

Hopf bifurcation for a size-structured model with resting phase

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The authors are pleased to dedicate this article to Jerry Goldstein on the occasion of his 70th birthday.

Abstract

This article investigates Hopf bifurcation for a size-structured population dynamic model that is designed to describe size dispersion among individuals in a given population. This model has a nonlinear and non-local boundary condition. We reformulate the problem as an abstract non-densely defined Cauchy problem, and study it in the frame work of integrated semigroup theory. We prove a Hopf bifurcation theorem and we present some numerical simulations to support our analysis.

Key words. Hopf bifurcation, size structured model, integrated semigroups.

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1 Introduction

In this work we investigate Hopf bifurcation for the following size-structured population dynamic model:

$$\left\{ \begin{array}{l} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial}{\partial s} (g j_g(t, s)) - \sigma^+ j_g(t, s) + \sigma^- j_r(t, s) - (\varsigma + \mu) j_g(t, s), \\ g j_g(t, 0) = \alpha h \left(\int_0^{+\infty} \gamma(s) (j_g(t, s) + j_r(t, s) + a(t, s)) ds \right), \\ \\ \frac{\partial j_r(t, s)}{\partial t} = -\sigma^- j_r(t, s) + \sigma^+ j_g(t, s) - (\varsigma + \mu) j_r(t, s), \\ \\ \frac{\partial a(t, s)}{\partial t} = \varsigma (j_g(t, s) + j_r(t, s)) - \mu a(t, s), \\ \\ j_g(0, \cdot) = j_{g,0} \in L_+^1((0, +\infty), \mathbb{R}), \\ j_r(0, \cdot) = j_{r,0} \in L_+^1((0, +\infty), \mathbb{R}), \\ \text{and} \\ a(0, \cdot) = a_0 \in L_+^1((0, +\infty), \mathbb{R}), \end{array} \right. \quad (1.1)$$

where $g > 0, \sigma^+ > 0, \sigma^- > 0, \varsigma > 0, \mu > 0, \alpha > 0, \gamma \in L_+^\infty((0, +\infty), \mathbb{R}) \setminus \{0\}$, and the map $h : [0, +\infty) \rightarrow [0, +\infty)$ is defined by

$$h(x) = x \exp(-\xi x), \forall x \geq 0,$$

with $\xi > 0$.

Model (1.1) combines the growth process of individuals in size, the mortality process and the reproduction of individuals. In this model, the total population is decomposed into juveniles and adults. Here, juveniles and adults have another meaning than the usual ones in ecology. Actually, juveniles are the individuals that can grow in size, while the adults have reached the maturity in size (i.e. definitively stopped growing in size). The resting phase, i.e. period while individuals stop growing, is introduced to the class of juveniles, resulting in two subpopulations, namely growing juveniles and non-growing juveniles. The population density $j_g(t, s)$, $j_r(t, s)$ and $a(t, s)$ are respectively the density of growing juveniles, non-growing juveniles and adults at time t with size s . For each $s_2 > s_1 \geq 0$ the quantity

$$\int_{s_1}^{s_2} j_g(t, s) ds, \quad \int_{s_1}^{s_2} j_r(t, s) ds, \quad \int_{s_1}^{s_2} a(t, s) ds,$$

are respectively the total number of individuals of growing juveniles, non-growing juveniles, adults, at time t in the size range (s_1, s_2) .

In this model the newborns are assumed to be in the class of growing juveniles with size zero. Moreover, the flux of newborns at time t is given by $\alpha h \left(\int_0^{+\infty} \gamma(s) (j_g(t, s) + j_r(t, s) + a(t, s)) ds \right)$, where α is the reproduction rate of individuals, and the function $\gamma(s) \in [0, 1]$ can be interpreted as the probability for an individual with size s to reproduce. The function $h(x) = x \exp(-\xi x)$

is a Ricker [48, 49] type birth function. This type of birth function has been commonly used in the literature, which describes a limitation for the birth whenever the population becomes large. We refer to Ducrot, Magal and Seydi [22] for a mathematical justification of the Ricker function by using a singular perturbation idea. For mathematical convenience, the mortality rate μ is supposed to be independent of the size.

If we neglect the birth and the death process in model (1.1), then it becomes

$$\begin{cases} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial}{\partial s} (gj_g(t, s)) - \sigma^+ j_g(t, s) + \sigma^- j_r(t, s) - \varsigma j_g(t, s), \\ gj_g(t, 0) = 0, \\ \frac{\partial j_r(t, s)}{\partial t} = -\sigma^- j_r(t, s) + \sigma^+ j_g(t, s) - \varsigma j_r(t, s), \\ \frac{\partial a(t, s)}{\partial t} = \varsigma (j_g(t, s) + j_r(t, s)). \end{cases}$$

Here $g > 0$ is the growth rate of growing juveniles. σ^+ (respectively σ^-) is the turning rate of juveniles passing from the growing phase to the resting phase (conversely from the resting phase to the growing phase). To be more precise, the average time spent by a juvenile in the growing phase (respectively in the resting phase) follows an exponential law with mean $\frac{1}{\sigma^+}$ (respectively $\frac{1}{\sigma^-}$). $\varsigma > 0$ is the transition rate from juvenile to adult stage.

Figure 1 summarizes model (1.1). For short, the new born individuals start in the growing phase. The juveniles then alternate between the growing phase and the resting phase, and this process stops when individuals become adults (in size).

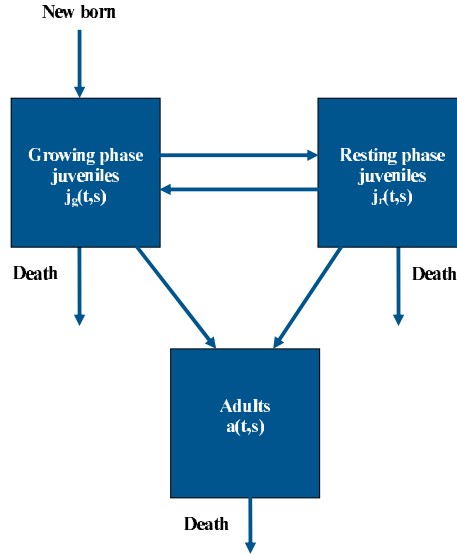


Figure 1: *Diagram flux of model (1.1).*

As far as we know, the first attempt to model size structured population can be attributed to Sinko and Streifer [46], Bell and Anderson [7]. Their model is a single transport equation. Since then, transport equations have been widely used and investigated size structured populations in the context of ecology and cell population dynamics. We refer to Metz and Diekmann [42], Cushing [17], Arino [2], Arino and Sanchez [3], Calsina and Saldana [10], Calsina and Sanchón [11], Webb [56] (and references therein) for studies on size-structured models.

With a single transport equation, two individuals having the same size at a given time keep the same size as long as they stay alive. However, it is observed that a group of individuals having the same size (for example at birth) exhibit distributed size after a period of time (see [6]). This phenomenon can be regarded as a dispersion process with respect to size.

The dispersion of individuals during the development process was probably introduced by Lee et al. [36] and modeled first by using a diffusion process in Metz and Diekmann [42]. Recently, this kind of model was investigated by Buffoni and Pasquali [9] with a linear boundary condition and by Chu, Ducrot, Magal and Ruan [13] with a nonlinear boundary condition.

Another approach to model this phenomenon is by allowing growth rates to vary for individuals with the same size. We refer to Huyer [30] and Banks et al. [6] for models with multiple growth rates. More recently, Chu, Magal and Yuan [14] modeled the size dispersion process by using a “random walk” like process by alternating a positive and negative growth speed. In particular, when the negative growth rate becomes null in the “random walk” model, one can derive a model similar to the model used to describe the quiescence of cells. Models with quiescence were first proposed by Gyllenberg and Webb [27] for tumor cells. We refer to [4, 23, 28, 50, 51] for studies on age and/or size-structured models with quiescence and results on this subject. We also refer to Bai and Cui [5], Farkas and Hinow [25] for size-structured cell models with two kinds of interchangeable but strictly positive growth rates.

From modeling point of view, the goal of model (1.1) is to describe this size dispersion process. To the best of our knowledge, the model (1.1) has not been considered in the context of size population dynamics.

From a mathematical point of view of (1.1), we can first consider some special cases. For example, if $\gamma(x) = 1, \forall x \in [0, +\infty)$, then the total number of individuals $U(t) := \int_0^{+\infty} u(t, s) ds$ satisfies the following ordinary differential equation

$$\begin{cases} \frac{dU(t)}{dt} = \alpha h(U(t)) - \mu U(t), \forall t \geq 0, \\ U(0) = \int_0^{+\infty} (j_{g,0} + j_{r,0} + a_0)(s) ds. \end{cases}$$

In this case, the positive equilibrium (when it exists) is globally asymptotically stable. Consequently, there will be no oscillations.

If we assume $\varsigma = 0$, then

$$a(t, s) = e^{-\mu t} a_0(s) \rightarrow 0 \text{ as } t \rightarrow +\infty.$$

Hence, the dynamical properties of (1.1) with $\varsigma = 0$ are captured by the following

system

$$\begin{cases} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial}{\partial s} (gj_g(t, s)) - \sigma^+ j_g(t, s) + \sigma^- j_r(t, s) - \mu j_g(t, s), \\ gj_g(t, 0) = \alpha h \left(\int_0^{+\infty} \gamma(s)(j_g(t, s) + j_r(t, s)) ds \right), \\ \frac{\partial j_r(t, s)}{\partial t} = -\sigma^- j_r(t, s) + \sigma^+ j_g(t, s) - \mu j_r(t, s), \\ j_g(0, \cdot) = j_{g,0} \in L_+^1(0, +\infty), \\ j_r(0, \cdot) = j_{r,0} \in L_+^1(0, +\infty), \end{cases} \quad (1.2)$$

which is an extreme case of the model studied in Chu, Magal and Yuan [14].

In particular, if $\sigma^+ = 0$ and $\varsigma = 0$, then the system becomes

$$\begin{cases} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial}{\partial s} (gj_g(t, s)) - \mu j_g(t, s), \\ gj_g(t, 0) = \alpha h \left(\int_0^{+\infty} \gamma(s)(j_g(t, s)) ds \right), \\ j_g(0, \cdot) = j_{g,0} \in L_+^1(0, +\infty). \end{cases} \quad (1.3)$$

With a simple change of variable, we can assume $g = 1$, then (1.3) is exactly the age-structured model considered in Magal and Ruan [40] and Chu, Ducrot, Magal and Ruan [13].

From mathematical point of view, the goal of this article is to study the existence of Hopf bifurcation for system (1.1). Our work is conducted by the early fundamental work of Engel and Nagel [24] and Goldstein [26] on linear semigroup theory. Some recent improvement about this theory allows to derive a center manifold theorem for abstract non-densely defined Cauchy problems (see Magal and Ruan [40]) as well as a Hopf bifurcation theorem (see Liu, Magal and Ruan [37]). These theorems have been successfully applied to study the existence of Hopf bifurcation for some age/size-structured models, see [40, 13, 14, 41]. We would like to point out that there are relatively few results concerning the non-trivial periodic solutions for age/size-structured population dynamical models. We refer to Cushing [18, 19], Prüss [43], Swart [47], Kostova and Li [35], Bertoni [8] for results in such a context. It is commonly believed that periodic solutions appeared in age/size-structured models are induced by Hopf bifurcations (Castillo-Chavez et al [12], Inaba [31, 32], Zhang et al [57]). Hopf bifurcation analysis has been considered for various classes of partial differential equations in Amann [1], Crandall and Rabinowitz [15], Da Prato and Lunardi [20], Guidotti and Merino [16], Koch and Antman [33], Sandstede and Scheel [44], and Simonett [45]. However, since there is a nonlinear and nonlocal boundary condition in our model (1.1), their results and techniques do not apply to (1.1).

The paper is organized as follows. In section 2, system (1.1) is reformulated as a non-densely defined Cauchy problem. In section 3, we study the existence and uniqueness of the positive equilibrium. In section 4, we linearize system (1.1) at the positive equilibrium, investigate the spectral properties of the linearized equation, and give the characteristic equation. The local stability of the

positive equilibrium is considered in section 5. In section 6, the existence of Hopf bifurcation is studied when α is considered as the bifurcation parameter. Finally, in section 7 we summarize the results of the paper and present some bifurcation diagrams as well as some numerical simulations of the model.

2 Preliminary

By making a simple change of variable ($\tilde{s} = \frac{s}{g}$), without loss of generality, we will always assume that $g = 1$. From here on, we consider the system

$$\left\{ \begin{array}{l} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial j_g(t, s)}{\partial s} - \sigma^+ j_g(t, s) + \sigma^- j_r(t, s) - (\varsigma + \mu) j_g(t, s), \\ j_g(t, 0) = \alpha h \left(\int_0^{+\infty} \gamma(s) (j_g(t, s) + j_r(t, s) + a(t, s)) ds \right), \\ \frac{\partial j_r(t, s)}{\partial t} = -\sigma^- j_r(t, s) + \sigma^+ j_g(t, s) - (\varsigma + \mu) j_r(t, s), \\ \frac{\partial a(t, s)}{\partial t} = \varsigma (j_g(t, s) + j_r(t, s)) - \mu a(t, s), \\ j_g(0, \cdot) = j_{g,0} \in L_+^1(0, +\infty), \\ j_r(0, \cdot) = j_{r,0} \in L_+^1(0, +\infty), \\ a(0, \cdot) = a_0 \in L_+^1(0, +\infty), \end{array} \right. \quad (2.1)$$

where $\sigma^+ > 0, \sigma^- > 0, \varsigma > 0, \mu > 0, \alpha > 0, \gamma \in L_+^\infty(0, +\infty) \setminus \{0\}$, and the map $h : \mathbb{R} \rightarrow \mathbb{R}$ is defined by

$$h(x) = x \exp(-\xi x), \forall x \in \mathbb{R},$$

with $\xi > 0$.

Let $L : D(L) \subset X \rightarrow X$ be a linear operator on a Banach space X . Denote by $\rho(L)$ the resolvent set of L . The spectrum of L is $\sigma(L) = \mathbb{C} \setminus \rho(L)$. The point spectrum of L is the set

$$\sigma_P(L) := \{\lambda \in \mathbb{C} : N(\lambda I - L) \neq \{0\}\}.$$

Let Y be a subspace of X . Then we denote by $L_Y : D(L_Y) \subset Y \rightarrow Y$ the part of L in Y , which is defined by

$$L_Y x = Lx, \forall x \in D(L_Y) := \{x \in D(L) \cap Y : Lx \in Y\}.$$

In particular, we denote L_0 the part of L in $\overline{D(L)}$.

Consider the Banach space

$$X := \mathbb{R} \times L^1(0, +\infty) \times L^1(0, +\infty) \times L^1(0, +\infty)$$

endowed with the usual product norm

$$\left\| \begin{pmatrix} \alpha \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} \right\| = |\alpha| + \|\varphi_1\|_{L^1(0, +\infty)} + \|\varphi_2\|_{L^1(0, +\infty)} + \|\varphi_3\|_{L^1(0, +\infty)}.$$

The positive cone of X is

$$X_+ := \mathbb{R}_+ \times L_+^1(0, +\infty) \times L_+^1(0, +\infty) \times L_+^1(0, +\infty).$$

Define the linear operator $A : D(A) \subset X \rightarrow X$ by

$$A \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} -\varphi_1(0) \\ -\varphi_1' \\ 0 \\ 0 \end{pmatrix}$$

with

$$D(A) := \{0\} \times W^{1,1}(0, +\infty) \times L^1(0, +\infty) \times L^1(0, +\infty).$$

Then

$$X_0 := \overline{D(A)} = \{0\} \times L^1(0, +\infty) \times L^1(0, +\infty) \times L^1(0, +\infty) \neq X.$$

Let $A_0 : D(A_0) \subset X_0 \rightarrow X_0$ be the part of A in X_0 , which is defined by

$$A_0 x = Ax, \quad \forall x \in D(A_0)$$

with

$$D(A_0) = \{x \in D(A), Ax \in X_0\}.$$

Define the linear operator $L : X_0 \rightarrow X_0$ by

$$L \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ -(\sigma^+ + \varsigma + \mu)\varphi_1 + \sigma^- \varphi_2 \\ -(\sigma^- + \varsigma + \mu)\varphi_2 + \sigma^+ \varphi_1 \\ \varsigma(\varphi_1 + \varphi_2) - \mu\varphi_3 \end{pmatrix}.$$

Define the map $H : X_0 \rightarrow X$ by

$$H \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} \alpha h \left(\int_0^{+\infty} \gamma(s) (\varphi_1(s) + \varphi_2(s) + \varphi_3(s)) ds \right) \\ 0 \\ 0 \\ 0 \end{pmatrix}.$$

By identifying $\begin{pmatrix} j_g(t, \cdot) \\ j_r(t, \cdot) \\ a(t, \cdot) \end{pmatrix}$ with $v(t) = \begin{pmatrix} 0 \\ j_g(t, \cdot) \\ j_r(t, \cdot) \\ a(t, \cdot) \end{pmatrix}$, the partial differential

equation (2.1) can be rewritten as the following non-densely defined Cauchy problem

$$\frac{dv(t)}{dt} = Av(t) + Lv(t) + H(v(t)), \quad \text{for } t \geq 0, \quad \text{and } v(0) = \begin{pmatrix} 0 \\ j_{g,0} \\ j_{r,0} \\ a_0 \end{pmatrix} \in X_0. \quad (2.2)$$

First we have the following lemma about the resolvent of A .

Lemma 2.1 We have $(0, +\infty) \subset \rho(A_0) = \rho(A)$, and for each $\lambda > 0$ we obtain the following explicit formula for the resolvent of A :

$$(\lambda I - A)^{-1} \begin{pmatrix} c \\ \psi_1 \\ \psi_2 \\ \psi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix}$$

\Leftrightarrow

$$\begin{cases} \varphi_1(s) = ce^{-\lambda s} + \int_0^s e^{-\lambda(s-l)} \psi_1(l) dl, \\ \varphi_2 = \frac{\psi_2}{\lambda}, \\ \varphi_3 = \frac{\psi_3}{\lambda}. \end{cases}$$

From the resolvent formula for A , we deduce that.

Lemma 2.2 The linear operator A is a Hille-Yosida operator on X . More precisely, we have $(0, +\infty) \subset \rho(A)$ (the resolvent set of A), and

$$\|(\lambda I - A)^{-1}\| \leq \frac{1}{\lambda}, \forall \lambda > 0.$$

Set

$$\Omega := \{\lambda \in \mathbb{C} : \operatorname{Re}(\lambda) > -\mu\}.$$

Next we obtain the following result.

Lemma 2.3 The linear operator $A + L$ is a Hille-Yosida operator on X . Moreover

$$\Omega \subset \rho(A + L),$$

and for each $\lambda \in \Omega$ the resolvent of $A + L$ is defined by

$$(\lambda I - (A + L))^{-1} \begin{pmatrix} c \\ \psi_1 \\ \psi_2 \\ \psi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix}$$

\Leftrightarrow

$$\begin{cases} \varphi_1(s) = ce^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} \\ \quad + \int_0^s e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)(s-l)} \left(\psi_1(l) + \frac{\sigma^-}{\lambda + \sigma^- + \varsigma + \mu} \psi_2(l)\right) dl, \\ \varphi_2(s) = \frac{1}{\lambda + \sigma^- + \varsigma + \mu} (\psi_2(s) + \sigma^+ \varphi_1(s)), \\ \varphi_3(s) = \frac{1}{\lambda + \mu} (\psi_3(s) + \varsigma (\varphi_1(s) + \varphi_2(s))). \end{cases}$$

Next since $L + \delta I$ is a positive linear operator for $\delta > 0$ large enough we obtain the following result.

Lemma 2.4 We have $(\lambda I - (A + L))^{-1} X_+ \subset X_+$ for $\lambda > 0$ large enough.

Set

$$X_{0+} := X_0 \cap X_+.$$

By using the results in Thieme [52], Magal [38], and Magal and Ruan [39], we can obtain the following theorem.

Theorem 2.5 (Existence) *There exists a unique continuous semiflow $\{V(t)\}_{t \geq 0}$ on X_{0+} such that $\forall v(0) \in X_{0+}$, $t \rightarrow V(t)v(0)$ is the unique integrated solution of system (2.2), or equivalently,*

$$V(t)v(0) = v(0) + A \int_0^t V(l)v(0) dl + L \int_0^t V(l)v(0) dl + \int_0^t H(V(l)v(0)) dl, \quad \forall t \geq 0.$$

3 Equilibrium

The equilibrium solutions of equation (2.2) are obtained by solving the equation

$$A \begin{pmatrix} 0 \\ \bar{j}_g \\ \bar{j}_r \\ \bar{a} \end{pmatrix} + L \begin{pmatrix} 0 \\ \bar{j}_g \\ \bar{j}_r \\ \bar{a} \end{pmatrix} + H \begin{pmatrix} 0 \\ \bar{j}_g \\ \bar{j}_r \\ \bar{a} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

and we obtain the following lemma.

Lemma 3.1 (Equilibrium) *There exists a positive equilibrium of system (2.1) (or system (2.2)) if and only if $R_0(\alpha) > 1$, where*

$$R_0(\alpha) := \alpha \left(1 + \frac{\zeta}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \zeta + \mu}\right) \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \zeta + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \zeta + \mu}\right)s} ds. \quad (3.1)$$

Moreover, when it exists, it is unique and the positive equilibrium $\bar{v} = \begin{pmatrix} 0 \\ \bar{j}_g \\ \bar{j}_r \\ \bar{a} \end{pmatrix}$

is given by the following formula:

$$\begin{aligned} \bar{j}_g(s) &= \frac{\alpha \ln R_0(\alpha)}{\xi R_0(\alpha)} e^{-\left(\sigma^+ + \zeta + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \zeta + \mu}\right)s}, \\ \bar{j}_r(s) &= \frac{\sigma^+}{\sigma^- + \zeta + \mu} \bar{j}_g(s), \\ \bar{a}(s) &= \frac{\zeta}{\mu} (\bar{j}_g(s) + \bar{j}_r(s)). \end{aligned}$$

4 Linearized equation

From now on, we set

$$\bar{v} = \begin{pmatrix} 0 \\ \bar{j}_g \\ \bar{j}_r \\ \bar{a} \end{pmatrix},$$

where $\bar{j}_g, \bar{j}_r, \bar{a}$ are given by Lemma 3.1.

The linearized system of (2.2) around \bar{v} is

$$\frac{dv(t)}{dt} = Av(t) + Lv(t) + DH(\bar{v})v(t) \text{ for } t \geq 0, \quad (4.1)$$

where

$$DH(\bar{v}) \begin{pmatrix} 0 \\ \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} \eta(\alpha) \int_0^{+\infty} \gamma(s) (\varphi_1(s) + \varphi_2(s) + \varphi_3(s)) ds \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

with

$$\eta(\alpha) = \alpha h' \left(\int_0^{+\infty} \gamma(s) (\bar{j}_g(s) + \bar{j}_r(s) + \bar{a}(s)) ds \right).$$

Since

$$h'(x) = e^{-\xi x} (1 - \xi x),$$

and by Lemma 3.1 we have

$$\begin{aligned} & \int_0^{+\infty} \gamma(s) (\bar{j}_g(s) + \bar{j}_r(s) + \bar{a}(s)) ds \\ &= \left(1 + \frac{\varsigma}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}\right) \frac{\alpha \ln R_0(\alpha)}{\xi R_0(\alpha)} \int_0^{+\infty} \gamma(s) e^{-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu}\right)s} ds \\ &= \frac{\ln R_0(\alpha)}{\xi}, \end{aligned}$$

it can be deduced that

$$\eta(\alpha) = \frac{\alpha}{R_0(\alpha)} (1 - \ln R_0(\alpha)). \quad (4.2)$$

The Cauchy problem (4.1) corresponds to the following linearized system:

$$\left\{ \begin{array}{l} \frac{\partial j_g(t, s)}{\partial t} = -\frac{\partial j_g(t, s)}{\partial s} - \sigma^+ j_g(t, s) + \sigma^- j_r(t, s) - (\varsigma + \mu) j_g(t, s), \\ j_g(t, 0) = \eta(\alpha) \int_0^{+\infty} \gamma(s) (j_g(t, s) + j_r(t, s) + a(t, s)) ds, \\ \frac{\partial j_r(t, s)}{\partial t} = -\sigma^- j_r(t, s) + \sigma^+ j_g(t, s) - (\varsigma + \mu) j_r(t, s), \\ \frac{\partial a(t, s)}{\partial t} = \varsigma (j_g(t, s) + j_r(t, s)) - \mu a(t, s), \\ j_g(0, \cdot) = j_{g,0} \in L_+^1(0, +\infty), \\ j_r(0, \cdot) = j_{r,0} \in L_+^1(0, +\infty), \\ a(0, \cdot) = a_0 \in L_+^1(0, +\infty). \end{array} \right.$$

Next we study the spectral properties of the linearized equation (4.1).

Definition 4.1 Let $L : D(L) \subset X \rightarrow X$ be the infinitesimal generator of a linear C_0 -semigroup $\{T_L(t)\}_{t \geq 0}$ on a Banach space X . We define $\omega_0(L) \in [-\infty, +\infty)$ the growth bound of L by

$$\omega_0(L) := \lim_{t \rightarrow +\infty} \frac{\ln \left(\|T_L(t)\|_{\mathcal{L}(X)} \right)}{t}.$$

The essential growth bound $\omega_{0,ess}(L) \in [-\infty, +\infty)$ of L is defined by

$$\omega_{0,ess}(L) := \lim_{t \rightarrow +\infty} \frac{\ln \left(\|T_L(t)\|_{ess} \right)}{t},$$

where $\|T_L(t)\|_{ess}$ is the essential norm of $T_L(t)$ defined by

$$\|T_L(t)\|_{ess} = \kappa(T_L(t)B_X(0,1)),$$

here $B_X(0,1) = \{x \in X : \|x\|_X \leq 1\}$, and for each bounded set $B \subset X$,

$\kappa(B) = \inf \{\varepsilon > 0 : B \text{ can be covered by a finite number of balls of radius } \leq \varepsilon\}$

is the Kuratovsky measure of non-compactness.

For the following result, the existence of the projector was first proved by Webb [54, 55] and the fact that there is a finite number of points of the spectrum is proved by Engel and Nagel [24].

Theorem 4.2 Let $L : D(L) \subset X \rightarrow X$ be the infinitesimal generator of a linear C_0 -semigroup $\{T_L(t)\}$ on a Banach space X . Then

$$\omega_0(L) = \max \left(\omega_{0,ess}(L), \max_{\lambda \in \sigma(L) \setminus \sigma_{ess}(L)} \operatorname{Re}(\lambda) \right).$$

Assume in addition that $\omega_{0,ess}(L) < \omega_0(L)$. Then for each $\gamma \in (\omega_{0,ess}(L), \omega_0(L)]$, $\{\lambda \in \sigma(L) : \operatorname{Re}(\lambda) \geq \gamma\} \subset \sigma_p(L)$ is non empty, finite and contains only poles of the resolvent of L . Moreover, there exists a finite rank bounded linear operator of projection $\Pi : X \rightarrow X$ satisfying the following properties:

- (a) $\Pi(\lambda - L)^{-1} = (\lambda - L)^{-1}\Pi, \forall \lambda \in \rho(L)$;
- (b) $\sigma(L_{\Pi(X)}) = \{\lambda \in \sigma(L) : \operatorname{Re}(\lambda) \geq \gamma\}$;
- (c) $\sigma(L_{(I-\Pi)(X)}) = \sigma(L) \setminus \sigma(L_{\Pi(X)})$.

To simplify the notation, we define $B_\alpha : D(B_\alpha) \subset X \rightarrow X$ as

$$B_\alpha x = Ax + Lx + DH(\bar{v})x \text{ with } D(B_\alpha) = D(A),$$

and denote by $(B_\alpha)_0$ the part of B_α in X_0 .

Lemma 4.3 For each $\lambda \in \Omega$, we have

$$\lambda \in \rho(B_\alpha) \Leftrightarrow \Delta(\alpha, \lambda) \neq 0,$$

where

$$\begin{aligned} \Delta(\alpha, \lambda) &= 1 - \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right) \\ &\quad \times \int_0^{+\infty} \gamma(s) e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} ds. \end{aligned}$$

Moreover, we deduce the following explicit formula:

$$(\lambda I - B_\alpha)^{-1} \begin{pmatrix} c \\ \psi_1 \\ \psi_2 \\ \psi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ \widehat{\psi}_1 \\ \widehat{\psi}_2 \\ \widehat{\psi}_3 \end{pmatrix}$$

\Leftrightarrow

$$\begin{cases} \widehat{\psi}_1(s) = \widehat{c} e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} \\ \quad + \int_0^s e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)(s-l)} \left(\psi_1(l) + \frac{\sigma^-}{\lambda + \sigma^- + \varsigma + \mu} \psi_2(l)\right) dl, \\ \widehat{\psi}_2(s) = \frac{1}{\lambda + \sigma^- + \varsigma + \mu} (\psi_2(s) + \sigma^+ \psi_1(s)), \\ \widehat{\psi}_3(s) = \frac{1}{\lambda + \mu} (\psi_3(s) + \varsigma (\psi_1(s) + \psi_2(s))), \end{cases}$$

where

$$\begin{aligned} \widehat{c} &= \Delta(\alpha, \lambda)^{-1} \left\{ c + \eta(\alpha) \int_0^{+\infty} \gamma(s) \left[\frac{1}{\lambda + \mu} \psi_3(s) + \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \frac{1}{\lambda + \sigma^- + \varsigma + \mu} \psi_2(s) \right. \right. \\ &\quad \left. \left. + \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right) \right. \right. \\ &\quad \left. \left. \times \left(\int_0^s e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)(s-l)} \left(\psi_1(l) + \frac{\sigma^-}{\lambda + \sigma^- + \varsigma + \mu} \psi_2(l)\right) dl \right) \right] ds \right\}, \end{aligned}$$

with $\eta(\alpha)$ defined in (4.2).

Proof. Since $\lambda \in \Omega$, it follows from Lemma 2.3 that $(\lambda I - (A + L))$ is invertible. Then

$$\lambda I - B_\alpha \text{ is invertible } \Leftrightarrow I - DH(\bar{v})(\lambda I - (A + L))^{-1} \text{ is invertible,}$$

and

$$(\lambda I - B_\alpha)^{-1} = (\lambda I - (A + L))^{-1} \left[I - DH(\bar{v})(\lambda I - (A + L))^{-1} \right]^{-1}.$$

The result follows by solving

$$\left[I - DH(\bar{v})(\lambda I - (A + L))^{-1} \right] \begin{pmatrix} \widehat{c} \\ \widehat{\psi}_1 \\ \widehat{\psi}_2 \\ \widehat{\psi}_3 \end{pmatrix} = \begin{pmatrix} c \\ \psi_1 \\ \psi_2 \\ \psi_3 \end{pmatrix}. \quad (4.3)$$

■

By using the above explicit formula for the resolvent of B_α we obtain the following lemma.

Lemma 4.4 *If $\lambda_0 \in \sigma(B_\alpha) \cap \Omega$, then λ_0 is a simple eigenvalue of B_α if and only if*

$$\frac{d\Delta(\alpha, \lambda_0)}{d\lambda} \neq 0.$$

Since $DH(\bar{v})$ is a bounded linear operator and $A + L$ is a Hille-Yosida operator, it follows that the linear operator B_α is also a Hille-Yosida operator. Consequently $(B_\alpha)_0$ generates a strongly continuous semigroup $\{T_{(B_\alpha)_0}(t)\}$ on X_0 . Moreover by using a perturbation result we obtain the following estimation.

Lemma 4.5 *The essential growth bound of $(B_\alpha)_0$ satisfies the following estimation:*

$$\omega_{0,ess}((B_\alpha)_0) \leq -\mu.$$

Proof. We have

$$\begin{aligned} \|T_{(A+L)_0}(t)\varphi\|_{L^1(0,+\infty)} &= \| \|T_{(A+L)_0}(t)\varphi\| \|_{L^1(0,+\infty)} \leq \|T_{(A+L)_0}(t)|\varphi|\|_{L^1(0,+\infty)} \\ &= \int_0^\infty T_{(A+L)_0}(t)|\varphi(x)| dx = \int_0^\infty e^{-\mu t} |\varphi(x)| dx \\ &= e^{-\mu t} \|\varphi\|_{L^1(0,+\infty)}. \end{aligned}$$

It follows that

$$\omega_{0,ess}((A+L)_0) \leq -\mu.$$

Since $DH(\bar{v})$ is compact, and $\omega_{0,ess}((A+L)_0) \leq \omega_0((A+L)_0) \leq -\mu$, by using the result in Thieme [53] or Ducrot, Liu and Magal [21, Theorem 1.2], we deduce that

$$\omega_{0,ess}((B_\alpha)_0) \leq \omega_{0,ess}((A+L)_0) \leq -\mu. \quad \blacksquare$$

Lemma 4.6 *We have*

$$\sigma((B_\alpha)_0) \cap \Omega = \sigma_p((B_\alpha)_0) \cap \Omega = \{\lambda \in \Omega : \Delta(\alpha, \lambda) = 0\}.$$

Proof. This Lemma follows directly from Lemma 4.5, Theorem 4.2 and Lemma 4.3. \blacksquare

5 Local stability

This section is devoted to study the local stability of the positive steady state \bar{v} . Recall that this positive equilibrium exists and is unique if and only if $R_0(\alpha) > 1$. Since the essential growth bound $\omega_{0,ess}((B_\alpha)_0) \leq -\mu < 0$, by the local stability result proved in Thieme [52] or in Magal and Ruan [39], it is sufficient to consider

$$\sigma((B_\alpha)_0) \cap \Omega = \{\lambda \in \Omega : \Delta(\alpha, \lambda) = 0\},$$

and to show that all the eigenvalues of the characteristic equation have negative real part.

Lemma 5.1 *If $R_0(\alpha) > 1$, then $\Delta(\alpha, 0) \neq 0$.*

Proof. After a simple of computation, we can deduce that

$$\Delta(\alpha, 0) = \ln R_0(\alpha),$$

and the result follows. ■

Theorem 5.2 *If*

$$1 < R_0 \leq e^2,$$

then the positive equilibrium \bar{v} of system (2.2) is locally asymptotically stable.

Proof. Consider the characteristic equation

$$1 = \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right) \int_0^{+\infty} \gamma(s) e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} ds,$$

where

$$\eta(\alpha) = \frac{\alpha}{R_0(\alpha)} (1 - \ln R_0(\alpha))$$

with

$$R_0(\alpha) = \alpha \left(1 + \frac{\varsigma}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}\right) \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu}\right)s} ds.$$

Thanks to Lemma 5.1, 0 is not an eigenvalue. It is easy to check that if $\text{Re}(\lambda) \geq 0$, then

$$\begin{aligned} \left|1 + \frac{\varsigma}{\lambda + \mu}\right| &< 1 + \frac{\varsigma}{\mu}, \\ \left|1 + \frac{\sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right| &< 1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}, \\ \text{Re}\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right) &> \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu}. \end{aligned}$$

Hence we can derive from the characteristic equation that

$$\begin{aligned} 1 &= \left| \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right) \int_0^{+\infty} \gamma(s) e^{-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} ds \right| \\ &< |\eta(\alpha)| \left(1 + \frac{\varsigma}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}\right) \int_0^{+\infty} \gamma(s) e^{-\text{Re}\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\lambda + \sigma^- + \varsigma + \mu}\right)s} ds \\ &< |\eta(\alpha)| \left(1 + \frac{\varsigma}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}\right) \int_0^{+\infty} \gamma(s) e^{-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu}\right)s} ds \\ &= |1 - \ln R_0(\alpha)|. \end{aligned}$$

So if

$$|1 - \ln R_0(\alpha)| \leq 1,$$

i.e.

$$0 \leq \ln R_0(\alpha) \leq 2,$$

then there will be no roots of the characteristic equation with non-negative real part, and the result follows. ■

6 Hopf bifurcation

In this section we will study the existence of Hopf bifurcation around the positive equilibrium \bar{v} when α is regarded as the bifurcation parameter of the system. Recall that by Theorem 5.2 we already know that the positive equilibrium \bar{v} of system (2.1) is locally asymptotically stable if

$$1 < R_0(\alpha) \leq e^2,$$

where

$$R_0(\alpha) := \alpha \left(1 + \frac{\zeta}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \zeta + \mu}\right) \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \zeta + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \zeta + \mu}\right)s} ds.$$

So in order to study Hopf bifurcation, we should consider the parameter α in the region $\{x \in \mathbb{R} : R_0(\alpha) > e^2\}$, i.e.

$$\alpha > e^2 \left(\left(1 + \frac{\zeta}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \zeta + \mu}\right) \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \zeta + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \zeta + \mu}\right)s} ds \right)^{-1}.$$

In this section, we will assume that

$$\gamma(x) = (x - \tau)^n e^{-\beta(x-\tau)} 1_{[\tau, +\infty)}(x)$$

with $\tau > 0$, $\beta \geq 0$, $n \in \mathbb{N}$, and

$$1_{[\tau, +\infty)}(x) = \begin{cases} 1, & \text{if } x \geq \tau, \\ 0, & \text{if } x \in [0, \tau). \end{cases}$$

We assume before that $\gamma(x) \in L_+^\infty(0, +\infty) \setminus \{0\}$, so the parameters in function $\gamma(\cdot)$ satisfy either $\tau > 0$, $\beta > 0$, $n \in \mathbb{N}$ or $\tau > 0$, $\beta = 0$, $n = 0$. Therefore, we make the following assumption for function $\gamma(\cdot)$.

Assumption 6.1

$$\gamma(x) = (x - \tau)^n e^{-\beta(x-\tau)} 1_{[\tau, +\infty)}(x)$$

with $\tau > 0$, $\beta > 0$, $n \in \mathbb{N}$ or $\tau > 0$, $\beta = 0$, $n = 0$.

Lemma 6.2 *Let Assumption 6.1 be satisfied. Then the characteristic equation becomes*

$$\begin{aligned} 1 &= \eta(\alpha) \left(1 + \frac{\zeta}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \zeta + \mu + \sigma^-}\right) \\ &\quad \times n! \exp\left(-\left(\lambda + \sigma^+ + \zeta + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \zeta + \mu + \sigma^-}\right)\tau\right) \\ &\quad \times \left(\beta + \lambda + \sigma^+ + \zeta + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \zeta + \mu + \sigma^-}\right)^{-(n+1)} \end{aligned}$$

for $\operatorname{Re}(\lambda) > -\mu$, where

$$\eta(\alpha) = \frac{\alpha}{R_0(\alpha)}(1 - \ln R_0(\alpha)) = \frac{1}{\chi}(1 - \ln(\alpha\chi))$$

with

$$R_0(\alpha) = \alpha\chi,$$

$$\begin{aligned} \chi &:= \left(1 + \frac{\varsigma}{\mu}\right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu}\right) \\ &\times n! \exp\left(-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\varsigma + \mu + \sigma^-}\right)\tau\right) \\ &\times \left(\beta + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\varsigma + \mu + \sigma^-}\right)^{-(n+1)}. \end{aligned}$$

Proof. We have

$$\begin{aligned} &\int_0^{+\infty} \gamma(s) \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)s\right) ds \\ &= \int_\tau^{+\infty} (s - \tau)^n e^{-\beta(s-\tau)} \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)s\right) ds \\ &= e^{\beta\tau} \int_\tau^{+\infty} (s - \tau)^n \exp\left(-\left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)s\right) ds \\ &= n! \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)\tau\right) \\ &\times \left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)^{-(n+1)}. \end{aligned}$$

In particular, taking $\lambda = 0$ in the above formula, we have

$$\begin{aligned} \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\sigma^- + \varsigma + \mu}\right)s} ds &= n! \exp\left(-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\varsigma + \mu + \sigma^-}\right)\tau\right) \\ &\times \left(\beta + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{\varsigma + \mu + \sigma^-}\right)^{-(n+1)}. \end{aligned}$$

Then the result follows by putting the above formulas into $\Delta(\alpha, \lambda) = 0$. \blacksquare

6.0.1 Existence of purely imaginary eigenvalues

Now we are in the position to look for purely imaginary roots $\lambda = \pm i\omega$ with $\omega > 0$.

Proposition 6.3 *Let Assumption 6.1 be satisfied, and $\varsigma > 0$, $\sigma^+ > 0$, $\sigma^- > 0$, $\mu > 0$, $\tau > 0$, $\beta \geq 0$, $n \in \mathbb{N}$ be fixed. Then the characteristic equation has a pair*

of purely imaginary solutions $\pm i\omega$ with $\omega > 0$ if and only if ω is a solution of equation

$$-\theta_1(\omega) + \arctan\left(\frac{\omega}{\mu}\right) + b(\omega)\tau + (n+1)\theta_2(\omega) = \pi + 2k\pi, k \in \mathbb{Z}, \quad (6.1)$$

and

$$\alpha = \frac{1}{\chi} \exp\left(1 + \chi\sqrt{\omega^2 + \mu^2} \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega) \times n!}\right),$$

where

$$a(\omega) := \varsigma + \mu + \frac{\sigma^+ [(\varsigma + \mu)(\varsigma + \mu + \sigma^-) + \omega^2]}{\omega^2 + (\varsigma + \mu + \sigma^-)^2}, \quad b(\omega) := \omega \left(1 + \frac{\sigma^+ \sigma^-}{\omega^2 + (\varsigma + \mu + \sigma^-)^2}\right),$$

$$r_1(\omega) := \sqrt{(a(\omega))^2 + (b(\omega))^2}, \quad r_2(\omega) := \sqrt{(\beta + a(\omega))^2 + (b(\omega))^2},$$

$$\theta_1(\omega) := \arctan\left(\frac{b(\omega)}{a(\omega)}\right), \quad \theta_2(\omega) := \arctan\left(\frac{b(\omega)}{\beta + a(\omega)}\right).$$

Moreover, for each $k \in \mathbb{N}$, there exists at least one solution ω_k of equation (6.1), and for each

$$\alpha = \alpha_k := \frac{1}{\chi} \exp\left(1 + \chi\sqrt{\omega_k^2 + \mu^2} \exp(a(\omega_k)\tau) \frac{r_2(\omega_k)^{(n+1)}}{r_1(\omega_k) \times n!}\right),$$

the characteristic equation has at least one pair of purely imaginary eigenvalues $\pm i\omega_k$ with $\omega_k > 0$. Furthermore

$$\omega_k \rightarrow +\infty \text{ and } \alpha_k \rightarrow +\infty, \text{ as } k \rightarrow +\infty.$$

Proof. Under Assumption 6.1 if the characteristic equation admits a pair of purely imaginary solutions $\pm i\omega$ with $\omega > 0$, then by Lemma 6.5, we have

$$1 = \eta(\alpha) \left(1 + \frac{\varsigma}{i\omega + \mu}\right) \left(1 + \frac{\sigma^+}{i\omega + \varsigma + \mu + \sigma^-}\right)$$

$$\times n! \exp\left(-\left(i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-}\right)\tau\right)$$

$$\times \left(\beta + i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-}\right)^{-(n+1)}.$$

Note that

$$\begin{aligned}
& i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-} \\
&= i\omega + \varsigma + \mu + \frac{\sigma^+ (i\omega + \varsigma + \mu)}{i\omega + \varsigma + \mu + \sigma^-} \\
&= \varsigma + \mu + \frac{\sigma^+ [(\varsigma + \mu)(\varsigma + \mu + \sigma^-) + \omega^2]}{\omega^2 + (\varsigma + \mu + \sigma^-)^2} \\
&+ i\omega \left(1 + \frac{\sigma^+ \sigma^-}{\omega^2 + (\varsigma + \mu + \sigma^-)^2} \right).
\end{aligned}$$

Now set

$$\begin{aligned}
a(\omega) &:= \varsigma + \mu + \frac{\sigma^+ [(\varsigma + \mu)(\varsigma + \mu + \sigma^-) + \omega^2]}{\omega^2 + (\varsigma + \mu + \sigma^-)^2}, \\
b(\omega) &:= \omega \left(1 + \frac{\sigma^+ \sigma^-}{\omega^2 + (\varsigma + \mu + \sigma^-)^2} \right).
\end{aligned}$$

Then

$$i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-} = a(\omega) + ib(\omega) := r_1(\omega) e^{i\theta_1(\omega)},$$

$$\begin{aligned}
& \left(1 + \frac{\varsigma}{i\omega + \mu} \right) \left(1 + \frac{\sigma^+}{i\omega + \varsigma + \mu + \sigma^-} \right) \\
&= \frac{i\omega + \mu + \varsigma}{i\omega + \mu} \times \frac{i\omega + \varsigma + \mu + \sigma^- + \sigma^+}{i\omega + \varsigma + \mu + \sigma^-} \\
&= \frac{1}{i\omega + \mu} \times \left(i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-} \right) \\
&= \frac{a(\omega) + ib(\omega)}{i\omega + \mu} = \frac{r_1(\omega) e^{i\theta_1(\omega)}}{i\omega + \mu},
\end{aligned}$$

$$\beta + i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega + \varsigma + \mu + \sigma^-} = \beta + a(\omega) + ib(\omega) := r_2(\omega) e^{i\theta_2(\omega)},$$

where

$$\begin{aligned}
r_1(\omega) &:= \sqrt{(a(\omega))^2 + (b(\omega))^2}, \\
r_2(\omega) &:= \sqrt{(\beta + a(\omega))^2 + (b(\omega))^2}, \\
\theta_1(\omega) &:= \arctan \left(\frac{b(\omega)}{a(\omega)} \right), \\
\theta_2(\omega) &:= \arctan \left(\frac{b(\omega)}{\beta + a(\omega)} \right).
\end{aligned}$$

So

$$\begin{aligned}
1 &= \eta(\alpha) \left(1 + \frac{\varsigma}{i\omega + \mu}\right) \left(1 + \frac{\sigma^+}{i\omega + \varsigma + \mu + \sigma^-}\right) \\
&\quad \times n! \exp\left(-\left(i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{i\omega + \varsigma + \mu + \sigma^-}\right)\tau\right) \\
&\quad \times \left(\beta + i\omega + \sigma^+ + \varsigma + \mu - \frac{\sigma^+\sigma^-}{i\omega + \varsigma + \mu + \sigma^-}\right)^{-(n+1)},
\end{aligned}$$

\Leftrightarrow

$$1 = \eta(\alpha) \frac{r_1(\omega) e^{i\theta_1(\omega)}}{\sqrt{\omega^2 + \mu^2} e^{i \arctan(\frac{\omega}{\mu})}} \times n! \exp(- (a(\omega) + ib(\omega)) \tau) \times \left(r_2(\omega) e^{i\theta_2(\omega)}\right)^{-(n+1)}.$$

By Theorem 5.2, in order to obtain pure imaginary eigenvalues for the characteristic equation, we must have $R_0(\alpha) > e^2$. Then by the definition of $\eta(\alpha)$ in equation (4.2) we have $\eta(\alpha) < 0$. Hence, the above equation is equivalent to

$$1 = -\eta(\alpha) \frac{r_1(\omega)}{\sqrt{\omega^2 + \mu^2}} \times n! \exp(-a(\omega)\tau) \times r_2(\omega)^{-(n+1)}, \quad (6.2)$$

$$-\theta_1(\omega) + \arctan\left(\frac{\omega}{\mu}\right) + b(\omega)\tau + (n+1)\theta_2(\omega) = \pi + 2k\pi, k \in \mathbb{Z}. \quad (6.3)$$

Denote by $f(\omega) := -\theta_1(\omega) + \arctan\left(\frac{\omega}{\mu}\right) + b(\omega)\tau + (n+1)\theta_2(\omega)$. Note that

$$b(\omega) \rightarrow +\infty, \text{ as } \omega \rightarrow +\infty,$$

$$\theta_1(\omega) \rightarrow \frac{\pi}{2}, \arctan\left(\frac{\omega}{\mu}\right) \rightarrow \frac{\pi}{2}, \theta_2(\omega) \rightarrow \frac{\pi}{2}, \text{ as } \omega \rightarrow +\infty,$$

it follows that

$$\lim_{\omega \rightarrow +\infty} f(\omega) = +\infty.$$

Moreover, since $f(\omega)$ is a continuous function with respect to ω and $f(0) = 0$, it can be obtained that equation (6.3) has at least one solution $\omega_k > 0$ for each $k \in \mathbb{N}$. Furthermore, we have

$$\omega_k \rightarrow +\infty, \text{ as } k \rightarrow +\infty.$$

Remember that

$$\eta(\alpha) = \frac{1}{\chi}(1 - \ln(\alpha\chi)).$$

Then it follows from (6.2) that

$$\frac{1}{\chi}(1 - \ln(\alpha\chi)) = -\sqrt{\omega^2 + \mu^2} \exp(a(\omega)\tau) \frac{(r_2(\omega))^{(n+1)}}{r_1(\omega) \times n!},$$

i.e.,

$$\alpha = \frac{1}{\chi} \exp \left(1 + \chi \sqrt{\omega^2 + \mu^2} \exp(a(\omega) \tau) \frac{(r_2(\omega))^{(n+1)}}{r_1(\omega) \times n!} \right).$$

■

Next we give the following lemma to show that for any given $\alpha > 0$ large enough, there exists at most one pair of purely imaginary solutions of the characteristic equation.

Lemma 6.4 *Let Assumption 6.1 be satisfied, and $\xi > 0, \varsigma > 0, \sigma^+ > 0, \sigma^- > 0, \mu > 0, \tau > 0, \beta \geq 0, n \in \mathbb{N}$ be fixed. Then there exists $\delta > 0$ large enough, such that for each $\alpha > \delta$, if*

$$\Delta(\alpha, i\omega_1) = \Delta(\alpha, i\omega_2) = 0, \omega_1, \omega_2 > 0,$$

then

$$\omega_1 = \omega_2.$$

In particular, if $\beta = n = 0$, then $\Delta(\alpha, i\omega_1) = \Delta(\alpha, i\omega_2) = 0, \omega_1, \omega_2 > 0$ implies $\omega_1 = \omega_2$ for each $\alpha > 0$.

Proof. By Proposition 6.3, we know that if $\Delta(\alpha, i\omega) = 0$, then

$$\alpha = \frac{1}{\chi} \exp \left(1 + \chi \sqrt{\omega^2 + \mu^2} \exp(a(\omega) \tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega) \times n!} \right),$$

In order to prove this lemma, we will first prove that $\frac{d\alpha}{d\omega} > 0$ for ω large enough, i.e.

$$\frac{d}{d\omega} \left(\sqrt{\omega^2 + \mu^2} \exp(a(\omega) \tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \right) > 0, \text{ for } \omega \text{ large enough.} \quad (6.4)$$

In fact, we have

$$\begin{aligned}
& \frac{d}{d\omega} \left(\sqrt{\omega^2 + \mu^2} \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \right) \\
&= \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \\
&+ \sqrt{\omega^2 + \mu^2} \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \times \frac{d}{d\omega} (a(\omega)) \tau \\
&+ \sqrt{\omega^2 + \mu^2} \exp(a(\omega)\tau) \frac{d}{d\omega} \left(\frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \right) \\
&= \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \\
&\times \left\{ \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} + \sqrt{\omega^2 + \mu^2} \times \frac{d}{d\omega} (a(\omega)) \tau \right. \\
&+ \left. \sqrt{\omega^2 + \mu^2} \left(\frac{(n+1) \frac{d}{d\omega} (r_2(\omega)) \times r_1(\omega) - r_2(\omega) \frac{d}{d\omega} (r_1(\omega))}{r_1(\omega) r_2(\omega)} \right) \right\} \\
&= \exp(a(\omega)\tau) \frac{r_2(\omega)^{(n+1)}}{r_1(\omega)} \times \Phi(\omega),
\end{aligned}$$

where

$$\begin{aligned}
\Phi(\omega) &:= \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} + \sqrt{\omega^2 + \mu^2} \times \frac{d}{d\omega} (a(\omega)) \tau \\
&+ \sqrt{\omega^2 + \mu^2} \left(\frac{(n+1) \frac{d}{d\omega} (r_2(\omega)) \times r_1(\omega) - r_2(\omega) \frac{d}{d\omega} (r_1(\omega))}{r_1(\omega) r_2(\omega)} \right) \\
&= \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} + \sqrt{\omega^2 + \mu^2} \times \frac{d}{d\omega} (a(\omega)) \tau \\
&+ (n+1) \frac{\sqrt{\omega^2 + \mu^2} \frac{d}{d\omega} (r_2(\omega))}{r_2(\omega)} - \frac{\sqrt{\omega^2 + \mu^2} \frac{d}{d\omega} (r_1(\omega))}{r_1(\omega)}.
\end{aligned}$$

So in order to prove equation (6.4), it is sufficient to show

$$\lim_{\omega \rightarrow +\infty} \Phi(\omega) > 0.$$

Since

$$\begin{aligned}
a(\omega) &= \varsigma + \mu + \frac{\sigma^+ [(\varsigma + \mu)(\varsigma + \mu + \sigma^-) + \omega^2]}{\omega^2 + (\varsigma + \mu + \sigma^-)^2}, \\
b(\omega) &= \omega \left(1 + \frac{\sigma^+ \sigma^-}{\omega^2 + (\varsigma + \mu + \sigma^-)^2} \right),
\end{aligned}$$

$$r_1(\omega) = \sqrt{(a(\omega))^2 + (b(\omega))^2},$$

$$r_2(\omega) = \sqrt{(\beta + a(\omega))^2 + (b(\omega))^2},$$

we have

$$\frac{da(\omega)}{d\omega} = \frac{2\omega\sigma^+\sigma^-(\varsigma + \mu + \sigma^-)}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)^2},$$

$$\begin{aligned} \frac{db(\omega)}{d\omega} &= 1 + \frac{\sigma^+\sigma^-}{\omega^2 + (\varsigma + \mu + \sigma^-)^2} - \frac{2\omega^2\sigma^+\sigma^-}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)^2} \\ &= \frac{\omega^4 + \omega^2(2(\varsigma + \mu + \sigma^-)^2 - \sigma^+\sigma^-) + (\varsigma + \mu + \sigma^-)^4 + \sigma^+\sigma^-(\varsigma + \mu + \sigma^-)^2}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)^2}, \end{aligned}$$

$$\frac{dr_1(\omega)}{d\omega} = \frac{1}{\sqrt{(a(\omega))^2 + (b(\omega))^2}} \left(a(\omega) \frac{d}{d\omega} (a(\omega)) + b(\omega) \frac{d}{d\omega} (b(\omega)) \right),$$

$$\frac{dr_2(\omega)}{d\omega} = \frac{1}{\sqrt{(\beta + a(\omega))^2 + (b(\omega))^2}} \left((\beta + a(\omega)) \frac{d}{d\omega} (a(\omega)) + b(\omega) \frac{d}{d\omega} (b(\omega)) \right).$$

Then we obtain

$$\lim_{\omega \rightarrow +\infty} a(\omega) = \sigma^+,$$

$$\lim_{\omega \rightarrow +\infty} \sqrt{\omega^2 + \mu^2} \frac{d}{d\omega} (a(\omega)) = 0,$$

$$\lim_{\omega \rightarrow +\infty} \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} = 1,$$

$$\lim_{\omega \rightarrow +\infty} \frac{da(\omega)}{d\omega} = 0, \quad \lim_{\omega \rightarrow +\infty} \frac{db(\omega)}{d\omega} = 1,$$

$$\lim_{\omega \rightarrow +\infty} \frac{\sqrt{\omega^2 + \mu^2}}{r_1(\omega)} = \lim_{\omega \rightarrow +\infty} \frac{\sqrt{\omega^2 + \mu^2}}{r_2(\omega)} = 1,$$

$$\lim_{\omega \rightarrow +\infty} \frac{b(\omega)}{\sqrt{(a(\omega))^2 + (b(\omega))^2}} = \lim_{\omega \rightarrow +\infty} \frac{b(\omega)}{\sqrt{(\beta + a(\omega))^2 + (b(\omega))^2}} = 1,$$

and it follows that

$$\lim_{\omega \rightarrow +\infty} \frac{dr_1(\omega)}{d\omega} = \lim_{\omega \rightarrow +\infty} \frac{dr_2(\omega)}{d\omega} = 1.$$

Therefore, we deduce

$$\lim_{\omega \rightarrow +\infty} \Phi(\omega) = \lim_{\omega \rightarrow +\infty} \left(1 + (n+1) \frac{dr_2(\omega)}{d\omega} - \frac{dr_1(\omega)}{d\omega} \right) = n+1 > 0,$$

and (6.4) is satisfied. Moreover, it is clear that

$$\alpha \rightarrow +\infty, \text{ as } \omega \rightarrow +\infty.$$

So we deduce that $\frac{d\alpha}{d\omega} > 0$ for α large enough.

In particular, if $\beta = n = 0$, then by Proposition 6.3, we know that if $\Delta(\alpha, i\omega) = 0$, then

$$\alpha = \mu \exp \left(\begin{array}{l} 1 + \left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu} \right) \tau \\ + \frac{\sqrt{\omega^2 + \mu^2}}{\mu} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \end{array} \right).$$

Obviously,

$$\begin{aligned} \frac{d\alpha}{d\omega} &= \exp \left(\begin{array}{l} 1 + \left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu} \right) \tau \\ + \frac{\sqrt{\omega^2 + \mu^2}}{\mu} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \end{array} \right) \times \\ &\frac{d}{d\omega} \left(\sqrt{\omega^2 + \mu^2} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \right), \end{aligned}$$

After some computations, we arrive at

$$\begin{aligned} &\frac{d}{d\omega} \left(\sqrt{\omega^2 + \mu^2} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \right) \\ &= \omega (\omega^2 + \mu^2)^{-\frac{1}{2}} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \\ &+ \sqrt{\omega^2 + \mu^2} \exp \left(\frac{\omega^2 \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)(\sigma^- + \varsigma + \mu)} \right) \\ &\times \frac{2\omega (\varsigma + \mu + \sigma^-) \sigma^- \sigma^+ \tau}{(\omega^2 + (\varsigma + \mu + \sigma^-)^2)^2} \\ &> 0. \end{aligned}$$

Thus, in this case, we have $\frac{d\alpha}{d\omega} > 0$ for each α satisfying $\Delta(\alpha, i\omega) = 0$, and the result follows. \blacksquare

6.0.2 Transversality condition

The aim of this section is to prove a transversality condition for the model.

Lemma 6.5 *If $R_0(\alpha) > 1$, $\text{Re}(\lambda) > -\mu$ and $\Delta(\alpha, \lambda) = 0$, then*

$$\frac{\partial \Delta(\alpha, \lambda)}{\partial \alpha} < 0.$$

Proof. We have

$$\begin{aligned}\Delta(\alpha, \lambda) &= 1 - \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-}\right) \\ &\quad \times \int_0^{+\infty} \gamma(s) \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)\right) ds,\end{aligned}$$

and

$$\begin{aligned}\frac{\partial \Delta(\alpha, \lambda)}{\partial \alpha} &= -\frac{d\eta(\alpha)}{d\alpha} \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-}\right) \\ &\quad \times \int_0^{+\infty} \gamma(s) \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)\right) ds \\ &= \frac{1}{R_0(\alpha)} \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-}\right) \\ &\quad \times \int_0^{+\infty} \gamma(s) \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)\right) ds.\end{aligned}$$

Thus if $\Delta(\alpha, \lambda) = 0$, we deduce that

$$\begin{aligned}\frac{\partial \Delta(\alpha, \lambda)}{\partial \alpha} &= \frac{1}{R_0(\alpha)} \times \frac{1}{\eta(\alpha)} \\ &= \frac{1}{R_0(\alpha)} \times \frac{1}{\frac{\alpha}{R_0(\alpha)} (1 - \ln R_0(\alpha))} \\ &= \frac{1}{\alpha (1 - \ln R_0(\alpha))},\end{aligned}$$

and the result follows. \blacksquare

Lemma 6.6 *Let Assumption 6.1 be satisfied, and $\xi > 0, \varsigma > 0, \sigma^+ > 0, \sigma^- > 0, \mu > 0, \tau > 0, \beta \geq 0, n \in \mathbb{N}$ be fixed. For each $k \geq 0$ large enough, let $\lambda_k = i\omega_k, \omega_k > 0$ be the purely imaginary root of the characteristic equation associated to $\alpha_k > 0$ (defined in Proposition 6.3), then we have*

$$\operatorname{Re} \frac{\partial \Delta(\alpha_k, i\omega_k)}{\partial \lambda} > 0.$$

Proof. Let Assumption 6.1 be satisfied, then the characteristic equation is

$\Delta(\alpha, \lambda) = 0$, where

$$\begin{aligned}\Delta(\alpha, \lambda) &= 1 - \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu}\right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-}\right) \\ &\quad \times n! \exp\left(-\left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right) \tau\right) \\ &\quad \times \left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-}\right)^{-(n+1)}.\end{aligned}$$

After some computations, we deduce that

$$\begin{aligned}
\frac{\partial \Delta(\alpha, \lambda)}{\partial \lambda} &= \eta(\alpha) \left(\frac{\varsigma}{(\lambda + \mu)^2} \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-} \right) + \left(1 + \frac{\varsigma}{\lambda + \mu} \right) \frac{\sigma^+}{(\lambda + \varsigma + \mu + \sigma^-)^2} \right) \\
&\times n! \exp \left(- \left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right) \tau \right) \\
&\times \left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right)^{-(n+1)} \\
&+ \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu} \right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-} \right) \\
&\times n! \exp \left(- \left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right) \tau \right) \\
&\times \left(1 + \frac{\sigma^+ \sigma^-}{(\lambda + \varsigma + \mu + \sigma^-)^2} \right) \tau \\
&\times \left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right)^{-(n+1)} \\
&+ \eta(\alpha) \left(1 + \frac{\varsigma}{\lambda + \mu} \right) \left(1 + \frac{\sigma^+}{\lambda + \varsigma + \mu + \sigma^-} \right) \\
&\times n! \exp \left(- \left(\lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right) \tau \right) \\
&\times (n+1) \left(\beta + \lambda + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{\lambda + \varsigma + \mu + \sigma^-} \right)^{-(n+2)} \\
&\times \left(1 + \frac{\sigma^+ \sigma^-}{(\lambda + \varsigma + \mu + \sigma^-)^2} \right).
\end{aligned}$$

Then if $\Delta(\alpha_k, i\omega_k) = 0$, we have

$$\begin{aligned}
1 &= \eta(\alpha_k) \left(1 + \frac{\varsigma}{i\omega_k + \mu} \right) \left(1 + \frac{\sigma^+}{i\omega_k + \varsigma + \mu + \sigma^-} \right) \\
&\times n! \exp \left(- \left(i\omega_k + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega_k + \varsigma + \mu + \sigma^-} \right) \tau \right) \\
&\times \left(\beta + i\omega_k + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega_k + \varsigma + \mu + \sigma^-} \right)^{-(n+1)}.
\end{aligned}$$

It follows that

$$\begin{aligned} \frac{\partial \Delta(\alpha_k, i\omega_k)}{\partial \lambda} &= \frac{\varsigma}{(i\omega_k + \mu)^2 + \varsigma(i\omega_k + \mu)} + \frac{\sigma^+}{(i\omega_k + \varsigma + \mu + \sigma^-)^2 + \sigma^+(i\omega_k + \varsigma + \mu + \sigma^-)} \\ &\quad + \left(1 + \frac{\sigma^+ \sigma^-}{(i\omega_k + \varsigma + \mu + \sigma^-)^2}\right) \tau \\ &\quad + (n+1) \left(\beta + i\omega_k + \sigma^+ + \varsigma + \mu - \frac{\sigma^+ \sigma^-}{i\omega_k + \varsigma + \mu + \sigma^-}\right)^{-1} \\ &\quad \times \left(1 + \frac{\sigma^+ \sigma^-}{(i\omega_k + \varsigma + \mu + \sigma^-)^2}\right). \end{aligned}$$

Since $\omega_k \rightarrow +\infty$ as $k \rightarrow +\infty$,

$$\lim_{k \rightarrow +\infty} \operatorname{Re} \left(\frac{\partial \Delta(\alpha_k, i\omega_k)}{\partial \lambda} \right) = \tau > 0,$$

and the result follows. \blacksquare

Theorem 6.7 *Let Assumption 6.1 be satisfied, and $\xi > 0, \varsigma > 0, \sigma^+ > 0, \sigma^- > 0, \mu > 0, \tau > 0, \beta \geq 0, n \in \mathbb{N}$ be fixed. For each $k \geq 0$ large enough, let $\lambda_k = i\omega_k, \omega_k > 0$ be the purely imaginary root of the characteristic equation associated to $\alpha_k > 0$ (defined in Proposition 6.3), then there exists $\rho_k > 0$ (small enough) and a C^1 -map $\widehat{\lambda}_k : (\alpha_k - \rho_k, \alpha_k + \rho_k) \rightarrow \mathbb{C}$ such that*

$$\widehat{\lambda}_k(\alpha_k) = i\omega_k, \quad \Delta(\alpha, \widehat{\lambda}_k(\alpha)) = 0, \quad \forall \alpha \in (\alpha_k - \rho_k, \alpha_k + \rho_k)$$

satisfying the transversality condition

$$\operatorname{Re} \left(\frac{d\widehat{\lambda}_k(\alpha_k)}{d\alpha} \right) > 0.$$

Proof. By Lemma 6.6 we can use the implicit function theorem around each $(\alpha_k, i\omega_k)$ provided by Proposition 6.3, and obtain that there exists $\rho_k > 0$ and a C^1 -map $\widehat{\lambda}_k : (\alpha_k - \rho_k, \alpha_k + \rho_k) \rightarrow \mathbb{C}$ such that

$$\widehat{\lambda}_k(\alpha_k) = i\omega_k, \quad \Delta(\alpha, \widehat{\lambda}_k(\alpha)) = 0, \quad \forall \alpha \in (\alpha_k - \rho_k, \alpha_k + \rho_k).$$

Moreover, we have

$$\frac{\partial \Delta(\alpha, \widehat{\lambda}_k(\alpha))}{\partial \alpha} + \frac{\partial \Delta(\alpha, \widehat{\lambda}_k(\alpha))}{\partial \lambda} \frac{d\widehat{\lambda}_k(\alpha)}{d\alpha} = 0, \quad \forall \alpha \in (\alpha_k - \rho_k, \alpha_k + \rho_k).$$

So

$$\frac{d\widehat{\lambda}_k(\alpha)}{d\alpha} = - \frac{1}{\frac{\partial \Delta(\alpha, \widehat{\lambda}_k(\alpha))}{\partial \lambda}} \frac{\partial \Delta(\alpha, \widehat{\lambda}_k(\alpha))}{\partial \alpha}, \quad \forall \alpha \in (\alpha_k - \rho_k, \alpha_k + \rho_k).$$

By using Lemma 6.5, we deduce that $\forall \alpha \in (\alpha_k - \rho_k, \alpha_k + \rho_k)$

$$\operatorname{Re} \left(\frac{d}{d\alpha} \widehat{\lambda}_k(\alpha) \right) > 0 \Leftrightarrow \operatorname{Re} \left(\frac{\partial \Delta(\alpha, \widehat{\lambda}_k(\alpha))}{\partial \lambda} \right) > 0.$$

In particular, we have

$$\operatorname{Re} \left(\frac{d}{d\alpha} \widehat{\lambda}_k(\alpha_k) \right) > 0 \Leftrightarrow \operatorname{Re} \left(\frac{\partial \Delta(\alpha_k, i\omega_k)}{\partial \lambda} \right) > 0.$$

By Lemma 6.6, the result follows. \blacksquare

6.1 Hopf bifurcations

$\omega_{0,ess}((B_\alpha)_0) < 0$ has been obtained in Lemma 4.5. The existence of a unique pair of pure imaginary eigenvalues of B_α has been obtained by Proposition 6.3 and Lemma 6.4. The simplicity of these pure imaginary eigenvalues follows directly from Lemmas 4.4 and 6.6. Moreover, the transversality condition is proved in Theorem 6.7. Hence by using the Hopf bifurcation Theorem proved in [37, Theorem 2.4], we obtain the following Hopf bifurcation result.

Theorem 6.8 (Hopf Bifurcation) *Let Assumptions 6.1 be satisfied. Then there exists $k_0 \in \mathbb{N}$ (large enough) such that for each $k \geq k_0$, the number α_k (defined in Proposition 6.3 is a Hopf Bifurcation point for system (2.1) parametrized by α , around the positive equilibrium \bar{v} given in Lemma 3.1.*

7 Summary and numerical simulations

We first summarize the main results of this study. They are essentially divided into three parts: (a) the existence of a positive equilibrium; (b) the local stability of this equilibrium; and (c) the Hopf bifurcation for this equilibrium. To be more precise, we obtain the following results.

- (i) There exists a positive equilibrium if and only if

$$R_0 > 1,$$

where

$$R_0(\alpha) := \alpha \left(1 + \frac{\varsigma}{\mu} \right) \left(1 + \frac{\sigma^+}{\sigma^- + \varsigma + \mu} \right) \int_0^{+\infty} \gamma(x) e^{-\left(\sigma^+ + \varsigma + \mu - \frac{\sigma^- \sigma^+}{\sigma^- + \varsigma + \mu} \right) s} ds.$$

Moreover, when it exists, it must be unique.

- (ii) The positive equilibrium is locally asymptotic stable if $1 < R_0 \leq e^2$.
(iii) To show the Hopf bifurcation we consider the following function $\gamma(x)$:

$$\gamma(x) = (x - \tau)^n e^{-\beta(x-\tau)} 1_{[\tau, +\infty)}(x)$$

for $\beta > 0, n \in \mathbb{N}, \tau > 0$, or $\beta = 0, n = 0, \tau > 0$.

Then regarding α as a parameter we obtain an infinity of Hopf bifurcating branches around the positive equilibrium. To be more precise, they are

$$\alpha_k = \frac{1}{\chi} \exp \left(1 + \chi \sqrt{\omega_k^2 + \mu^2} \exp(a(\omega_k)\tau) \frac{r_2(\omega_k)^{(n+1)}}{r_1(\omega_k) \times n!} \right) \quad (7.1)$$

for k large enough, where ω_k is a solution of

$$-\theta_1(\omega) + \arctan\left(\frac{\omega}{\mu}\right) + b(\omega)\tau + (n+1)\theta_2(\omega) = \pi + 2k\pi,$$

$$a(\omega_k) = \varsigma + \mu + \frac{\sigma^+ [(\varsigma + \mu)(\varsigma + \mu + \sigma^-) + \omega_k^2]}{\omega_k^2 + (\varsigma + \mu + \sigma^-)^2},$$

$$b(\omega_k) = \omega_k \left(1 + \frac{\sigma^+ \sigma^-}{\omega_k^2 + (\varsigma + \mu + \sigma^-)^2} \right),$$

$$r_1(\omega_k) = \sqrt{(a(\omega_k))^2 + (b(\omega_k))^2},$$

$$r_2(\omega_k) = \sqrt{(\beta + a(\omega_k))^2 + (b(\omega_k))^2}.$$

By using Proposition 6.3, we can investigate numerically the bifurcations in the space of parameters. Figures 2, 3, 4 and 5 are drawn to show the influence of σ^+, σ^- and ς on the bifurcation diagram.

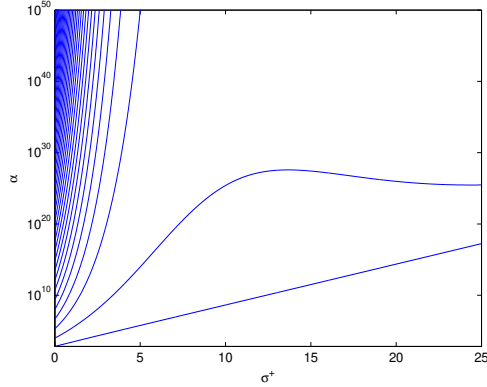


Figure 2: In this figure, we plot curves given by (7.1) in the (σ^+, α) -plane for $\sigma^- = 1, \varsigma = 1, \mu = 1, n = 0, \beta = 0$ and $\tau = 2$.

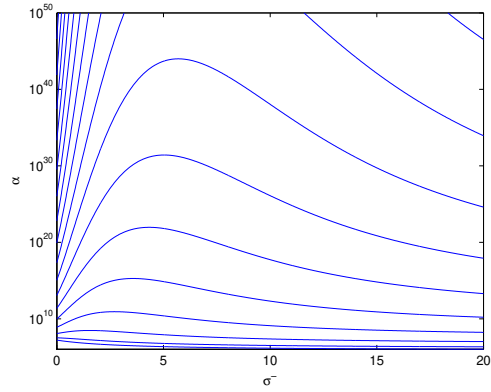


Figure 3: In this figure, we plot curves given by (7.1) in the (σ^-, α) -plane for $\sigma^+ = 1, \zeta = 1, \mu = 2, n = 1, \beta = 1$ and $\tau = 3$.

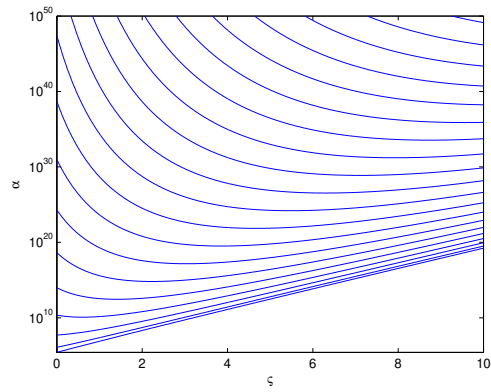


Figure 4: In this figure, we plot curves given by (7.1) in the (ζ, α) -plane for $\sigma^+ = 1, \sigma^- = 1, \mu = 2, n = 1, \beta = 1$ and $\tau = 3$.

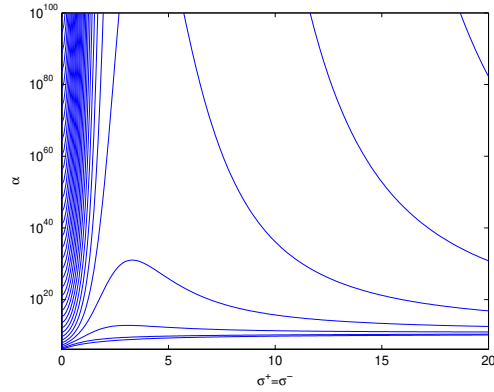


Figure 5: In this figure, assuming that $\sigma^+ = \sigma^-$, we plot curves given by (7.1) in the (σ^+, α) -plane for $\zeta = 1, \mu = 1, n = 1, \beta = 2$ and $\tau = 5$.

Next we provide some numerical simulations in order to illustrate the stability of the positive equilibrium and the Hopf bifurcation for system (2.1) when taking α as the bifurcation parameter. In the following figures, we choose the following parameters $\gamma(x) = 1_{[5,20]}(x), \sigma^+ = 0.01, \sigma^- = 0.05, \zeta = 0.01, \mu = 0.1$ and $\xi = 0.5$.

In Figure 6, we plot the total number of individuals in the stage of adults, growing juveniles and non-growing juveniles, i.e. L^1 -norm of $a(t, \cdot), j_g(t, \cdot)$ and $j_r(t, \cdot)$, respectively. Moreover, we plot the surface solutions of $j(t, s)$ for various values of α , see Figures 7, 8 and 9.

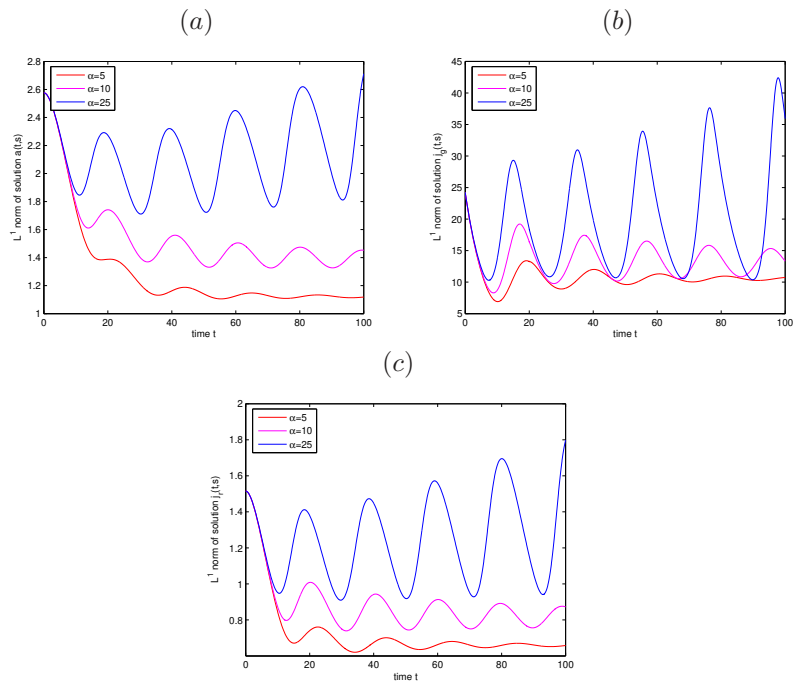


Figure 6: Figures (a), (b) and (c) describe the evolution of the L^1 norm respectively of $a(t, \cdot)$, $j_g(t, \cdot)$ and $j_r(t, \cdot)$ as a function of time.

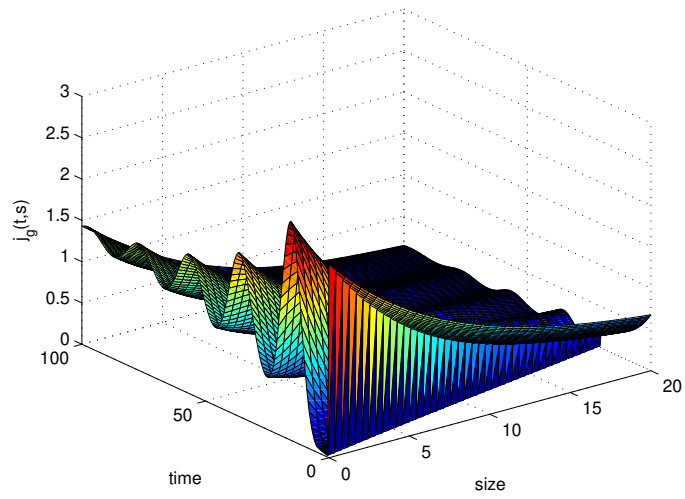


Figure 7: Surface solution of $j_g(t, s)$ when $\alpha = 5$.

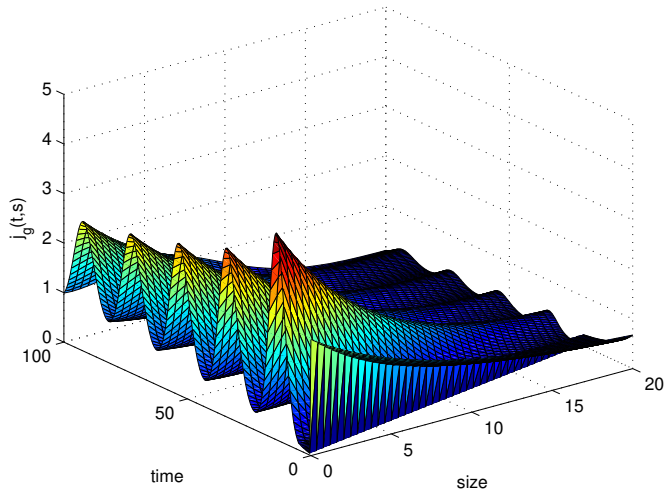


Figure 8: *Surface solution of $j_g(t, s)$ when $\alpha = 10$.*

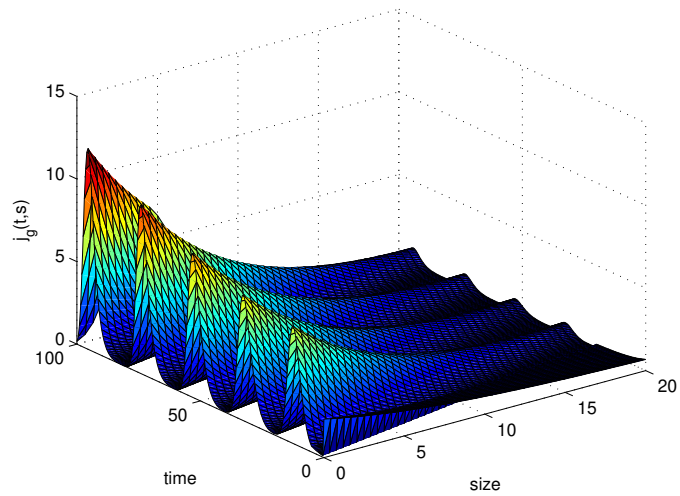


Figure 9: *Surface solution of $j_g(t, s)$ when $\alpha = 25$.*

It can be observed from the above figures that when α is relatively small, the positive equilibrium is locally asymptotically stable; when α is relatively large, the positive equilibrium becomes unstable. We conclude that increasing α from 5 to 25 tends to destabilize the positive equilibrium and leads to undamped oscillating solutions.

Next we choose parameter α carefully in order to observe the Hopf bifurcating periodic solution. In fact, if $\gamma(x) = 1_{[5,+\infty)}(x)$, $\sigma^+ = 0.01$, $\sigma^- = 0.05$, $\varsigma = 0.01$, $\mu = 0.1$ and $\xi = 0.5$, then by Proposition 6.3 and Lemma 6.4, the characteristic equation admits a unique pair of purely imaginary solution $\pm 0.3663i$ at $\alpha = \alpha_0 = 22.8509$. Moreover, when $\gamma(x) = 1_{[5,+\infty)}(x)$ and if $\Delta(\alpha, i\omega) = 0$, following the lines of Lemma 6.6, we can arrive at

$$\operatorname{Re}\left(\frac{\partial\Delta(\alpha, i\omega)}{\partial\lambda}\right) = \frac{\mu}{\omega^2 + \mu^2} + \left(1 + \frac{\sigma^+\sigma^-\left((\varsigma + \mu + \sigma^-)^2 - \omega^2\right)}{\left((\varsigma + \mu + \sigma^-)^2 + \omega^2\right)^2}\right)\tau.$$

In particular, under the chosen parameters, it can be derived that

$$\operatorname{Re}\left(\frac{\partial\Delta(\alpha_0, 0.3663i)}{\partial\lambda}\right) = 5.6919 > 0.$$

Consequently, the simplicity of eigenvalues $\pm 0.3663i$ follows. Moreover, according to the proof of Theorem 6.7, the transversality condition is also satisfied. From the above analysis, we can conclude that the number $\alpha = \alpha_0 = 22.8509$ should be a Hopf bifurcation point. Therefore, we choose $\alpha = 23 > \alpha_0$, and depict the following figures:

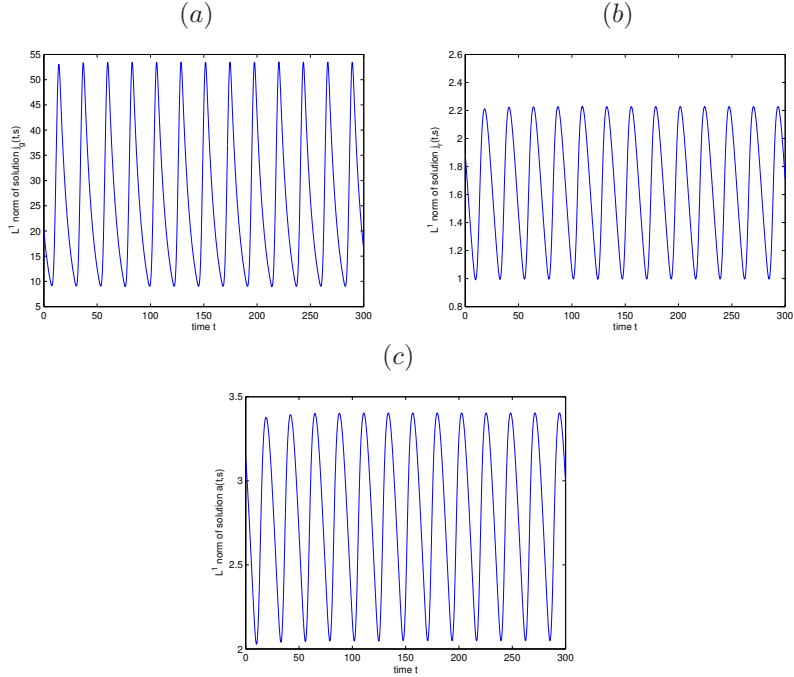


Figure 10: Figures (a), (b) and (c) describe the evolution of L^1 -norm of respectively $j_g(t, \cdot)$, $j_r(t, \cdot)$ and $a(t, \cdot)$ in function of time when $\alpha = 23$.

The above figures 6-10 indicate the existence of periodic solutions, which support our analysis.

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