Mathematical study of a bacteria–fish model with level of infection structure

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Abstract

In this paper, we propose a mathematical model to study a bacteria–fish system, based upon the interactions between *Clostridium botulinum* and tilapia, *Oerochromis mossambicus*. The fish population is divided into susceptible and infected, and the infected fish population is considered structured by the level of infection. The model is thus a system with the infected fish equation being an evolution equation, while those corresponding to the susceptible fish and bacteria in water are ordinary differential equations. The model is firstly transformed into a system with distributed delay for susceptible fish and bacteria and, further, under some assumptions, into a system with discrete delay. The study of this system gives us some results concerning the existence, uniqueness, positivity and boundedness of solutions; we also discuss the existence and stability of its equilibrium points, including conditions for the appearance of Hopf bifurcation. The theoretical results are illustrated by some numerical simulations.
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1. Introduction

Clostridium botulinum is a worldwide contaminant of fish and the causative agent of the foodborne disease referred to as botulism in man, bankruptcy disease or also botulism in fish and avian botulism in birds. *C. botulinum* elaborates toxins that are among the most powerful neuroparalytic poisons which we have knowledge of. Its incidence in fish and incrimination in outbreaks of food-poisoning have been extensively studied, see [1] and the references therein. Botulinal spores are widely distributed in the environment: soils, marine sediments and aquatic habitats throughout the world. The first organisms in getting infected use to be fish which makes the infection reach men and birds. Concerning men, it can be introduced into processed foods through raw materials or by post-processing contamination

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[1] This paper is dedicated to the memory of our dear friend Abdelaziz Kacha, who passed away a few days before the submission of this work.

of foods resulting in man botulism; development of new-generation foods, which are mildly processed, contain few or no preservatives, are packaged in vacuum or modified atmospheres to ensure long shelf life and rely primarily on refrigeration for preservation, has raised concerns of potential increases in botulism risk [2].

In the case of birds, important outbreaks of avian botulism having fish as the source of infection have been reported. A paradigmatic case occurred in recent years in the Salton Sea in southern California (USA) [3]. During 1996, avian botulism killed over 15 000 birds, among them 9000 western white pelicans, *Pelecanus erythrorhynchos* and 1200 endangered Californian brown pelicans *Pelecanus occidentalis californicus*. The source of the toxin for these fish-eating birds is considered to be fish, notably Mozambique tilapia, *Oerochromis mossambicus*, which is one the most abundant fish species in the Sea and predominant food source for pelicans. The distribution and ecology of *C. botulinum* in fish and aquatic environments are studied in [4], its growth and toxin production in a certain kind of fish and shrimp are analyzed in [5] and the particular sensitivity of tilapia *O. mossambicus* to *C. botulinum* toxins is described in [3,6].

A modelling effort to study the prey–predator system tilapia–pelican under the influence of botulism in the Salton Sea has been carried out by Chattopadyay and collaborators [7–9]. They proposed and studied a three-dimensional model consisting of susceptible fish population, infected fish population and their predator, the Pelican population. They concluded that for the persistence of a system a considerable reduction of tilapia population density should be carried out. These works are included in the so-called eco-epidemiological models which is rather a young subject of study, which tries to merge the epidemic models with some demographic issues, [10–15], to take into account the important effects of transmissible diseases in ecological relationships between species. One of the basic goals for the study of eco-epidemiological models is to find conditions for which the system becomes disease free.

In this work we propose a mathematical model to study a bacteria–fish system, based upon the interactions between *C. botulinum* and tilapia, *O. mossambicus*. In contrast with works [7–9], we include explicitly the variable corresponding to bacteria density and, on the other hand, we do not include the predator population variable. Bacteria live in water but they only can grow in fish. Once a fish gets bacteria spores they start growing till the fish dies. In that sense our model could be considered a host–parasitoid system in continuous time. The fish death always happen if the amount of bacteria in it attains a specified threshold. The fish population is divided into susceptible and infected individuals. The infected fish population, as proposed in [16], is structured by the level of infection. The model is a system of differential equations with initial and boundary conditions. The infected fish equation is an evolution equation, while those corresponding to the susceptible fish and bacteria in water are ordinary differential equations. We firstly transform this system by integrating the infected equation by means of the characteristics method obtaining a system of two differential equations with distributed delay for susceptible fish and bacteria in the water. The delay appears as function of the minimal amount of bacteria in a fish to be considered infected, the growth rate of bacteria in fish and the amount threshold of bacteria provoking fish death; it represents the time interval needed for a susceptible fish to attain the infection threshold. Similar models describing the epidemics induced by bacteriophages in marine bacteria populations are presented in [17,18]; in contrast with the delay system discussed in [18] our model does not introduce the delay explicitly in the equations but it is a consequence of the level of infection structure given to the infected fish population together with the threshold condition related to the growth of bacteria in fish. The distributed delay system is proved to reduce to a discrete delay system by assuming that most of the fish die when its level of infection is closed to the threshold.

In this work we analyze the discrete delay system. We obtain some results concerning the existence, uniqueness, positivity and boundedness of solutions. We also discuss the existence and stability of equilibrium points of the system, establishing conditions for Hopf bifurcation to occur. The theoretical results are illustrated by some numerical simulations.

The paper is organized as follows. The model is presented in Section 2. In Section 3 the use of the characteristic lines method allows us to integrate the infected fish equation to get a system of two ordinary differential equations with delay for the susceptible fish and the bacteria. In Section 4, the distributed delay of the system is transformed in a discrete delay. The study of this last system is performed in Section 5. Section 6 is devoted to some numerical simulations and a conclusion is developed in Section 7.

2. Model

We present the following model of two interacting populations of bacteria and fish:

Infected fish dynamics

$$\frac{\partial I\,(b,t)}{\partial t} + \frac{\partial}{\partial b}\,(\beta b I\,(b,t)) = -\upsilon\,(b)\,I\,(b,t)\,. \tag{1a}$$

$$\beta b_0 I\,(b_0,t) = S\,(t)\,f\,(B\,(t))\,. \tag{1b}$$

Susceptible fish dynamics

$$\frac{\mathrm{d}S\,(t)}{\mathrm{d}t} = r S\,(t)\,(K - S\,(t)) - S\,(t)\,f\,(B(t))\,. \tag{1c}$$

Bacteria dynamics

$$\frac{\mathrm{d}B\,(t)}{\mathrm{d}t} = -\mu B\,(t) + \int_{b_0}^{\bar{b}} b\upsilon(b)I\,(b,t)\,\mathrm{d}b. \tag{1d}$$

Initial conditions

$$I\,(b,0) = I_0\,(b)\,, \qquad S(0) = S_0, \qquad B(0) = B_0. \tag{1e}$$

We denote by $B(t)$ the total number of bacteria in water. Fish get infected by bacteria spores and we distinguish between susceptible and infected fish. We denote by $S(t)$ the total number of susceptible fish. While bacteria and susceptible fish populations are taken to be non-structured we consider the infected fish population to be disease structured. The individual state variable for this population is the number of bacteria in the fish which is denoted by b. So, $I\,(b,t)$ denotes the density function representing the distribution of infected fish in terms of b at time t. This means that the total number of infected fish having between b_1 and b_2 bacteria in their organisms is given by the following integral

$$\int_{b_1}^{b_2} I\,(b,t)\mathrm{d}b.$$

We assume that in the absence of bacteria the fish population grows according to a logistic equation with carrying capacity K and a ratio intrinsic growth rate to carrying capacity r.

We consider infected any fish with disease level $b \geq b_0$ and we suppose that no fish survive when its disease level attains value $\bar{b}$. Thus the total number of infected fish is

$$I\,(t) = \int_{b_0}^{\bar{b}} I\,(b,t)\mathrm{d}b.$$

Infected fish neither reproduce nor contribute to the carrying capacity of fish population.

Bacteria only grow and divide in the host. The growth of bacteria in an infected fish is governed by the equation

$$\frac{\mathrm{d}b}{\mathrm{d}t} = \beta b, \qquad b(0) = b_0,$$

with β denoting the intrinsic growth rate of bacteria in fish. We see then that the maximal life span of an infected fish is: $\tau = \frac{1}{\beta}\ln(\frac{\bar{b}}{b_0})$. In the absence of fish, bacteria population decreases according to a constant mortality rate μ.

The rate of infection, i.e the inflow rate to the infected fish compartment, $\beta b_0 I\,(b_0,t)$, is taken to be equal to $S(t)f\,(B(t))$ where $f\,(B(t))\mathrm{d}t$ represents the ratio of the number of newly infected fish to the number of susceptible fish during a small interval of time $(t, t+\mathrm{d}t)$.

The individual mortality rate for infected fish, $\upsilon(b)$, is dependent on the structurant variable b. The fact that no fish survive for $b \geq \bar{b}$ is imposed by the following assumption:

$$\int_{b_0}^{\bar{b}} \upsilon(b)\mathrm{d}b = +\infty. \tag{2}$$

When fish die they disintegrate in water and the bacteria grown in them up to that moment increase the total number of bacteria in water, $B(t)$, at a rate equal to $\int_{b_0}^{\bar{b}} b\upsilon(b)I\,(b,t)\mathrm{d}b$.

3. A distributed delay version of the model

To begin with the study of system (1) we find the solution of Eq. (1a) following the characteristic lines and substitute it into Eq. (1d) obtaining a distributed delay differential equation for the dynamics of bacteria population.

The characteristic lines, $(\widetilde{b}(s), \widetilde{t}(s))$, are the trajectories made by vector field $(\beta \widetilde{b}, 1)$ in the *level of disease $\times$ time* space, where s is a local time new variable. Solving:

$$\begin{cases} \dfrac{\mathrm{d}\widetilde{b}}{\mathrm{d}s} = \beta \widetilde{b}, & \widetilde{b}(0) = \widetilde{b}_0 \\[2mm] \dfrac{\mathrm{d}\widetilde{t}}{\mathrm{d}s} = 1, & \widetilde{t}(0) = \widetilde{t}_0 \end{cases}$$

we obtain the characteristic line

$$\begin{cases} \widetilde{b}(s) = \widetilde{b}_0 \exp(\beta s) \\ \widetilde{t}(s) = s + \widetilde{t}_0. \end{cases}$$

If we denote

$$\widetilde{I}(s) = I\left(\widetilde{b}(s), \widetilde{t}(s)\right)$$

then Eq. (1a) can be written as

$$\frac{\mathrm{d}\widetilde{I}}{\mathrm{d}s} = -\left(\beta + \upsilon\left(\widetilde{b}_0 \exp(\beta s)\right)\right)\widetilde{I}$$

and, thus, we obtain

$$\widetilde{I}(s) = \widetilde{I}(0) \exp\left(-\int_0^s \left(\beta + \upsilon\left(\widetilde{b}_0 \exp(\beta \sigma)\right)\right)\mathrm{d}\sigma\right)$$

$$I\left(\widetilde{b}(s), \widetilde{t}(s)\right) = I\left(\widetilde{b}_0, \widetilde{t}_0\right) \exp\left(-\int_0^s \left(\beta + \upsilon\left(\widetilde{b}_0 \exp(\beta \sigma)\right)\right)\mathrm{d}\sigma\right).$$

Now, for a given pair (b, t), we take:

- $\widetilde{t}_0 = 0$, $s = t$ and $\widetilde{b}_0 = b \exp(-\beta t)$, if $b\exp(-\beta t) > b_0$.
- $\widetilde{b}_0 = b_0$, $s = \frac{1}{\beta}\ln\left(\frac{b}{b_0}\right)$ and $t_0 = t - \frac{1}{\beta}\ln\left(\frac{b}{b_0}\right)$, if $b\exp(-\beta t) \le b_0$.

This yields

$$I(b, t) = \begin{cases} I_0(b\exp(-\beta t)) \exp\left(-\int_0^t (\beta + \upsilon(b\exp(\beta(\sigma - t))))\mathrm{d}\sigma\right), & \text{if } b\exp(-\beta t) > b_0, \\[3mm] I\left(b_0, t - \dfrac{1}{\beta}\ln\left(\dfrac{b}{b_0}\right)\right) \exp\left(-\int_0^{\frac{1}{\beta}\ln\left(\frac{b}{b_0}\right)} (\beta + \upsilon(b_0\exp(\beta\sigma)))\mathrm{d}\sigma\right), & \text{if } b\exp(-\beta t) \le b_0. \end{cases} \quad (3)$$

Substituting (3) into Eq. (1d), we obtain the following system of differential equations

$$\begin{cases} \dfrac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \displaystyle\int_{b_0}^{\bar{b}} b\upsilon(b) I_0(b\exp(-\beta t)) \exp\left(-\int_0^t (\beta + \upsilon(b\exp(\beta(\sigma - t))))\mathrm{d}\sigma\right)\mathrm{d}b \\ \qquad \text{if } b\exp(-\beta t) > b_0 \\ \dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = rS(t)(K - S(t)) - S(t)f(B(t)) \end{cases} \quad (4)$$

and

$$\begin{cases} \dfrac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \displaystyle\int_{b_0}^{\bar{b}} b\upsilon(b) I\left(b_0, t - \dfrac{1}{\beta}\ln\left(\dfrac{b}{b_0}\right)\right) \exp\left(-\int_0^{\frac{1}{\beta}\ln\left(\frac{b}{b_0}\right)} (\beta + \upsilon(b_0\exp(\beta\sigma)))\mathrm{d}\sigma\right)\mathrm{d}b \\ \qquad \text{if } b\exp(-\beta t) \le b_0 \\ \dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = rS(t)(K - S(t)) - S(t)f(B(t)). \end{cases} \quad (5)$$

System (4) can be written in the following form

$$
\begin{cases}
\dfrac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + h(t) \\[2mm]
\dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = S(t)(K - S(t)) - S(t) f(B(t))
\end{cases}
\tag{6}
$$

with

$$
h(t) = \int_{b_0}^{\bar{b}} b\upsilon(b) I_0(b \exp(-\beta t)) \exp\left(-\int_0^t (\beta + \upsilon(b_0 \exp(\beta(\sigma - t)))) \,\mathrm{d}\sigma\right) \mathrm{d}b.
$$

It is an o.d.e. system the solution of which is

$$
\begin{cases}
B(t) = B(0) \exp(-\mu t) + \displaystyle\int_0^t \exp(-\mu(t - \sigma)) h(\sigma) \,\mathrm{d}\sigma \\[3mm]
S(t) = \dfrac{S_0}{\exp\left(-\int_0^t (K - f(B(s))) \,\mathrm{d}s\right) + S_0 \int_0^t \exp\left(-\int_s^t (K - f(B(\sigma))) \,\mathrm{d}\sigma\right) \mathrm{d}s}.
\end{cases}
$$

Now, it suffices to study system (5) which is a distributed delay differential system.

If we put

$$
\pi(b) = \exp\left(-\int_0^{\frac{1}{\beta} \ln\left(\frac{b}{b_0}\right)} (\beta + \upsilon(b_0 \exp(\beta\sigma))) \,\mathrm{d}\sigma\right)
$$

and

$$
g(t, b) = \frac{1}{\beta b_0} S\left(t - \frac{1}{\beta} \ln\left(\frac{b}{b_0}\right)\right) f\left(B\left(t - \frac{1}{\beta} \ln\left(\frac{b}{b_0}\right)\right)\right)
$$

system (5) becomes

$$
\begin{cases}
\dfrac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \displaystyle\int_{b_0}^{\bar{b}} b\upsilon(b)\pi(b)g(t, b)\mathrm{d}b \\[3mm]
\dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = rS(t)(K - S(t)) - S(t)f(B(t)).
\end{cases}
\tag{7}
$$

4. A case with concentrated mortality by infection

We study in the following the model (7) in a particular case, namely when the mortality by infection is concentrated in a neighborhood of $b = \bar{b}$.

Starting from a function υ which has support in the interval $[b_1, \bar{b}[$, $b_0 < b_1 < \bar{b}$, we define the family υ_ε by

$$
\upsilon_\varepsilon(b) := \upsilon\left(\frac{\bar{b} - b_1}{\varepsilon}(b - (\bar{b} - \varepsilon)) + b_1\right),
$$

that verifies $\mathrm{supp}(\upsilon_\varepsilon) = [\bar{b} - \varepsilon, \bar{b}]$ and $\int_{b_0}^{\bar{b}} \upsilon_\varepsilon(b) \,\mathrm{d}b = +\infty$, if we replace $\upsilon(b)$ by $\upsilon_\varepsilon(b)$ in the first equation of system (7), we get

$$
\frac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \int_{b_0}^{\bar{b}} b\upsilon_\varepsilon(b)\pi_\varepsilon(b) g(t, b) \,\mathrm{d}b,
\tag{8}
$$

where

$$
\pi_\varepsilon(b) = \exp\left(-\int_0^{\frac{1}{\beta}\ln\left(\frac{b}{b_0}\right)} (\beta + \upsilon_\varepsilon(b_0 \exp(\beta\sigma))) \,\mathrm{d}\sigma\right).
$$

The latter, by means of the change of variables $u = b_0 \exp(\beta\sigma)$, becomes

$$\pi_\varepsilon(b) = \frac{b_0}{b} \exp\left(-\int_{b_0}^{b} \frac{\upsilon_\varepsilon(u)}{\beta u} du\right).$$

Since g is continuous in $(t, \bar{b})$, then $\forall \varsigma > 0, \exists \eta_0 > 0$ such that $\forall \varepsilon \leq \eta_0$ and $\forall b \in [\bar{b} - \varepsilon, \bar{b}]$, the following inequalities hold

$$(1 - \varsigma) g(t, \bar{b}) \leq g(t, b) \leq (1 + \varsigma) g(t, \bar{b}), \tag{9}$$

and thus we also have

$$(1 - \varsigma) g(t, \bar{b}) \int_{b_0}^{\bar{b}} b\upsilon_\varepsilon(b) \pi_\varepsilon(b) \, db \leq \int_{b_0}^{\bar{b}} b\upsilon_\varepsilon(b) \pi_\varepsilon(b) g(t, b) \, db$$

$$\leq (1 + \varsigma) g(t, \bar{b}) \int_{b_0}^{\bar{b}} b\upsilon_\varepsilon(b) \pi_\varepsilon(b) \, db.$$

The fact that $\text{supp}(\upsilon_\varepsilon(b)) = [\bar{b} - \varepsilon, \bar{b}]$ implies that

$$\frac{1}{\beta\bar{b}} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds \leq \int_{b_0}^{b} \frac{\upsilon_\varepsilon(s)}{\beta s} ds \leq \frac{1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds,$$

from which we obtain

$$\exp\left(\frac{-1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right) \leq \exp\left(-\int_{b_0}^{b} \frac{\upsilon_\varepsilon(s)}{\beta s} ds\right) \leq \exp\left(\frac{-1}{\beta\bar{b}} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right),$$

and finally

$$\begin{cases} \int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(\dfrac{-1}{\beta(\bar{b} - \varepsilon)} \displaystyle\int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right) db \leq \int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(-\displaystyle\int_{b_0}^{b} \dfrac{\upsilon_\varepsilon(s)}{\beta s} ds\right) db, \\[4mm] \int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(-\displaystyle\int_{b_0}^{b} \dfrac{\upsilon_\varepsilon(s)}{\beta s} ds\right) db \leq \int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(\dfrac{-1}{\beta\bar{b}} \displaystyle\int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right) db. \end{cases}$$

Calling $\chi(b) = \exp(-\frac{1}{\beta(\bar{b}-\varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(u) du)$ we have $\chi'(b) = -\frac{1}{\beta(\bar{b}-\varepsilon)} \upsilon_\varepsilon(b) \exp(-\frac{1}{\beta(\bar{b}-\varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(u) du)$, and thus, having in mind that $\text{supp}\, \upsilon_\varepsilon \subset [\bar{b} - \varepsilon, \bar{b}]$,

$$\int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(\frac{-1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right) db = b_0 \beta(\bar{b} - \varepsilon) \int_{b_0}^{\bar{b}} (-\chi'(b)) db$$

$$= \beta b_0(\bar{b} - \varepsilon)(-\chi(\bar{b}) + \chi(\bar{b} - \varepsilon)).$$

On the other hand, we have $\int_{b_0}^{\bar{b}} \upsilon_\varepsilon(u) du = +\infty$ which is a direct consequence of assumption (2), and then we get

$$\chi(\bar{b}) = \exp\left(-\frac{1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{\bar{b}} \upsilon_\varepsilon(u) du\right) = 0$$

which makes

$$\int_{b_0}^{\bar{b}} b_0 \upsilon_\varepsilon(b) \exp\left(\frac{-1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{b} \upsilon_\varepsilon(s) \, ds\right) db = b_0 \beta(\bar{b} - \varepsilon) \exp\left(\frac{-1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{\bar{b}-\varepsilon} \upsilon_\varepsilon(s) \, ds\right)$$

and thus we obtain the following inequality

$$b_0 \beta(\bar{b} - \varepsilon) \exp\left(\frac{-1}{\beta(\bar{b} - \varepsilon)} \int_{b_0}^{\bar{b}-\varepsilon} \upsilon_\varepsilon(s) \, ds\right) db \leq \int_{b_0}^{\bar{b}} b\upsilon_\varepsilon(b) \pi_\varepsilon(b) \, db.$$

The same arguments used out of $\chi(b)$ to get the previous inequality give us the next one out of $\psi(b) = \exp(-\frac{1}{\beta \bar{b}} \int_{b_0}^{b} \upsilon_\varepsilon(u) \mathrm{d}u)$,

$$\int_{b_0}^{\bar{b}} b \upsilon_\varepsilon(b) \pi_\varepsilon(b) \, \mathrm{d}b \le b_0 \beta \, \bar{b} \exp \left(\frac{-1}{\beta \bar{b}} \int_{b_0}^{\bar{b}-\varepsilon} \upsilon_\varepsilon(s) \, \mathrm{d}s \right).$$

Having in mind that $\mathrm{supp} \left(\upsilon_\varepsilon(b) \right) = \left[\bar{b} - \varepsilon, \bar{b} \right]$, we have

$$b_0 \beta \left(\bar{b} - \varepsilon \right) \le \int_{b_0}^{\bar{b}} b \upsilon_\varepsilon(b) \pi_\varepsilon(b) \, \mathrm{d}b \le b_0 \beta \bar{b}. \tag{10}$$

From inequalities (9) and (10) we obtain

$$(1 - \varsigma) \, g\left(t, \bar{b}\right) b_0 \beta \left(\bar{b} - \varepsilon\right) \le \int_{b_0}^{\bar{b}} b \upsilon_\varepsilon(b) \pi_\varepsilon(b) g(t, b) \, \mathrm{d}b \le (1 + \varsigma) \, g\left(t, \bar{b}\right) b_0 \beta \, \bar{b}$$

and so

$$\lim_{\varepsilon \to 0} \int_{b_0}^{\bar{b}} b \upsilon_\varepsilon(b) \pi_\varepsilon(b) g(t, b) \, \mathrm{d}b = g\left(t, \bar{b}\right) \bar{b}.$$

Consequently, Eq. (8) becomes a discrete retarded differential equation

$$\frac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \bar{b} S \left(t - \frac{1}{\beta} \ln \left(\frac{\bar{b}}{b_0} \right) \right) f \left(B \left(t - \frac{1}{\beta} \ln \left(\frac{\bar{b}}{b_0} \right) \right) \right).$$

The model (5) can be written as

$$\begin{cases} \dfrac{\mathrm{d}B(t)}{\mathrm{d}t} = -\mu B(t) + \bar{b} S(t - \tau) f\left(B(t - \tau)\right) \\ \dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = r S(t) \left(K - S(t)\right) - S(t) f\left(B(t)\right) \\ (B_0, S_0) = \varphi \in \Omega_0, \end{cases} \tag{11}$$

where $\Omega_0 = \{\varphi = (\varphi_1, \varphi_2) \in C([-\tau, 0]; \mathbb{R}^2) : \varphi_1 > 0, \varphi_2 > 0\}$ and $\tau = \frac{1}{\beta} \ln(\frac{\bar{b}}{b_0})$.

5. Study of the model with discrete delay

In this section we study system (11) with the following function $f(x)$ which is of Michaelis–Menten type:

$$f(x) = \frac{x}{K_1 + x},$$

where K_1 is the bacteria density at which half of the maximum infection rate is reached.

5.1. Existence and uniqueness of the solution

System (11) can be written as

$$\begin{cases} x'(t) = A x(t) + F(x_t) \\ x_0 = \varphi, \end{cases} \tag{12}$$

where $A = \begin{bmatrix} -\mu & 0 \\ 0 & rK \end{bmatrix}$, $x(t) = \begin{pmatrix} B(t) \\ S(t) \end{pmatrix}$ and $F : C\left([-\tau, 0]; \mathbb{R}^2\right) \to \mathbb{R}^2$ is defined by

$$F(\varphi) = \begin{pmatrix} \bar{b} \varphi_2(-\tau) f\left(\varphi_1(-\tau)\right) \\ -\left(\varphi_2(0)\right)^2 r - \varphi_2(0) f\left(\varphi_1(0)\right) \end{pmatrix}.$$

Since f is a C^∞ function then F is locally Lipschitz, and it is well known (see [19] Chapter 2, [20] Chapter 9) that this assures the existence and uniqueness of a maximal solution of system (12) which is given by

$$x(t) = \exp(tA)\varphi(0) + \int_0^t \exp((t-s)A) F(x_s) \, ds, \quad \text{for } t \in \left[-\tau, T_\varphi\right[.$$

5.2. Positivity of the solution

Proposition 5.1. *If $\varphi > 0$, then the solution $(B(t), S(t))$ of system (11) is non-negative on $\left[-\tau, T_\varphi\right[$.*

Proof. Let $0 < t < \tau$. We have

$$\frac{dB(t)}{dt} = -\mu B(t) + \bar{b}\varphi_2(t-\tau)f(\varphi_1(t-\tau)).$$

It follows that

$$\frac{dB(t)}{dt} \geq -\mu B(t).$$

By integration, we get

$$B(t) \geq \varphi_1(0)\exp(-\mu t) \quad \text{for any } 0 \leq t \leq \tau,$$

from where

$$B(t) \geq 0 \quad \forall t \in [0, \tau].$$

On the other hand, we have

$$\frac{dS(t)}{dt} = S(t)l(t),$$

where $l(t) = r(K - S(t)) - f(B(t))$. So we get

$$S(t) = S(0)\exp\left(\int_0^t l(\sigma)\,d\sigma\right).$$

Since $S(0) > 0$, the solution is positive for any $t \in [0, \tau[$. Let $\left(\widehat{B}(t), \widehat{S}(t)\right)$ be a non-negative solution of Eq. (11) on $[0, \tau]$ and let $\tau < t < 2\tau$, we then have

$$\frac{dB(t)}{dt} = -\mu B(t) + \bar{b}\widehat{S}(t-\tau)f\left(\widehat{B}(t-\tau)\right) \quad \text{for any } t \in [\tau, 2\tau].$$

Thus

$$\frac{dB(t)}{dt} \geq -\mu B(t) \quad \text{for any } t \in [\tau, 2\tau],$$

which implies that

$$B(t) \geq \widehat{B}(\tau)\exp(-\mu t) \quad \text{for any } t \in [\tau, 2\tau],$$

and so

$$B(t) \geq 0 \quad \text{for any } t \in [\tau, 2\tau].$$

The solution $(B(t), S(t))$ of system (11) is non-negative on $[\tau, 2\tau]$. Proceeding as previously we prove by induction the positivity of solution $(B(t), S(t))$ on $\left[-\tau, T_\varphi\right]$. $\quad\square$

5.3. Boundedness of the solution

Proposition 5.2. *The solution* $(B(t), S(t))$ *of system* (11) *is bounded on* $\left[-\tau, T_\varphi\right[$.

Proof. Proposition 5.1 and the choice of $f(x)$ give $S(t) f(B(t)) > 0$ and so in the second equation of system (11) we have $\frac{dS(t)}{dt} < rS(t)(K - S(t))$.

Then $S(t)$ verifies $S(t) < \hat{S}(t)$ where $\hat{S}(t)$ is the solution of the next initial value problem:

$$\frac{d\hat{S}(t)}{dt} = r\hat{S}(t)\left(K - \hat{S}(t)\right), \quad \hat{S}(0) = S_0$$

which is a logistic equation that assures that

$$S(t) < \hat{S}(t) \leq \max(S_0, K) := M.$$

This bound for $S(t)$ applied to the first equation of system (11) and the fact that $f(x) \in (0, 1)$ for $x > 0$ give us:

$$\frac{dB(t)}{dt} < -\mu B(t) + \bar{b}M$$

which yields

$$B(t) \leq \exp(-\mu t)B(0) + (1 - \exp(-\mu t))\frac{\bar{b}M}{\mu} \leq \max\left(B(0), \frac{\bar{b}}{\mu}M\right). \quad \square$$

Proposition 5.3. *System* (11) *has a unique global solution.*

Proof. Let us suppose that $X(t) = (B(t), S(t))$ for $t \in [0, T_\varphi[$ is a maximal solution of system (11). It verifies $\frac{dX(t)}{dt} = AX(t) + F(X_t) := G(X_t)$ which is a continuous function of X. As $X(t)$ is bounded on $[0, T_\varphi[$, $\frac{dX(t)}{dt}$ is bounded on $[0, T_\varphi[$ and thus $X(t)$ is uniformly continuous on $[0, T_\varphi[$. So we can extend $X(t)$ to the right of T_φ which contradicts our assumption on maximality. This fact implies $T_\varphi = +\infty$ that is equivalent to the global existence of the solution.

5.4. Equilibrium points

System (11) has a trivial equilibrium $E_0 = (0, 0)$, an axial equilibrium $E_1 = (0, K)$ and possibly a positive equilibrium $E^* = (B^*, S^*)$ where B^* and S^* satisfy the following system:

$$\begin{cases} -\mu B^* + \dfrac{\bar{b}S^*B^*}{K_1 + B^*} = 0 \\ rS^*(K - S^*) - \dfrac{S^*B^*}{K_1 + B^*} = 0 \\ B^* > 0, \ S^* > 0. \end{cases} \tag{13}$$

Hence $S^* = \frac{\mu}{\bar{b}}(K_1 + B^*)$ and B^* verifies the equation:

$$\frac{-\mu r}{\bar{b}}\left(K_1 + B^*\right)^2 + (rK - 1)(K_1 + B^*) + K_1 = 0.$$

The only root of this equation which can be positive is

$$B^* = -K_1 - \frac{\bar{b}}{2\mu r}\left(1 - rK - \sqrt{(rK - 1)^2 + 4\mu r K_1/\bar{b}}\right). \tag{14}$$

The condition for this to hold is

$$\mu K_1 < \bar{b}K \tag{15}$$

and we obtain for S^*:

$$S^* = \frac{\mu}{\bar{b}}\left(K_1 + B^*\right) = \frac{1}{2r}\left(rK - 1 + \sqrt{(rK-1)^2 + 4\mu r K_1/\bar{b}}\right). \tag{16}$$

5.5. Local stability of equilibrium points

To linearize system (11) about an equilibrium point $(\bar{B}, \bar{S})$ we define the local variables

$$\begin{cases} x(t) = B(t) - \bar{B}, \\ y(t) = S(t) - \bar{S}. \end{cases}$$

We then obtain the linearized system

$$\begin{cases} \dfrac{dx}{dt} = -\mu x(t) + \bar{b}f(\bar{B})y(t-\tau) + \bar{b}\bar{S}f'(\bar{B})x(t-\tau) \\ \dfrac{dy}{dt} = (rK - 2r\bar{S} - f(\bar{B}))y(t) - \bar{S}f'(\bar{B})x(t), \end{cases} \tag{17}$$

the associated characteristic equation of which is given by $\det(M(\lambda, \tau)) = 0$ where

$$M(\lambda, \tau) = \begin{bmatrix} -\mu + \bar{b}\bar{S}f'(\bar{B})\exp(-\lambda\tau) - \lambda & \bar{b}f(\bar{B})\exp(-\lambda\tau) \\ -\bar{S}f'(\bar{B}) & rK - 2r\bar{S} - f(\bar{B}) - \lambda \end{bmatrix}.$$

A straightforward calculation finally gives

$$\lambda^2 + \left(\mu - rK + 2r\bar{S} + f(\bar{B})\right)\lambda + (2r\bar{S} + f(\bar{B}) - rK)\mu + (rK - 2r\bar{S} - \lambda)\bar{b}\bar{S}f'(\bar{B})\exp(-\lambda\tau) = 0. \tag{18}$$

5.5.1. Local stability around $E_0 = (0, 0)$

Proposition 5.4. *The equilibrium point $E_0 = (0, 0)$ is unstable and if $rK > 1$ then it is also repulsive.*

Proof. In this case the characteristic equation is

$$\lambda^2 + (\mu - rK)\lambda - \mu rK = 0,$$

the roots of which are $\lambda_1 = -\mu < 0$ and $\lambda_2 = rK > 0$. So E_0 is a saddle point.

To prove the second assertion of the proposition we use the second equation of system (11) which is of Bernoulli type and can be written in the form:

$$-\frac{d}{dt}\left(\frac{1}{S}\right) = \frac{1}{S(t)}\left(rK - f(B(t))\right) - r.$$

Hence

$$\frac{1}{S} = \frac{1}{S_0}\exp\left(-\int_0^t (rK - f(B(s)))\,ds\right) + \int_0^t r\exp\left(-\int_s^t (rK - f(B(\sigma)))\,d\sigma\right)ds,$$

that is

$$S(t) = \frac{S_0}{\exp\left(-\int_0^t (rK - f(B(s)))\,ds\right) + S_0\int_0^t r\exp\left(-\int_s^t (rK - f(B(\sigma)))\,d\sigma\right)ds}.$$

Since $f(B(t)) < 1$ we have

$$S(t) \geq \frac{S_0}{\exp-(rK-1)t + \frac{rS_0}{rK-1}(1 - \exp(-(rK-1)t))},$$

thus

$$\liminf_{t\to+\infty} S(t) \geq \frac{rK-1}{r} > 0,$$

which proves that E_0 is repulsive.

5.5.2. Local stability around $E_1 = (0, K)$

Now the characteristic equation becomes

$$\lambda^2 + (\mu + rK)\lambda + rK\mu - \frac{rK^2}{K_1}\bar{b}\exp(-\lambda\tau) - \bar{b}\frac{K}{K_1}\lambda\exp(-\lambda\tau) = 0$$

or

$$(\lambda + rK)\left(\lambda + \mu - \bar{b}\frac{K}{K_1}\exp(-\lambda\tau)\right) = 0. \tag{19}$$

This implies that

$$\lambda = -rK \quad \text{or} \quad \lambda + \mu - \bar{b}\frac{K}{K_1}\exp(-\lambda\tau) = 0. \tag{20}$$

So, $\lambda = -rK < 0$ is always an eigenvalue of (19) and we, therefore, focus on the equation

$$\lambda + \mu - \bar{b}\frac{K}{K_1}\exp(-\lambda\tau) = 0. \tag{21}$$

Function $f(\lambda) = \lambda + \mu - \bar{b}\frac{K}{K_1}\exp(-\lambda\tau)$, considering λ to be real, is increasing and its range is $(-\infty, +\infty)$, hence Eq. (21) possesses a unique real root λ_0. We are now proving that any other root $\lambda = \alpha + i\omega \neq \lambda_0$ of Eq. (21) verifies $\alpha < \lambda_0$. Taking the real part in Eq. (21), we obtain

$$\alpha - \lambda_0 = \frac{\bar{b}K}{K_1}(\exp(-\alpha\tau)\cos(\omega\tau) - \exp(-\lambda_0\tau)).$$

If we suppose that $\alpha > \lambda_0$ we get a contradiction since, in this case, the first term of the equality is positive while the second term is negative. So $\alpha \leq \lambda_0$. If we now assume that $\alpha = \lambda_0$ then this equality implies that $\cos(\omega\tau) = 1$ and, therefore, $\sin(\omega\tau) = 0$. But considering the imaginary part of (21) we get $\omega + \frac{\bar{b}K}{K_1}\sin(\omega\tau)e^{-\alpha\tau} = 0$, so $\omega = 0$ yielding $\lambda = \lambda_0$ in contradiction with the assumption that $\lambda \neq \lambda_0$. Thus, $\alpha < \lambda_0$.

The real root λ_0 is negative if $\mu K_1 > \bar{b}K$ and, in this case, all eigenvalues of (19) have negative real parts. We summarize the previous study in the following proposition.

Proposition 5.5. *Let $E_1 = (0, K)$ be the axial equilibrium point of system (11). If $\mu K_1 > \bar{b}K$ then E_1 is locally asymptotically stable and if $\mu K_1 < \bar{b}K$ then it is unstable.*

Remark 1. *If $\mu K_1 = \bar{b}K$ then the unique real root of (19) is $\lambda_0 = 0$ and all other eigenvalues have negative real parts. One can check that λ_0 is a simple root of (21) and, thus, the linear system is stable, but still we cannot conclude on the stability of E_1 without further analysis.*

We notice that the condition for $E_1 = (0, K)$ to be unstable coincides with condition (15) for the existence of the positive equilibrium $E^* = (B^*, S^*)$.

5.5.3. Local stability around $E^* = (B^*, S^*)$

In the following we assume condition (15), $\mu K_1 < \bar{b}K$, that assures the existence of the positive equilibrium $E^* = (B^*, S^*)$. The characteristic equation, using that $f(B^*) = r(K - S^*)$, can be written as:

$$D(\lambda, \tau) = \lambda^2 + (\mu + rS^*)\lambda + \mu rS^* + (r(K - 2S^*) - \lambda)\bar{b}S^*f'(B^*)\exp(-\lambda\tau) = 0. \tag{22}$$

In this section, we use some basic results on zeros of some transcendental functions (see [21,22]).

Proposition 5.6. *The characteristic equation associated to the linearized system of (11) about the positive equilibrium $E^* = (B^*, S^*)$ does not have $\lambda = 0$ as a root.*

Proof. If we make $\lambda = 0$ in Eq. (22) we obtain

$$\mu rS^* + r(K - 2S^*)\bar{b}S^*f'(B^*) = 0. \tag{23}$$

From Eq. (13) we can deduce the following equality:

$$\bar{b}S^* f'(B^*) = \frac{\mu^2 K_1}{\bar{b}S^*} \tag{24}$$

and substituting in Eq. (23) we have the following second degree equation for S^*:

$$\bar{b}(S^*)^2 - 2\mu K_1 S^* + \mu K K_1 = 0$$

which does not have positive solutions if and only if $\mu K_1 < \bar{b}K$.

Now we study the case without delay.

Proposition 5.7. *For $\tau = 0$, a necessary and sufficient condition for the roots of the characteristic equation associated to the linearized system of* (11) *about the positive equilibrium $E^* = (B^*, S^*)$ to have negative real parts is that the following two inequalities hold:*

$$\begin{cases} (\mu + rK - 1)\bar{b}S^* + \mu K_1(1 - \mu) > 0 \\ \left((rK - 1)\bar{b} - 2r\mu K_1\right) S^* + \mu K_1(rK + 1) > 0. \end{cases} \tag{25}$$

Proof. For $\tau = 0$ the characteristic equation (22) simplifies to

$$D(\lambda, 0) = \lambda^2 + \left(\mu + rS^*\right)\lambda + \mu rS^* + \left(r(K - 2S^*) - \lambda\right)\bar{b}S^* f'(B^*) = 0 \tag{26}$$

which is a second degree equation $\lambda^2 + a_1\lambda + b_1 = 0$ where

$$a_1 = \mu + rS^* - \bar{b}S^* f'(B^*)$$

and

$$b_1 = \mu rS^* + r(K - 2S^*)\bar{b}S^* f'(B^*).$$

The roots of the characteristic equations have negative real parts if and only $a_1 > 0$ and $b_1 > 0$. That is,

$$\begin{cases} a_1 = \mu + rS^* - \bar{b}S^* f'(B^*) > 0 \\ b_1 = \mu rS^* + r(K - 2S^*)\bar{b}S^* f'(B^*) > 0. \end{cases}$$

Then, using equality (24), we obtain:

$$\begin{cases} \mu + rS^* - \dfrac{\mu^2 K_1}{\bar{b}S^*} > 0 \\ \mu rS^* + r(K - 2S^*)\dfrac{\mu^2 K_1}{\bar{b}S^*} > 0 \end{cases}$$

and, thus,

$$\begin{cases} r\bar{b}(S^*)^2 + \bar{b}\mu S^* - \mu^2 K_1 > 0 \\ \bar{b}(S^*)^2 - 2\mu K_1 S^* + \mu K K_1 > 0. \end{cases}$$

From Eq. (13) one can deduce that

$$r\bar{b}(S^*)^2 = \mu K_1 - \bar{b}(1 - rK)S^*$$

which, when substituted in the previous inequalities gives us conditions (25). $\quad\square$

In the next corollary we state some sufficient conditions to get the same result of Proposition 5.7.

We now explore the possibility of finding imaginary roots of the characteristic equation for particular values of the delay τ. Let $\lambda = i\omega (\omega \in \mathbb{R})$ be a root of (22), that is,

$$D(i\omega, \tau) = -\omega^2 + \left(\mu + rS^*\right)i\omega + \mu rS^* + (r(K - 2S^*) - i\omega)\bar{b}S^* f'(B^*) \exp(-i\omega\tau) = 0. \tag{27}$$

Thus

$$\exp\left(-i\omega\tau\right) = \frac{\omega^2 - (\mu + rS^*)\,i\omega - \mu r S^*}{(r(K - 2S^*) - i\omega)\bar{b}S^* f'(B^*)}.$$

Since $|\exp\left(-i\omega\tau\right)|^2 = 1$, then

$$(\omega^2 - \mu r S^*)^2 + (\mu + rS^*)^2\omega^2 = (r^2(K - 2S^*)^2 + \omega^2)(\bar{b}S^* f'(B^*))^2,$$

which is polynomial equation of degree four

$$\omega^4 + \left(\mu^2 + r^2(S^*)^2 - \left(\bar{b}S^* f'(B^*)\right)^2\right)\omega^2 + (\mu r S^*)^2 - r^2(K - 2S^*)^2\left(\bar{b}S^* f'(B^*)\right)^2 = 0.$$

Using equalities (24) the equation is written as

$$\omega^4 - C_1\omega^2 + C_2 = 0 \tag{28}$$

with

$$C_1 = \frac{1}{(S^*)^2\bar{b}^2}\left(K_1^2\mu^4 - \left(\mu^2 + r^2(S^*)^2\right)(S^*)^2\bar{b}^2\right)$$

$$C_2 = \frac{\mu^2 r^2}{(S^*)^2\bar{b}^2}\left(\bar{b}^2(S^*)^4 - (K - 2S^*)^2\mu^2 K_1^2\right).$$

The fact that Eq. (28) could be transformed, letting $\omega^2 = x$, into the second degree equation $x^2 - C_1x + C_2 = 0$ allows us to discuss the existence of imaginary roots of the characteristic equation (22) in a simple way in terms of the values of C_1 and C_2.

We, now, establish in the following two theorems sufficient conditions for the positive equilibrium $E^* = (B^*, S^*)$ to be asymptotically stable for any value of τ, in the first one, and for the system (11) to undergo Hopf bifurcations at E^* for certain values of τ, in the second one.

Theorem 5.1. *Let $E^* = (B^*, S^*)$ be the positive equilibrium of system* (11) *and assume that inequalities* (25) *hold. Let C_1 and C_2 be the coefficients in Eq.* (28), *if, either $C_1 < 0$ and $C_2 > 0$, or $0 < C_1 < 2\sqrt{C_2}$ then E^* is locally asymptotically stable for all $\tau \geq 0$.*

Proof. The assumptions on C_1 and C_2 implies that Eq. (28) has no real roots and thus that the characteristic equation (22) has no imaginary roots for any $\tau \geq 0$. Since we are also assuming that for $\tau = 0$ the roots of (22) have negative real parts we conclude, using the results in [22], that E^* is locally asymptotically stable for all $\tau \geq 0$. $\quad\square$

In the next theorem we assume that $C_2 < 0$ which implies that Eq. (28) possesses a unique positive root

$$\omega_0 = \sqrt{\frac{1}{2}\left(C_1 + \sqrt{C_1^2 - 4C_2}\right)}.$$

Thus, there is sequence τ_k ($k = 0, 1, 2, \ldots$) of positive values of the delay τ such that $(i\omega_0, \tau_k)$ is a solution of Eq. (27), i.e. $D\left(i\omega_0, \tau_k\right) = 0$. If we call τ_0 the only one of these values of τ for which $\omega_0\tau_0 \in (0, 2\pi)$ then we have

$$\tau_k = \tau_0 + \frac{2\pi}{\omega_0}k \quad \text{for } k = 0, 1, 2, \ldots.$$

Theorem 5.2. *Let $E^* = (B^*, S^*)$ be the positive equilibrium of system* (11), *assume that inequalities* (25) *hold and let the coefficient C_2 in Eq.* (28) *be negative. Then E^* is locally asymptotically stable for $0 \leq \tau < \tau_0$ and unstable for $\tau > \tau_0$. Moreover, if $\tau = \tau_k$ ($k = 0, 1, 2, \ldots$) and*

$$(\mu + rS^*)\omega_0^2\left((\mu + rS^*)\bar{b}S^* - \mu^2 K_1 \cos(\omega_0\tau_k)\right) + \left(\omega_0^3 - \mu r S^*\omega_0)(2\omega_0\bar{b}S^* + \mu^2 K_1 \sin(\omega_0\tau_k)\right) > 0,$$

then system (11) *undergoes a Hopf bifurcation at E^*.*

Proof. Since $C_2 < 0$, then Eq. (28) has one positive root and the characteristic equation (22) has a unique imaginary root $i\omega_0$ associated to the value τ_0 of the delay in the conditions of the theorem. Having in mind that for $\tau = 0$ the roots of (22) have negative real parts we conclude, using the results in [22], that E^* is locally asymptotically stable for all $\tau < \tau_0$.

To prove the existence of Hopf bifurcations at $\tau = \tau_k$ we need to verify the following transversality condition:

$$\Re\left(\frac{d\lambda}{d\tau}\right)\bigg|_{\substack{\tau=\tau_k \\ \lambda=i\omega_0}} > 0.$$

Considering λ as a function of τ and differentiating (22) with respect to τ we obtain

$$\frac{d\lambda}{d\tau} = \frac{(r(K-2S^*)-\lambda)\bar{b}S^*f'(B^*)\lambda\exp(-\lambda\tau)}{2\lambda+\mu+rS^*-(1+(r(K-2S^*)-\lambda)\tau)\bar{b}S^*f'(B^*)\exp(-\lambda\tau)}. \tag{29}$$

From (22) we have

$$(r(K-2S^*)-\lambda)\bar{b}S^*f'(B^*)\exp(-\lambda\tau) = -\left(\lambda^2+\left(\mu+rS^*\right)\lambda+\mu rS^*\right).$$

So (29) can be written as

$$\frac{d\lambda}{d\tau} = \frac{-\lambda\left(\lambda^2+(\mu+rS^*)\lambda+\mu rS^*\right)}{2\lambda+\mu+rS^*-\bar{b}S^*f'(B^*)\exp(-\lambda\tau)+\tau\left(\lambda^2+(\mu+rS^*)\lambda+\mu rS^*\right)}. \tag{30}$$

Using that $\bar{b}S^*f'(B^*) = \frac{\mu^2 K_1}{\bar{b}S^*}$ we, thus, obtain substituting $\tau = \tau_k$ and $\lambda = i\omega_0$ in (30)

$$\frac{d\lambda}{d\tau}\bigg|_{\substack{\tau=\tau_k \\ \lambda=i\omega_0}} = \frac{(\mu+rS^*)\omega_0^2+i(\omega_0^3-\mu rS^*\omega_0)}{\left(\mu+rS^*-\frac{\mu^2 K_1}{\bar{b}S^*}\cos(\omega_0\tau_k)+\tau_k(\mu rS^*-\omega_0^2)\right)+i\left(2\omega_0+\frac{\mu^2 K_1}{\bar{b}S^*}\sin(\omega_0\tau_k)+\tau_k(\mu+rS^*)\omega_0\right)}.$$

From this expression it is straightforward to prove the transversality condition stated in the theorem. $\quad\square$

6. Numerical simulations

In this section we present graphically some simulations (MATLAB, dde23) of the solution of system (11) for different values of the delay τ but using the same set of values for the other parameters, namely: $\mu = 0.2$, $\bar{b} = 10$, $K_1 = 12$, $K = 25$ and $r = 0.027$. As $\mu K_1 = 2.4 < 250 = \bar{b}K$ we have the existence of the positive equilibrium $E^* = (B^*, S^*) = (22.8994, 0.6980)$.

In Fig. 1 it is presented the case without delay, $\tau = 0$. The conditions (25) for E^* to be asymptotically stable in this case are satisfied: $a_1 = 0.1501 > 0$ and $b_1 = 0.0476 > 0$.

If we calculate the coefficients in Eq. (28) we obtain: $C_1 = -0.0356 < 0$ and $C_2 = -0.0019 < 0$. Thus, we can apply Theorem 5.2, where $\omega_0 = 0.1713$ and $\tau_0 = 4.1418$, obtaining that E^* still is asymptotically stable for $\tau < \tau_0$ (see Fig. 2 where $\tau = 3$) while E^* is unstable for $\tau > \tau_0$.

The transversality condition appearing in Theorem 5.2 is also verified,

$$\Re\left(\frac{d\lambda}{d\tau}\right)\bigg|_{\substack{\tau=4.1418 \\ \lambda=i0.1713}} = 0.0093 > 0.$$

So, a Hopf bifurcation occurs at E^* for $\tau = \tau_0$. See Fig. 3 where a periodic solution appears for that value of τ.

7. Discussion

In this work we propose a mathematical model to study a bacteria–fish system. The fish population is divided into susceptible and infected individuals, and the infected fish population is structured by the level of infection. The model, which is a system of differential equations with initial and boundary conditions, is first transformed into a system of two differential equations with distributed delay for susceptible fish and bacteria in the water and further reduced to a discrete delay system by assuming that fish mortality is mainly due to infection attaining the lethal threshold.
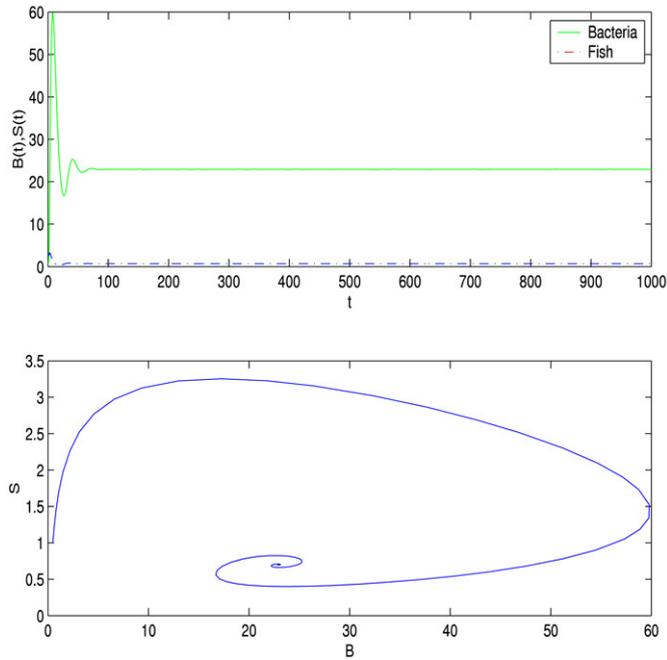
Fig. 1. Solution of system (11) for $\mu = 0.2$, $\bar{b} = 10$, $K_1 = 12$, $K = 25$, $r = 0.027$ and $\tau = 0$.
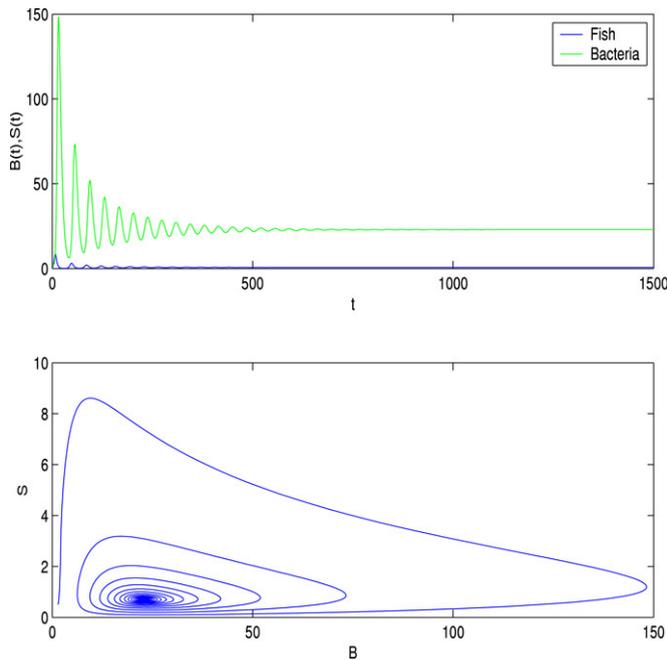

Fig. 2. Solution of system (11) for $\mu = 0.2$, $\bar{b} = 10$, $K_1 = 12$, $K = 25$, $r = 0.027$ and $\tau = 3$.

The analysis of this latter system gives the existence, for any parameter values, of two feasible equilibria: $E_0 = (0, 0)$, which is unstable and is only reachable if there is no fish in the initial conditions, and $E_1 = (0, K)$, the disease free equilibrium. E_1 is asymptotically stable if $\mu > \frac{\bar{b}K}{K_1}$, i.e. if bacteria mortality rate is larger than a certain quantity that may become small if either the fish environmental carrying capacity or the lethal disease level are themselves small. Bacteria mortality rate decreasing under this quantity, i.e. $\mu < \frac{\bar{b}K}{K_1}$, allows the existence of a
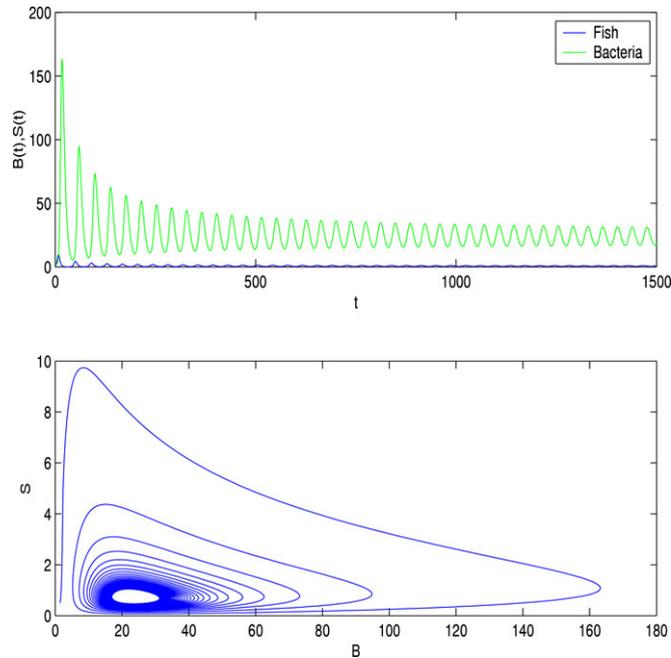
Fig. 3. Solution of system (11) for $\mu = 0.2$, $\bar{b} = 10$, $K_1 = 12$, $K = 25$, $r = 0.027$ and $\tau = 4.1418$.

positive equilibrium $E^* = (B^*, S^*)$, the endemic equilibrium. If conditions (25) hold then E^* is asymptotically stable for zero delay, $\tau = 0$. This can be extended for $\tau \in (0, \tau_0)$ where τ_0 is always positive and maybe infinite, depending on parameter values. If $\tau_0 < \infty$ a Hopf bifurcation occurs at E^* as seen in Fig. 3. An easy-to-analyze case happens when $rK > 1$, i.e. when the susceptible fish intrinsic growth rate is greater than one. Recall that this is the condition for $E_0 = (0, 0)$ to be repulsive. In this case it is straightforward to see that for small enough μ conditions (25) will be certainly satisfied and, having in mind that $\lim_{\mu \to 0^+} S^* = K - 1/r$, it is also possible to find values of μ for which the coefficients in Eq. (28) are $C_1 < 0$ and $C_2 > 0$ yielding from Theorem 5.1 the asymptotic stability of the endemic equilibrium for any value of the delay.

Acknowledgments

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