = 0$.

Define $\limsup_{t \rightarrow \infty} |u(t)| := S \in [0, \infty)$. For any $\varepsilon > 0$, we find $t_* > 0$ large enough so that

$$|u(t)| \leq S + \varepsilon$$

for all $t > t_*$. Thus, by condition (2.3), the inequality $|f(u(t))| \leq k(S + \varepsilon)$ holds for all $t > t_*$. Using this estimate, it follows that

$$\limsup_{t \rightarrow \infty} e^{-\gamma t} C(t) \leq (S + \varepsilon) \left(1 - \left(|be^{\gamma(\tau-\sigma)} - c| + |b|(1 - e^{\gamma(\tau-\sigma)}) \right) \frac{k}{\gamma} \right),$$

and

$$\limsup_{t \rightarrow \infty} e^{-\gamma t} B_* = 0.$$

Now we use the expression (2.2) and the previous estimates to arrive at

$$\limsup_{t \rightarrow \infty} |u(t)| = S \leq (S + \varepsilon) \left(1 - \left(|be^{\gamma(\tau-\sigma)} - c| + |b|(1 - e^{\gamma(\tau-\sigma)}) \right) \frac{k}{\gamma} \right).$$

As a consequence of condition (2.4) we deduce that $S = 0$ and the proof is complete. □

The purpose of this theorem was to develop delay-dependent criteria of global attraction in (1.2) when $f : \mathbb{R} \rightarrow \mathbb{R}$ is a smooth function defined on \mathbb{R} . Our result covers the best delay-independent condition of global attraction for (1.2), namely

$$(|b| + |c|)|f'(0)| < \gamma,$$

see [9]. The case $\tau > \sigma$ can be treated analogously by imposing the condition

$$\left(|b - ce^{\gamma(\sigma-\tau)}| + |c|(1 - e^{\gamma(\sigma-\tau)}) \right) k < \gamma,$$

replacing b by c in the proof of the previous theorem (these parameters can have any sign).

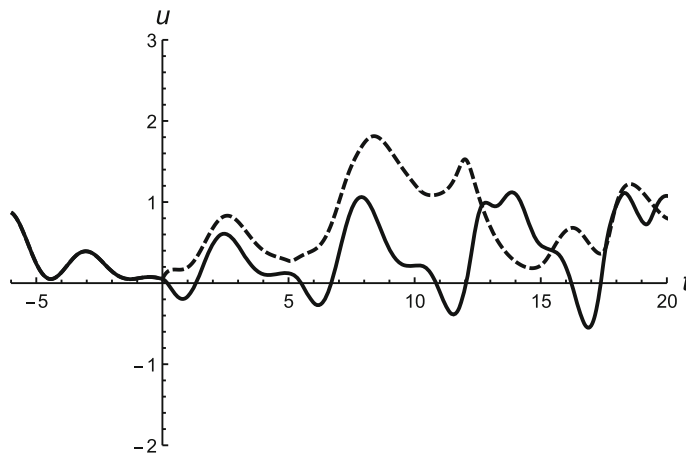


FIG. 1. Negative solution generated by positive initial data. The *dashed curve* is the solution of $u'(t) = \frac{\beta\theta^n u(t-\tau)}{\theta^n + u(t-\tau)^n} - \gamma u(t)$, and the *solid curve* is the solution of $u'(t) = -\frac{\beta\theta^n u(t-\sigma) \exp(-\gamma(\sigma-\tau))}{\theta^n + u(t-\sigma)^n} + \frac{\beta\theta^n u(t-\tau)}{\theta^n + u(t-\tau)^n} - \gamma u(t)$, where the parameters are chosen as $(\gamma, \theta, \beta, n) = (1, 1, 3, 10)$. The delays are $\tau = 5, \sigma = 6$, and the initial function is $\phi = (e^{-0.1t} - 1) \sin(t - \tau)^2 + 0.05$ in both cases. One can calculate that $\phi \notin \mathcal{A}$

3. Positive solutions and global attraction of nontrivial equilibria in (1.2)

Next we discuss some dynamical properties of (1.2) when $f : [0, \infty) \rightarrow [0, \infty)$ typically represents a recruitment function of some population models. Throughout this section we impose the following hypotheses **(H)**:

- f is smooth and bounded,
- $f(0) = 0$ and $f(x) > 0$ for all $x > 0$,
- $b > c > 0$ and $\sigma > \tau > 0$.

In the presence of the term $-cf(u(t-\sigma))$ in (1.2), there exist nonnegative initial conditions producing negative solutions; see Fig. 1 for an example. To exclude this behavior, which is undesirable in population models, we only focus on initial conditions taken from the set

$$\mathcal{A} = \left\{ \phi \in \mathcal{C}([- \sigma, 0], \mathbb{R}^+) : \phi(0) - ce^{\gamma\sigma} \int_{-\sigma}^{-\tau} e^{\gamma s} f(\phi(s)) ds \geq 0 \right\}$$

when

$$\gamma \leq \frac{\ln(\frac{b}{c})}{\sigma - \tau}. \tag{3.1}$$

From expression (2.1), an initial condition in \mathcal{A} clearly generates a solution remaining positive for all time, (note that (3.1) implies that $be^{\gamma\tau} - ce^{\gamma\sigma} > 0$).

As a first step we investigate the case of global extinction in (1.2). We stress that by the assumption of f being bounded, any solution of (1.2) is bounded for all $t > 0$.

Theorem 3.1. *Assume **(H)** and that (1.2) has no positive equilibria. Then the trivial solution is a global attractor in \mathcal{A} .*

Proof. Let $u(t)$ be a solution of (1.2) with an initial condition in \mathcal{A} . Our aim is to prove that if $M := \limsup_{t \rightarrow +\infty} u(t)$, then $M = 0$.

Pick $\varepsilon > 0$ and a time t_* large enough so that $u(t) \leq M + \varepsilon$ for all $t \geq t_*$. Next take $t_0 \geq t_* + \sigma$ satisfying that

$$\begin{aligned} \max\{0, M - \varepsilon\} &\leq u(t_0), \\ \left| e^{-\gamma t_0} (be^{\gamma\tau} - ce^{\gamma\sigma}) \frac{e^{\gamma t_*}}{\gamma} \right| &< \varepsilon, \\ e^{-\gamma t_0} B_* &< \varepsilon, \end{aligned}$$

[see (2.2) for the definition of B_*]. By expression (2.2), we have that

$$u(t_0) \leq \varepsilon + e^{-\gamma t_0} \left((be^{\gamma\tau} - ce^{\gamma\sigma}) \int_{t_*}^{t_0-\sigma} e^{\gamma s} f(u(s)) ds + be^{\gamma\tau} \int_{t_0-\sigma}^{t_0-\tau} e^{\gamma s} f(u(s)) ds \right). \tag{3.2}$$

Consequently,

$$\begin{aligned} M - \varepsilon \leq u(t_0) &\leq \varepsilon + e^{-\gamma t_0} \max\{f(x) : x \in [0, M + \varepsilon]\} \cdot \left((be^{\gamma\tau} - ce^{\gamma\sigma}) \frac{e^{\gamma(t_0-\sigma)} - e^{\gamma t_*}}{\gamma} \right. \\ &\quad \left. + be^{\gamma\tau} \left(\frac{e^{\gamma(t_0-\tau)} - e^{\gamma(t_0-\sigma)}}{\gamma} \right) \right), \end{aligned}$$

and, after simple computations,

$$M - \varepsilon \leq u(t_0) \leq \varepsilon + \max\{f(x) : x \in [0, M + \varepsilon]\} \left(\frac{(b-c)}{\gamma} - e^{-\gamma t_0} (be^{\gamma\tau} - ce^{\gamma\sigma}) \frac{e^{\gamma t_*}}{\gamma} \right).$$

By the choice of ε and t_0 , we deduce that

$$M \leq \left(\frac{(b-c)}{\gamma} + \varepsilon \right) \max\{f(x) : x \in [0, M + \varepsilon]\} + 2\varepsilon.$$

Then, by making $\varepsilon \rightarrow 0$, we arrive at

$$M \leq \frac{b-c}{\gamma} \max\{f(x) : x \in [0, M]\}. \tag{3.3}$$

On the other hand, as (1.2) has no positive equilibria, clearly

$$0 \leq \frac{b-c}{\gamma} f(x) < x$$

for all $x > 0$, and by using (3.3), we conclude $M = 0$. □

Remark 3.1. The condition on boundedness of f can be relaxed. Specifically, it is enough to impose that all solutions are defined for all $t > 0$.

Next we discuss criteria of uniform persistence and global attraction of nontrivial equilibria in model (1.2).

Theorem 3.2. *Assume (H) and*

$$f'(0) > \frac{\gamma}{b-c}. \tag{3.4}$$

Then $\liminf_{t \rightarrow \infty} u(t) > 0$ for any positive solution of (1.2).

Proof. First, take $l > 1$ and $\varepsilon > 0$ so that

$$\frac{b-c}{\gamma} f(x) \geq lx \tag{3.5}$$

for all $x \in [0, \varepsilon]$. Next, assume by contradiction that there is a positive solution so that $\liminf_{t \rightarrow \infty} u(t) = 0$. In such a case we can pick a strictly increasing sequence $\{t_n\}$ tending to ∞ so that $u(t_n) = \min\{u(t) : t \leq t_n\}$ with $\lim_{n \rightarrow \infty} u(t_n) = 0$.

By expression (2.1) and applying mean value theorem, we deduce that there are two values $\alpha_1(t) \in (-\tau, t - \sigma)$ and $\alpha_2(t) \in (t - \sigma, t - \tau)$ so that

$$\begin{aligned} u(t) &= e^{-\gamma t} \Theta + e^{-\gamma t} (be^{\gamma\tau} - ce^{\gamma\sigma}) \frac{e^{\gamma(t-\sigma)} - e^{-\gamma\tau}}{\gamma} f(u(\alpha_1(t))) \\ &\quad + be^{-\gamma t} e^{\gamma\tau} \frac{e^{\gamma(t-\tau)} - e^{\gamma(t-\sigma)}}{\gamma} f(u(\alpha_2(t))). \end{aligned} \tag{3.6}$$

From this expression, if $\lim_{n \rightarrow \infty} u(t_n) = 0$ then $\lim_{n \rightarrow \infty} f(u(\alpha_1(t_n))) = \lim_{n \rightarrow \infty} f(u(\alpha_2(t_n))) = 0$. Recall that

$$\begin{aligned} \frac{e^{-\gamma\sigma}(be^{\gamma\tau} - ce^{\gamma\sigma})}{\gamma} &> 0, \\ \frac{b(1 - e^{\gamma(\tau-\sigma)})}{\gamma} &> 0. \end{aligned}$$

As $f(x) = 0$ if and only if $x = 0$, we can find $n_0 > 0$ large enough such that $\alpha_i(t_n), u(t_n) \in [0, \varepsilon]$ for all $n > n_0$. Consequently, by (3.5) and the definition of t_n ,

$$f(u(\alpha_i(t_n))) \geq l \frac{\gamma}{b-c} u(\alpha_i(t_n)) \geq \frac{l\gamma}{b-c} u(t_n)$$

with $n \geq n_0$. Observe that, by incorporating the previous estimates in (3.6)

$$\begin{aligned} u(t_n) &\geq e^{-\gamma t_n} \left(u(0) - ce^{\gamma\sigma} \int_{-\sigma}^{-\tau} e^{\gamma s} f(u(s)) ds \right) \\ &\quad + \frac{be^{\gamma\tau} - ce^{\gamma\sigma}}{\gamma} (e^{-\gamma\sigma} - e^{-\gamma(t_n+\sigma)}) \frac{\gamma l}{b-c} u(t_n) + \frac{b}{\gamma} (1 - e^{\gamma(\tau-\sigma)}) \frac{\gamma l}{b-c} u(t_n). \end{aligned}$$

After some manipulations, we find

$$u(t_n) \geq e^{-\gamma t_n} \left(c - be^{\gamma(\tau-\sigma)} \right) \frac{lu(t_n)}{b-c} + lu(t_n)$$

what implies, by dividing by $u(t_n)$, $l \leq 1$, contradicting the choice of l . □

Theorem 3.3. *Assume that (H) and (3.4) are satisfied. For each solution $u(t)$ of (1.2) with initial condition in \mathcal{A} , there exist $0 < L \leq M$ and $M^*, L^* \in [L, M]$ such that the following statements hold:*

(i)

$$\begin{aligned} \liminf_{t \rightarrow \infty} u(t) &= L, \\ \limsup_{t \rightarrow \infty} u(t) &= M, \end{aligned}$$

and, for $G(x) := \frac{b-c}{a} f(x)$,

$$M \leq G(M^*), \quad L \geq G(L^*). \tag{3.7}$$

(ii) If $\bar{x} > 0$ is the unique positive equilibrium of (1.2), then

$$M^* < \bar{x} < L^* \quad \text{or} \quad L = M = \bar{x}. \quad (3.8)$$

In particular, when $\bar{x} > 0$ is a global attractor in $(0, +\infty)$ of

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

then \bar{x} is a global attractor of (1.2) in \mathcal{A} .

Proof. The existence of L with

$$\liminf_{t \rightarrow \infty} u(t) = L > 0$$

is a consequence of Theorem 3.2. By the remark preceding Theorem 3.1, there is $M > 0$, such that

$$\limsup_{t \rightarrow \infty} u(t) = M.$$

By arguing exactly as in Theorem 3.1, we deduce that

$$M \leq \max\{G(x) : x \in [L, M]\}.$$

The proof of the other inequality can be deduced reversing the inequalities in the previous part. This argument proves (i).

Using $G'(0) > 1$ and the boundedness of f , we easily see that in the case of a unique equilibrium, the function G satisfies

$$(G(x) - x)(x - \bar{x}) < 0 \quad (3.9)$$

for all $x \neq \bar{x}$. The first part of (ii) is a direct consequence of (3.7) and (3.9). Finally, we apply [7, Lemma 2.5] when G has a unique fixed point to exclude the existence of different $L^* > M^*$. Thus, $L = M = \bar{x}$. \square

This result allows us to deduce a result of practical permanence according to the related literature, see [25]. The key difference with respect to classical results on persistence is that we estimate an explicit lower bound for the long-term of the solutions.

Corollary 3.1. *Assume that (H) and (3.4) are satisfied. Then (1.2) is uniformly persistent. In particular, $\liminf_{t \rightarrow \infty} u(t) \geq L$ for any positive solution in \mathcal{A} , where $[L, M]$ is an attractive interval for the discrete equation*

$$x_{n+1} = G(x_n).$$

4. Applications

This section is devoted to present some applications of our results in different biological contexts: Bélair–Mackey’s model of mammalian platelet production, neural networks, and population dynamics. Equation (1.2) was deduced from a more general age-structured model in [3]. Here we provide a direct derivation, as this approach allows us to determine the set of biologically meaningful initial conditions in a clear manner.

4.1. Bélair–Mackey’s model as an age-structured model and the set of biologically meaningful initial data

Consider a biological population structured by age and let $n(t, a)$ denote the density of individuals at time t with respect to age a . Then the total population $N(t)$ is given by

$$N(t) = \int_0^\infty n(t, a) da.$$

Introducing an age-dependent mortality rate $\mu(a)$, the density satisfies

$$n(t + h, a + h) = e^{-\int_a^{a+h} \mu(s) ds} n(t, a)$$

and differentiating with respect to h and letting $h \rightarrow 0$, we find that the density is governed by the equation

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) n(t, a) = -\mu(a)n(t, a). \tag{4.1}$$

Assume now that individuals can be divided into three stages: juveniles, adults, elder, which are characterized by age, with $a \in [0, \tau)$, $a \in [\tau, \sigma)$, $a \in [\sigma, \infty)$, respectively. If we denote by $u(t)$ the adult population and suppose that only adults participate in reproduction according to a birth function $f(u(t))$, then we get the boundary condition

$$n(t, 0) = f(u(t)) \text{ where } u(t) = \int_\tau^\sigma n(t, a) da. \tag{4.2}$$

The initial condition at $t = 0$ corresponds to the initial age distribution, say

$$n(0, a) = \rho(a). \tag{4.3}$$

Collecting all the information, Eqs. (4.1), (4.2), and (4.3) allow us to define a Cauchy problem. By solving this problem along the characteristic lines $t - a = c$ and using (4.2), we find that, for $a \leq t$,

$$n(t, a) = n(t - a, 0)e^{-\int_0^a \mu(s) ds} = f(u(t - a))e^{-\int_0^a \mu(s) ds}. \tag{4.4}$$

In particular, for $\tau \leq t$,

$$n(t, \tau) = f(u((t - \tau)))e^{-\int_0^\tau \mu(s) ds} \tag{4.5}$$

and for $\sigma - \tau \leq t$,

$$n(t, \sigma) = n(t - \sigma + \tau, \tau)e^{-\int_\tau^\sigma \mu(s) ds}. \tag{4.6}$$

Now we differentiate $u(t)$ in the second equation in (4.2) and use (4.1) to obtain

$$u'(t) = n(t, \tau) - n(t, \sigma) - \int_\tau^\sigma \mu(a)n(t, a) da. \tag{4.7}$$

In the special case $\mu(a) = 0$ for $a < \tau$ and $\mu(a) = \gamma$ for $a \in (\tau, \sigma)$, we arrive at the delay differential equation

$$u'(t) = f(u((t - \tau))) - e^{-\gamma(\sigma - \tau)} f(u((t - \sigma))) - \gamma u(t). \tag{4.8}$$

Note that due to the term $e^{-\gamma(\sigma - \tau)} f(u(t - \sigma))$ there are non-feasible positive initial conditions producing negative solutions, roughly speaking, when the population at 0 is too small compared to its history in the interval $[-\sigma, -\tau]$. Motivated by this remark, we describe the biologically realistic initial conditions for the previous age-structured model.

An initial data of (4.8) is a continuous function ϕ defined on the interval $[-\sigma, 0]$. Observe that for $t \leq \tau$, Eq. (4.8) is

$$u'(t) = f(\phi((t-\tau))) - e^{-\gamma(\sigma-\tau)} f(\phi((t-\sigma))) - \gamma u(t), \quad (4.9)$$

while if $\tau \leq t \leq \sigma$, (4.8) is written as

$$u'(t) = f(u((t-\tau))) - e^{-\gamma(\sigma-\tau)} f(\phi((t-\sigma))) - \gamma u(t). \quad (4.10)$$

From the PDE model, the following relations hold:

$$n(t, \tau) = \rho(\tau - t) \text{ if } t \leq \tau, \quad (4.11)$$

$$n(t, \sigma) = \rho(\sigma - t) e^{-\gamma(\sigma-\tau)} \text{ if } \sigma - \tau \leq t \leq \sigma, \quad (4.12)$$

$$n(t, \sigma) = \rho(\sigma - t) e^{-\gamma t} \text{ if } t \leq \sigma - \tau. \quad (4.13)$$

Thus, to keep the DDE and the PDE consistent for all $t \geq 0$, we need to require

$$\rho(a) = f(\phi(-a)) \text{ if } a \leq \tau, \quad (4.14)$$

$$\rho(a) = f(\phi(-a)) e^{-\gamma(a-\tau)} \text{ if } \tau \leq a \leq \sigma. \quad (4.15)$$

Since $\phi(0) = \int_{\tau}^{\sigma} \rho(a) da$, we conclude that a biologically meaningful initial condition ϕ satisfies

$$\phi(0) = \int_{\tau}^{\sigma} f(\phi(-a)) e^{-\gamma(a-\tau)} da. \quad (4.16)$$

The set \mathcal{A} introduced in Sect. 3 contains all biologically meaningful initial conditions, which is obvious if we recall that

$$\mathcal{A} = \left\{ \phi \in \mathcal{C}([-\sigma, 0], \mathbb{R}_+) : \phi(0) \geq \int_{\tau}^{\sigma} f(\phi(-a)) e^{-\gamma(a-\tau)} da \right\}.$$

In a recent paper [27], Zhuge, Sun, and Lei showed that the ω -limit set for any positive solution of (4.19) is contained in

$$\mathcal{H} = \left\{ \phi \in \mathcal{C}([-\sigma, 0], \mathbb{R}^+) : \phi(0) = \int_{\tau}^{\sigma} f(\phi(-a)) e^{-\gamma(a-\tau)} da \right\}, \quad (4.17)$$

which is exactly the set defined by the relation we derived in (4.16).

4.2. Bifurcation and attraction in the Bélair–Mackey model: the role of the removal term

In this subsection we analyze the biological response of the model

$$u'(t) = -\gamma u(t) + f(u(t-\tau)) \quad (4.18)$$

with $f(x) = \frac{\beta_0 \theta^n x}{\theta^n + x^n}$ to the introduction of a mortality at age $\sigma - \tau > 0$, i.e., the biological role of $e^{-\gamma(\sigma-\tau)} f(u(t-\sigma))$ on

$$u'(t) = -\gamma u(t) + f(u(t-\tau)) - e^{-\gamma(\sigma-\tau)} f(u(t-\sigma)). \quad (4.19)$$

Choosing the mortality time $\sigma - \tau$ as a bifurcation parameter, our results establish the following behavior.

Corollary 4.1. *Consider equation (4.19) with $f(x) = \frac{\beta_0 \theta^n x}{\theta^n + x^n}$. Then we have the following:*

- (i) *if $\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} \leq 1$ then 0 is a global attractor of (4.19);*

(ii) if $\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} > 1$, then (4.19) is uniformly persistent. Moreover, the equilibrium $\bar{x} = \theta \sqrt[n]{\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} - 1}$ is the global attractor, provided

$$\left| \frac{\gamma + \gamma\left(\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} - 1\right)(1-n)}{\beta_0(1-e^{-\gamma(\sigma-\tau)})} \right| \leq 1.$$

Proof. Consider

$$x_{n+1} = \frac{(1 - e^{-\gamma(\sigma-\tau)})}{\gamma} f(x_n). \tag{4.20}$$

By a simple analysis, if $\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} \leq 1$ then 0 is a global attractor of (4.19). Now the first statement is clear from Theorem 3.1. To prove the second claim, we use that $\frac{(1-e^{-\gamma(\sigma-\tau)})}{\gamma} f(x_n)$ has negative Schwarzian derivative, see [26]. After simple computations,

$$\left| \frac{\gamma + \gamma\left(\frac{\beta_0(1-e^{-\gamma(\sigma-\tau)})}{\gamma} - 1\right)(1-n)}{\beta_0(1-e^{-\gamma(\sigma-\tau)})} \right| \leq 1$$

says that the positive equilibrium of (4.20) is locally asymptotically stable. Then, by Singer [26], that equilibrium is a global attractor for (4.20). Finally, we apply Theorem 3.3. The conclusion on persistence is clear from Corollary 3.1. \square

The introduction of a removal term in (4.18) produces, apart from the natural reduction of the equilibrium size of the population, a stabilizing effect. It is well known that Eq. (4.18) exhibits complex behaviors for suitable values of the parameters, typically, when the discrete equation

$$x_{n+1} = g(x_n) := \frac{1}{\gamma} f(x_n)$$

displays chaotic dynamics. However, any oscillatory behavior in (4.18) can be damped by adding the removal term, as we can see from the results for Eq. (4.19). Specifically, it is always possible to find two thresholds $\rho_1 < \rho_2$ with the following properties:

- if $\rho_1 < \sigma - \tau < \rho_2$ then a nontrivial equilibrium is a global attractor in (4.19);
- if $0 < \sigma - \tau < \rho_1$, then there is global extinction.

The mathematical explanation is as follows. We know that the global attraction in

$$x_{n+1} = (1 - e^{-\gamma(\sigma-\tau)})g(x_n)$$

implies global attraction in (4.19). On the other hand, by Liz [15], see also [4,16], one can deduce that there are $\rho_1 < \rho_2 \leq 1$ so that for all $k \in [0, \rho_1]$, 0 is a global attractor of

$$x_{n+1} = kg(x_n)$$

and for all $k \in (\rho_1, \rho_2)$, there is a positive global attractor for

$$x_{n+1} = kg(x_n).$$

In our case, we take $k = (1 - e^{-\gamma(\sigma-\tau)})$. The stabilizing role of the removal term and possible transitions between various dynamics are illustrated in the bifurcation diagram Fig. 2, whereas in Figure 3 we plotted some sample solutions representing different behaviors. Comparisons between the dashed and solid curves elucidate the role of the removal term.

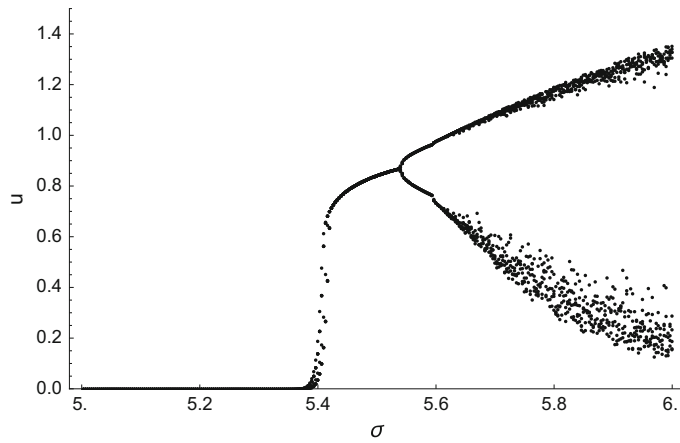


FIG. 2. Bifurcation diagram with respect to σ . Minima and maxima on an interval of solutions of $u'(t) = -\frac{\beta\theta^n u(t-\sigma)\exp(-\gamma(\sigma-\tau))}{\theta^n+u(t-\sigma)^n} + \frac{\beta\theta^n u(t-\tau)}{\theta^n+u(t-\tau)^n} - \gamma u(t)$ for different initial functions are plotted after long integration where the parameters are chosen as $(\gamma, \theta, \beta, n, \tau) = (1, 1, 3, 10, 5)$. The delay σ varies between 5 and 6. The figure illustrates the variety of possible dynamics and the transitions between them

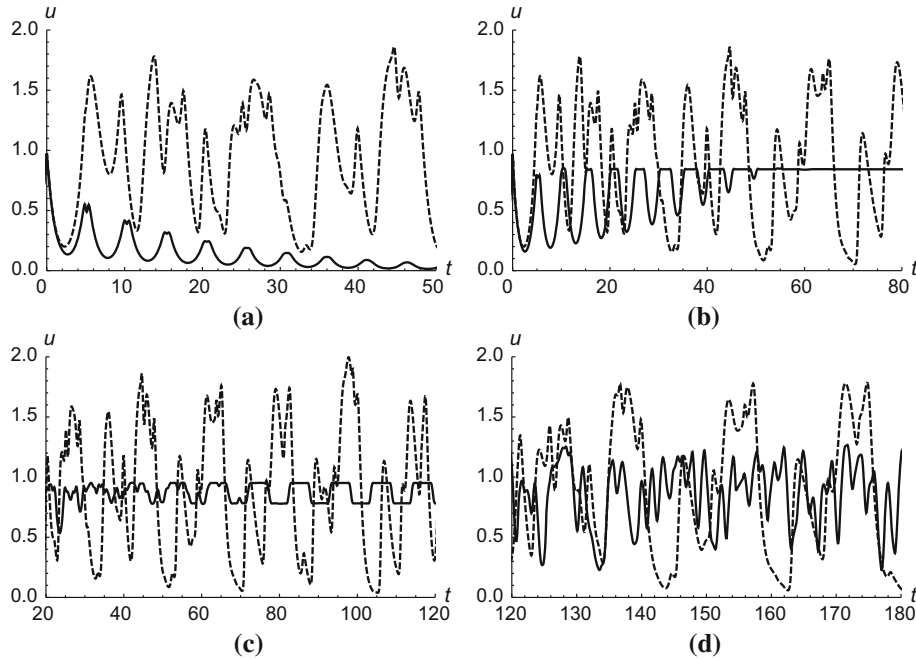


FIG. 3. Sample solutions showing a variety of dynamics for various σ . The *dotted curves* are solutions of $u'(t) = \frac{\beta\theta^n u(t-\tau)}{\theta^n+u(t-\tau)^n} - \gamma u(t)$, and the *solid curves* are solutions of $u'(t) = -\frac{\beta\theta^n u(t-\sigma)\exp(-\gamma(\sigma-\tau))}{\theta^n+u(t-\sigma)^n} + \frac{\beta\theta^n u(t-\tau)}{\theta^n+u(t-\tau)^n} - \gamma u(t)$, where the parameters are chosen as $(\gamma, \theta, \beta, n, \tau) = (1, 1, 3, 10, 5)$, with initial function $\phi = e^t$ in all cases. The delay σ equals to 5.3, 5.5, 5.58, 5.9, respectively in (a–d). The solutions show extinction, convergence to positive equilibrium, convergence to periodic solution and complicated behavior, matching the corresponding σ value in the bifurcation diagram of Fig. 2

4.3. Neural model

In this subsection we consider (1.2) as a neural model with an excitatory and an inhibitory loop assuming the same nonlinearity for the two delayed activation functions. A typically used activation function in neural models is $f(x) = \alpha \tanh(\beta x)$ [11], but non-monotone functions also have been proposed [22]. We can apply the results of Sect. 2 for both cases, to derive the following.

Corollary 4.2. *Consider (1.2) with*

$$f(x) = \alpha \tanh(\beta x).$$

Then 0 is a global attractor, provided

$$(|be^{-\gamma(\tau-\sigma)} - c| + |b|(1 - e^{-\gamma(\tau-\sigma)}))|\alpha\beta| < \gamma. \tag{4.21}$$

Proof. Since $f(0) = 0$ and $|f'(x)| = \left| \frac{d}{dx} \alpha \tanh(\beta x) \right| = |\alpha\beta \operatorname{sech}^2(\beta x)| \leq |\alpha\beta|$, Theorem 2.1 applies in a direct way. □

Corollary 4.3. *Consider (1.2) with the Morita activation function*

$$f(x) = \frac{1 - \exp(-\beta_1 x)}{1 + \exp(-\beta_1 x)} \frac{1 + k \exp(\beta_2(|x| - h))}{1 + \exp(\beta_2(|x| - h))}.$$

Then 0 is a global attractor, provided

$$(|be^{-\gamma(\tau-\sigma)} - c| + |b|(1 - e^{-\gamma(\tau-\sigma)}))(2\beta_1(|k| + e^{\beta_2 h}) + \beta_2|k - 1|) < \gamma. \tag{4.22}$$

Proof. First note that $f(x) = -f(-x)$. For $x > 0$, a straightforward calculation gives

$$f'(x) = \frac{2\beta_1 e^{\beta_1 x} (e^{\beta_2(x-h)} + 1) (k e^{\beta_2(x-h)} + 1) + \beta_2(k - 1) (e^{2\beta_1 x} - 1) e^{\beta_2(x-h)}}{(e^{\beta_1 x} + 1)^2 (e^{\beta_2(x-h)} + 1)^2}.$$

For $x > 0$ we have $|f(x)| \leq \int_0^x |f'(s)| ds \leq x \sup_{s \in [0, x]} |f'(s)|$. Simple estimations yield

$$|f'(x)| \leq 2\beta_1(|k| + e^{\beta_2 h}) + \beta_2|k - 1|,$$

hence the result follows from Theorem 2.1. During the calculation we used the assumption on the activation function as in [22] that all parameters are positive except k which may be negative as well. □

4.4. Three-stage populations

Motivated by Gourley et al. [8], we consider the population of a species whose lifetime can be divided into three stages: juvenile, adult, and old. Assuming that both the juvenile and the adult stages have fixed lengths τ and $\sigma - \tau$ (i.e., σ is the total length of juvenile and adult periods), and that only adults reproduce, a general model has the form (1.3). Next we consider the dynamics for two typical birth functions.

Corollary 4.4. *For Beverton–Holt-type birth function in (1.2), i.e., $f(y) = \frac{ay}{1+by}$, we have the following.*

- (i) *If $\frac{a(1-e^{-\gamma(\sigma-\tau)})}{\gamma} \leq 1$ then 0 is a global attractor.*
- (ii) *If $\frac{a(1-e^{-\gamma(\sigma-\tau)})}{\gamma} > 1$, then $\bar{x} = \frac{a(1-e^{-\gamma(\sigma-\tau)})-1}{b\gamma}$ is a global attractor.*

Proof. This result is a particular case of Corollary 4.1 with $a = \beta_0, b = \theta^{-1}$. □

The proof in case of a Ricker-type nonlinearity is also analogous, so we omit it and only state the result.

Corollary 4.5. *Let the birth function in (1.2) be Ricker-type, i.e., $f(y) = rye^{-y}$. Then,*

- (i) if $\frac{r(1-e^{-\gamma(\sigma-\tau)})}{\gamma} \leq 1$, then 0 is a global attractor of (1.3);
- (ii) if $1 < \frac{r(1-e^{-\gamma(\sigma-\tau)})}{\gamma} \leq e^2$, then the positive equilibrium $\bar{x} = \log\left(\frac{r(1-e^{-\gamma(\sigma-\tau)})}{\gamma}\right)$ is a global attractor of (1.3).

Acknowledgements

Parts of this work has been done while the authors were visiting Universidade de Vigo. The warm hospitality of the Departamento de Matemática Aplicada II and professor E. Liz is gratefully acknowledged. GR was supported by ERC StG 259559 and OTKA K109782. ARH was supported by Spanish Grant MTM2013-43404-P.

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(Received: September 2, 2015; revised: March 12, 2016)