Oscillations in Age-Structured Models of Consumer-Resource Mutualisms

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September 8, 2015

In Memory of Paul Waltman

Abstract

In consumer-resource interactions, a resource is regarded as a biotic population that helps to maintain the population growth of its consumer, whereas a consumer exploits a resource and then reduces its growth rate. Bi-directional consumer-resource interactions describe the cases where each species acts as both a consumer and a resource of the other, which is the basis of many mutualisms. In uni-directional consumer-resource interactions one species acts as a consumer and the other as a material and/or energy resource while neither acts as both. In this paper we consider an age-structured model for uni-directional consumer-resource mutualisms in which the consumer species has both positive and negative effects on the resource species, while the resource has only a positive effect on the consumer. Examples include a predator-prey system in which the prey is able to kill or consume predator eggs or larvae and the insect pollinator and the host plant relationship in which the plants provide food, seeds, nectar and other resources for the pollinators while the pollinators have both positive and negative effects on the plants. By carrying out local analysis and bifurcation analysis of the model, we discuss the stability of the positive equilibrium and show that under some conditions a non-trivial periodic solution through Hopf bifurcation appears when the maturation parameter passes through some critical values.

*Research was partially supported by NSFC (No. 11471044 and No. 11371058).

†Research was partially supported by the French Ministry of Foreign and European Affairs program France-China PFCC EGIDE (20932UL).

‡Research was partially supported by NSF (DMS-1412454).

Key words. Consumer-resource interaction, age-structure, stability, Hopf bifurcation, periodic solutions.
AMS Subject Classification. 35B32, 35Q92, 92D30

1 Introduction

Consumer-resource interactions are closely related the process of energy and/or nutrient transfer between a consumer organism and a resource. Here a resource is regarded as a biotic population that helps to maintain the population growth of its consumer, whereas a consumer exploits a resource and then reduces its growth rate. Modeling consumer-resource interactions and understanding the nonlinear dynamics of such interactions has been one of the most important and active topics in ecology in the last four decades (MacArthur [13], Murdoch et al. [21]). Traditionally a consumer-resource interaction is modeled by using $(+\ -)$ (predation, parasitism) type relation in which the consumer gains some material benefit at the cost of the resource, such as the classical predator-prey or parasite-host models (Rosenzweig and MarArthur [23], May [19]).

Recently, mutualism has been studied explicitly in terms of consumer-resource interactions, such as $(+\ 0)$ (commensalism), $(-\ 0)$ (amensalism), and $(+\ +)$ (mutualism), based on the balance between benefit and cost for the interacting species. For example, a mutualistic consumer exploits a resource (nutrient or nectar) supplied by another mutualistic species so that both the consumer and resource benefit from their interaction, which is described by a $(+\ +)$ type relation. Such mutualisms tend to be bi-directional, including coral mutualisms and mycorrhizal mutualisms (Holland and DeAngelis [7, 8]), in which each species acts as both a consumer and a resource of the other. For instance, the coral polyp passes nitrogen from captured prey to the photosynthetic zooxanthellae while the zooxanthellae provide energy in the form of glucose to the coral animals. Terrestrial plants and mycorrhizal fungi in the rhizosphere of the root system have a mutualistic relationship (Wang et al. [30]).

The uni-directional consumer-resource mutualisms are consistent with the traditional consumer-resource interaction, in which one species acts as a consumer and the other as a material and/or energy resource, while neither acts as both. Resources produced by a mutualistic species (N_1) attract and reward a consumer (N_2), which in the process of exploring the resource provinsions N_1 with a service of dispersal or defense (Holland and DeAngelis [7, 8], Wang et al. [30]). By assuming that the consumer species is age-structured, we consider the following consumer-resource interaction model coupled by an ordinary differential equation (ODE) and a partial differential equation (PDE)

$$
\begin{cases}
\dfrac{dN_1(t)}{dt} = N_1(t)\left[r - d_1 N_1(t) + \underbrace{\dfrac{\alpha_{12}\int_0^{+\infty}\beta(a)N_2(t,a)da}{\gamma_2 + \int_0^{+\infty}\beta(a)N_2(t,a)da}}_{\text{mutualist effect}} - \underbrace{\beta_1 \displaystyle\int_0^{+\infty}\beta(a)N_2(t,a)da}_{\text{consumtion effect}} \right], \\
\dfrac{\partial N_2(t,a)}{\partial t} + \dfrac{\partial N_2(t,a)}{\partial a} = -d_2 N_2(t,a), \quad a \geq 0, \\
N_2(t,0) = \underbrace{\dfrac{\alpha_{21}N_1(t)\int_0^{+\infty}\beta(a)N_2(t,a)da}{\gamma_1 + N_1(t)}}_{\text{flux of new borns}}, \\
N_1(0) = N_{10} \geq 0, \ \ N_2(0,\cdot) = N_{20} \in L^1_+\left((0,+\infty),\mathbb{R}\right),
\end{cases}
\tag{1.1}
$$

where $N_1(t)$ represents the density of the resource species at time t and $N_2(t,a)$ represents the density of the consumer species at time t with age a. The number r is the intrinsic growth rate of the resource species and $d_1 > 0$ represents a logistic type limitation of the resource species (i.e. limitation for space, foods, etc.) so that $r/d_1 > 0$ is its carrying capacity when in isolation from the consumer. The function $\beta(a)$ is the age-dependent maturation function so that

$$
A(t) := \int_0^{+\infty} \beta(a)N_2(t,a)da \tag{1.2}
$$

is the the number of matured (reproducing) consumers. The term $\dfrac{\alpha_{12}N_1(t)A(t)}{\gamma_2 + A(t)}$ describes the positive feedback on the growth of the resource species N_1 due to mutualistic interactions with the consumer species N_2, where α_{12} denotes the saturation level of the functional response of the consumer species and γ_2 denotes the half-saturation density of resource species; $\beta_1 N_1(t)A(t)$ represents the consumption level of resource species by matured consumer species. The number d_2 denotes the death rate of the consumer species. The term $\dfrac{\alpha_{21}N_1(t)A(t)}{\gamma_1 + N_1(t)}$ in the boundary condition denotes the new population births of the consumer species N_2 depending on resource supplied by N_1, which saturates with resource density (N_1) according to an Michaelis-Menton function, where α_{21} is the interaction strength and γ_1 is the half-saturation constant.

System (1.1) is a generalization of the ODE model (2.1) of Wang and DeAngelis [29] on uni-directional consumerresource interactions. As pointed out by Wang et al. [30], such interactions may be modeled by age-structured models. This is the motivation of this article. Moreover, Wang and DeAngelis [29] showed that there is no periodic orbit in their ODE model and all solutions converge to a steady state. We will show that under some conditions a nontrivial periodic solution of the age-structured model (1.1) appears through a Hopf bifurcation when the maturation parameter passes through some critical values.

The insect pollinator and the host plant relationship is an example of the uni-directional consumer-resource mutualisms as the insect provides no material resource to the plant (though it provides a pollination service), see Holland and DeAngelis [7]. Pollinators travel from their nest to a foraging patch, collecting food, flying back to their nests, and unloading food. Interacting with flowers individually, the pollinators remove nectar, contact pollen, and provide pollination service. Therefore, the plants provide food, seeds, nectar and other resources for the pollinators, while the pollinators have both positive and negative effects on the plants. The positive effect of pollinators on plants is described by the Michaelis-Meton functional response $\alpha_{12}N_1(t)A(t)/(\gamma_2 + A(t))$, where the parameter α_{12} is regarded as the plants efficiency in translating plant-pollinator interactions into fitness and α_{21} is the corresponding value for the pollinators; β_1 denotes the per-capita negative effect of pollinators on plants (Holland and DeAngelis [7], Wang, DeAngelis and Holland [31], and Mitchell et al. [20]).

Another example of consumer-resource interaction is introduced by Barkai and McQuaid [1] where they consider in some South African islands, rock lobsters feed on whelks, but in other areas whelks may be in such high abundance that they overwhelm and consume the lobsters. Also, Magalhães et al. [18] observed that small juvenile predatory mites may be killed by their thrips prey. Polis et al. [22] noted that 90 species of jellyfish and ctenophores eat fish eggs or larvae, while the older fish feed on these same species.

Before presenting our analysis and simulations of model (1.1), we make the following assumption.

Assumption 1.1 *Assume that*

$$\beta(a) = \beta^* 1_{[\tau,+\infty)}(a) = \begin{cases} \beta^*, & \text{if } a \geq \tau \\ 0, & \text{otherwise} \end{cases}$$

and

$$\int_0^{+\infty} \beta(a) e^{-d_2 a} da =: R_0,$$

where $\tau \geq 0, \beta^* > 0$ *and* $0 < R_0 < +\infty$.

Assumption 1.1 indicates that there is a maturation period $\tau > 0$, so that the maturation rate of the consumer species is $\beta^* > 0$ when the age a is less than τ and zero when the age a is greater than τ. We will use the maturation period τ as the bifurcation parameter to study the stability of the positive equilibrium and the existence of a Hopf bifurcation in the age-structured model (1.1).

The rest of the paper is organized as follows. in next section we recall the general Hopf bifurcation theorem for the semilinear Cauchy problem with a non-densely defined domain. Section 3 deals with the stability of the positive steady state and existence of Hopf bifurcation in the age-structured consumer-resource model (1.1). Some numerical simulations and a brief discussion are given in section 4.

2 Hopf Bifurcation Theorem for Nondensely Defined Cauchy Problems

For convenience, we recall the general Hopf bifurcation theorem we established in Liu et al. [11]. Consider the semilinear Cauchy problem:

$$\frac{du(t)}{dt} = Au(t) + F\left(\mu, u\left(t\right)\right), \forall t > 0, u(0) = x \in \overline{D\left(A\right)}, \tag{2.1}$$

where $\mu \in \mathbb{R}$ is the bifurcation parameter, $A : D(A) \subset X \to X$ is a linear operator on a Banach space X with $\overline{D(A)}$ not dense in X and A not necessary a Hille-Yosida operator, $F : \mathbb{R} \times \overline{D\left(A\right)} \to X$ is a C^k map with ($k \geq 4$). Denote by $A_Y : D(A_Y) \subset Y \to Y$ the part of A in Y, which is defined by

$$A_Y x = Ax, \;\; \forall x \in D(A_Y) = \left\{x \in D(A) \cap Y : Ax \in Y\right\}.$$

Set

$$X_0 := \overline{D\left(A\right)}.$$

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

$$A_0 x = Ax, \;\; \forall x \in D(A_0) = \left\{x \in D\left(A\right) : Ax \in X_0\right\}.$$

We denote by $\left\{T_A(t)\right\}_{t\geq 0}$ the strongly continuous semigroup of bounded linear operators on X (respectively $\left\{S_A(t)\right\}_{t\geq 0}$ the integrated semigroup) generated by A. The essential growth bound $\omega_{0,ess}\left(L\right) \in (-\infty, +\infty)$ of L is defined by

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

We make the following assumptions on the linear operator A and the nonlinear map F.

Assumption 2.1 *Assume that $A : D(A) \subset X \to X$ is a linear operator on a Banach space $(X, \|\cdot\|)$ such that there exist two constants $\omega_A \in \mathbb{R}$ and $M_A \geq 1$, such that $(\omega_A, +\infty) \subset \rho(A)$ and the following properties are satisfied*

(i) $\lim\limits_{\lambda\to+\infty} \left(\lambda I - A\right)^{-1} x = 0, \forall x \in X;$

(ii) $\|\left(\lambda I - A\right)^{-k}\|_{\mathcal{L}(X_0)} \leq \frac{M_A}{(\lambda-\omega_A)^k}, \forall \lambda > \omega_A, \forall k \geq 1.$

Assumption 2.2 *There exists a function $\delta : [0, +\infty) \to [0, +\infty)$ with*

$$\lim_{t(>0)\to 0} \delta\left(t\right) = 0,$$

such that for each $\tau > 0$ and $f \in C\left([0, \tau], X\right), t \to \int_0^t S_A(t - s)f(s)ds$ is continuously differentiable and

$$\left\|\frac{d}{dt}\int_0^t S_A(t-s)f(s)ds\right\| \leq \delta(t) \sup_{s\in[0,t]} \|f(s)\|, \;\; \forall t \in [0, \tau].$$

Assumption 2.3 *Let $\varepsilon > 0$, $F \in C^k((-\varepsilon,\varepsilon) \times B_{X_0}(0,\varepsilon); X), k \geq 4$. Assume that the following conditions are satisfied*

(i) $F(\mu,0) = 0, \forall \mu \in (-\varepsilon,\varepsilon)$, *and* $\partial_x F(0,0) = 0$.

(ii) (Transversality condition) *For each $\mu \in (-\varepsilon,\varepsilon)$, there exists a pair of conjugated simple eigenvalues of $(A + \partial_x F(\mu,0))_0$, denoted by $\lambda(\mu)$ and $\overline{\lambda(\mu)}$, such that*

$$\lambda(\mu) = \alpha(\mu) + i\omega(\mu),$$

the map $\mu \to \lambda(\mu)$ is continuously differentiable,

$$\omega(0) > 0,\ \alpha(0) = 0,\ \frac{d\alpha(0)}{d\mu} \neq 0,$$

and

$$\sigma(A_0) \bigcap i\mathbb{R} = \left\{\lambda(0), \overline{\lambda(0)}\right\}.$$

(iii) The essential growth bound of $\{T_{A_0}(t)\}_{t\geq 0}$ is strictly negative, that is,

$$\omega_{0,\mathrm{ess}}(A_0) < 0.$$

Now we can state the Hopf bifurcation theorem obtained in Liu et al. [11].

Theorem 2.4 *Let Assumptions 2.1-2.3 be satisfied. Then there exist $\varepsilon^* > 0$, three C^{k-1} maps, $\varepsilon \to \mu(\varepsilon)$ from $(0,\varepsilon^*)$ into $\mathbb{R}$, $\varepsilon \to x_\varepsilon$ from $(0,\varepsilon^*)$ into $\overline{D(A)}$, and $\varepsilon \to \gamma(\varepsilon)$ from $(0,\varepsilon^*)$ into $\mathbb{R}$, such that for each $\varepsilon \in (0,\varepsilon^*)$ there exists a $\gamma(\varepsilon)$-periodic function $u_\varepsilon \in C^k(\mathbb{R}, X_0)$, which is an integrated solution of (2.1) with the parameter value equals $\mu(\varepsilon)$ and the initial value equals x_ε. So for each $t \geq 0$, u_ε satisfies*

$$u_\varepsilon(t) = x_\varepsilon + A\int_0^t u_\varepsilon(l)dl + \int_0^t F(\mu(\varepsilon), u_\varepsilon(l))\, dl.$$

Moreover, we have the following properties

(i) There exist a neighborhood N of 0 in X_0 and an open interval I in $\mathbb{R}$ containing 0, such that for $\widehat{\mu} \in I$ and any periodic solution $\widehat{u}(t)$ in N with minimal period $\widehat{\gamma}$ close to $\frac{2\pi}{\omega(0)}$ of (2.1) for the parameter value $\widehat{\mu}$, there exists $\varepsilon \in (0,\varepsilon^*)$ such that $\widehat{u}(t) = u_\varepsilon(t+\theta)$ (for some $\theta \in [0,\gamma(\varepsilon))$), $\mu(\varepsilon) = \widehat{\mu}$, and $\gamma(\varepsilon) = \widehat{\gamma}$.

(ii) The map $\varepsilon \to \mu(\varepsilon)$ is a C^{k-1} function and we have the Taylor expansion

$$\mu(\varepsilon) = \sum_{n=1}^{[\frac{k-2}{2}]} \mu_{2n}\varepsilon^{2n} + O(\varepsilon^{k-1}),\ \forall \varepsilon \in (0,\varepsilon^*),$$

where $[\frac{k-2}{2}]$ is the integer part of $\frac{k-2}{2}$.

(iii) The period $\gamma(\varepsilon)$ of $t \to u_\varepsilon(t)$ is a C^{k-1} function and

$$\gamma(\varepsilon) = \frac{2\pi}{\omega(0)}[1 + \sum_{n=1}^{[\frac{k-2}{2}]} \gamma_{2n}\varepsilon^{2n}] + O(\varepsilon^{k-1}), \forall \varepsilon \in (0, \varepsilon^*),$$

where $\omega(0)$ is the imaginary part of $\lambda(0)$ defined in Assumption 2.3.

3 Equilibrium stability and Hopf bifurcation

In this section we investigate the stability and Hopf bifurcation of the age-structured consumer-resource model (1.1).

3.1 Rescaling time and age

In order to use the parameter τ as a bifurcation parameter (i.e. in order to obtain a smooth dependency of the system (1.1) with respect to τ) we first normalize τ in (1.1) by the time-scaling and age-scaling

$$\widehat{a} = \frac{a}{\tau} \text{ and } \widehat{t} = \frac{t}{\tau}$$

and consider the following distribution

$$\widehat{N}_1(\widehat{t}) = N_1(\tau\widehat{t}) \text{ and } \widehat{N}_2(\widehat{t},\widehat{a}) = \tau N_2(\tau\widehat{t},\tau\widehat{a}). \tag{3.1}$$

By dropping the hat notation we obtain, after this change of variable, the new system

$$\begin{cases} \frac{dN_1(t)}{dt} = \tau N_1(t)\left[r + \frac{\alpha_{12}\int_0^{+\infty}\beta(a)N_2(t,a)da}{\gamma_2+\int_0^{+\infty}\beta(a)N_2(t,a)da} - \beta_1\int_0^{+\infty}\beta(a)N_2(t,a)da - d_1N_1(t)\right], \\ \dfrac{\partial N_2(t,a)}{\partial t} + \dfrac{\partial N_2(t,a)}{\partial a} = -\tau d_2 N_2(t,a), \quad a \geq 0, \\ N_2(t,0) = \tau\frac{\alpha_{21}N_1(t)\int_0^{+\infty}\beta(a)N_2(t,a)da}{\gamma_1+N_1(t)}, \\ N_1(0) = N_{10} \geq 0, \ N_2(0,\cdot) = N_{20} \in L^1((0,+\infty),\mathbb{R}), \end{cases} \tag{3.2}$$

with the new function $\beta(a)$ defined by

$$\beta(a) = \beta^* 1_{[1,+\infty)}(a) = \begin{cases} \beta^*, & \text{if } a \geq 1 \\ 0, & \text{otherwise} \end{cases}$$

and

$$\int_\tau^{+\infty} \beta^* e^{-d_2 a}da = R_0 \Leftrightarrow \beta^*\frac{e^{-d_2\tau}}{d_2} = R_0 \Leftrightarrow \beta^* = R_0 d_2 e^{d_2\tau}$$

where $\tau \geq 0, \beta^* > 0$ and $0 < R_0 < +\infty$.

3.2 The transformation of the Cauchy problem

Consider the Banach space

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

with

$$\left\| \left(\begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \varphi \end{pmatrix} \right) \right\| = |\alpha_1| + |\alpha_2| + \|\varphi\|_{L^1((0,+\infty),\mathbb{R})}.$$

Let $\delta > 0$ be fixed. Define the linear operator $L : D(L) \to X$ by

$$L \left(\begin{pmatrix} N_1 \\ 0_{\mathbb{R}} \\ N_2 \end{pmatrix} \right) = \left(\begin{pmatrix} -\delta N_1 \\ -N_2(0) \\ -N_2' - \delta N_2 \end{pmatrix} \right)$$

with

$$D(L) = \mathbb{R} \times 0_{\mathbb{R}} \times W^{1,1}((0,+\infty), \mathbb{R}) \neq X.$$

Notice that L is non-densely defined since

$$X_0 := \overline{D(L)} = \mathbb{R} \times 0_{\mathbb{R}} \times L^1((0,+\infty), \mathbb{R}). \tag{3.3}$$

Let $F : \overline{D(L)} \to X$ be the nonlinear operator defined by

$$F \left(\begin{pmatrix} N_1 \\ 0_{\mathbb{R}} \\ N_2(.) \end{pmatrix} \right) = \begin{pmatrix} \tau N_1 \left[r - d_1 N_1 + \frac{\alpha_{12} A_2}{\gamma_2 + A_2} - \beta_1 A_2 + \delta N_1 \right] \\ \tau \frac{\alpha_{21} N_1 A_2}{\gamma_1 + N_1} \\ (-\tau d_2 + \delta) N_2(.) \end{pmatrix}.$$

where

$$A_2 := \int_0^{+\infty} \beta(a) N_2(a) da.$$

Then setting

$$x(t) = \left(\begin{pmatrix} N_1(t) \\ 0_{\mathbb{R}} \\ N_2(t,.) \end{pmatrix} \right),$$

we can rewrite system (3.2) as the following non-densely defined abstract Cauchy problem

$$\begin{cases} \dfrac{dx(t)}{dt} = Lx(t) + F(x(t)), \quad t \geq 0, \\ x(0) = \left(\begin{pmatrix} N_{10} \\ 0_{\mathbb{R}} \\ N_{20} \end{pmatrix} \right) \in \overline{D(L)}. \end{cases} \tag{3.4}$$

The global existence and uniqueness of solutions of system (3.4) follow from the results of Magal [14] and Magal and Ruan [16].

3.3 Existence of equilibria

If $\overline{x}(a) = \begin{pmatrix} \overline{N}_1 \\ 0_{\mathbb{R}} \\ \overline{N}_2(a) \end{pmatrix} \in X_0$ is an equilibrium of (3.4), we have

$$\begin{pmatrix} \overline{N}_1 \\ 0_{\mathbb{R}} \\ \overline{N}_2(a) \end{pmatrix} \in D(L) \text{ and } L \begin{pmatrix} \overline{N}_1 \\ 0_{\mathbb{R}} \\ \overline{N}_2(a) \end{pmatrix} + F \begin{pmatrix} \overline{N}_1 \\ 0_{\mathbb{R}} \\ \overline{N}_2(a) \end{pmatrix} = 0_X,$$

which is equivalent to

$$\begin{pmatrix} \tau \overline{N}_1 \left[r + \frac{\alpha_{12} \int_0^{+\infty} \beta(a) \overline{N}_2(a) da}{\gamma_2 + \int_0^{+\infty} \beta(a) \overline{N}_2(a) da} - \beta_1 \int_0^{+\infty} \beta(a) \overline{N}_2(a) da - d_1 \overline{N}_1 \right] \\ \tau \frac{\alpha_{21} \overline{N}_1 \int_0^{+\infty} \beta(a) \overline{N}_2(a) da}{\gamma_1 + \overline{N}_1} - \overline{N}_2(0) \\ -\tau d_2 \overline{N}_2(\cdot) - \overline{N}_2' \end{pmatrix} = 0_X.$$

By solving the above equations, we obtain the following lemma.

Lemma 3.1 *The system (3.4) has always the equilibria*

$$\overline{x}_1 = \begin{pmatrix} 0_{\mathbb{R}} \\ 0_{\mathbb{R}} \\ 0_{L^1((0,+\infty),\mathbb{R})} \end{pmatrix} \text{ and } \overline{x}_2 = \begin{pmatrix} \frac{r}{d_1} \\ 0_{\mathbb{R}} \\ 0_{L^1((0,+\infty),\mathbb{R})} \end{pmatrix}.$$

Furthermore, there exists a unique positive equilibrium of system (3.4)

$$\overline{x}(a) = \begin{pmatrix} \overline{N}_1 \\ 0_{\mathbb{R}} \\ \overline{N}_2(a) \end{pmatrix}$$

with

$$\overline{N}_1 = \frac{\gamma_1}{\alpha_{21} R_0 - 1},$$

$$\overline{N}_2(a) = \left(\frac{\alpha_{21} \overline{N}_1 \tau \left(\begin{array}{c} \left(\alpha_{12} - \beta_1 \gamma_2 - d_1 \overline{N}_1 + r\right) + \\ \sqrt{\left(\alpha_{12} - \beta_1 \gamma_2 - d_1 \overline{N}_1 + r\right)^2 + 4 \beta_1 \gamma_2 \left(r - d_1 \overline{N}_1\right)} \end{array} \right)}{2 \beta_1 \left(\gamma_1 + \overline{N}_1\right)} \right) e^{-d_2 \tau a}$$

if and only if

$$\alpha_{21} > \frac{d_1 \gamma_1 + r}{R_0 r}.$$

3.4 The characteristic equation

In order to get the linearized equation around the positive equilibrium $\overline{x}(a)$, we make the following change of variable

$$y(t) := x(t) - \overline{x}(a).$$

We obtain

$$\begin{cases} \dfrac{dy(t)}{dt} = Ly(t) + F(y(t) + \overline{x}(a)) - F(\overline{x}(a)), \quad t \geq 0, \\ y(0) = \begin{pmatrix} N_{10} - \overline{N}_1 \\ 0_{\mathbb{R}} \\ N_{20} - \overline{N}_2(a) \end{pmatrix} =: y_0 \in \overline{D(L)}. \end{cases} \tag{3.5}$$

Therefore the linearized equation of (3.5) around the equilibrium 0 is given by

$$\frac{dy(t)}{dt} = Ly(t) + DF(\overline{x})y(t) \ , \ t \geq 0, \ y(0) \in X_0.$$

Then (3.5) can be written as

$$\frac{dy(t)}{dt} = Ay(t) + H(y(t)), \quad t \geq 0, \tag{3.6}$$

where

$$A = L + DF(\overline{x})$$

is a linear operator and

$$H(y(t)) = F(y(t) + \overline{x}) - F(\overline{x}) - DF(\overline{x})y(t),$$

satisfying $H(0) = 0$, and $DH(0) = 0$.

Let

$$\upsilon := \min\{\delta, \tau d_2\}.$$

Denote

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

For $\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2(.) \end{array}\right) \end{array}\right) \in D(L)$, we have

$$
\begin{aligned}
& DF(\overline{x})\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2(.) \end{array}\right) \end{array}\right) \\
= & \left(\begin{array}{ccc} \delta-\tau d_1 \overline{N}_1 & 0 & 0 \\ \frac{\tau \alpha_{21} \gamma_1 \int_0^{+\infty} \beta(a) \overline{N}_2(a) da}{\left(\gamma_1+\overline{N}_1\right)^2} & 0 & 0 \\ 0 & 0 & -\tau d_2+\delta \end{array}\right)\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2(.) \end{array}\right) \end{array}\right) \\
+ & \left(\begin{array}{ccc} 0 & 0 & \tau \overline{N}_1\left[\frac{\alpha_{12} \gamma_2}{\left(\gamma_2+\int_0^{+\infty} \beta(a) \overline{N}_2(a) da\right)^2}-\beta_1\right] \\ 0 & 0 & \frac{\tau \alpha_{21} \overline{N}_1\left(\gamma_1+\overline{N}_1\right)}{\left(\gamma_1+\overline{N}_1\right)^2} \\ 0 & 0 & 0 \end{array}\right) \int_0^{+\infty} \beta(a)\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2(.) \end{array}\right) \end{array}\right) da .
\end{aligned}
$$

Let

$$
\widehat{L}\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2 \end{array}\right) \end{array}\right):=\left(\begin{array}{c} -\delta N_1 \\ \left(\begin{array}{c} -N_2(0) \\ -N_2^{\prime}-\tau d_2 N_2 \end{array}\right) \end{array}\right)
$$

and

$$
\begin{aligned}
& B\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2 \end{array}\right) \end{array}\right):= \\
= & \left(\begin{array}{ccc} \delta-\tau d_1 \overline{N}_1 & 0 & 0 \\ \frac{\tau \alpha_{21} \gamma_1 \int_0^{+\infty} \beta(a) \overline{N}_2(a) da}{\left(\gamma_1+\overline{N}_1\right)^2} & 0 & 0 \\ 0 & 0 & 0 \end{array}\right)\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2 \end{array}\right) \end{array}\right) \\
+ & \left(\begin{array}{ccc} 0 & 0 & \tau \overline{N}_1\left[\frac{\alpha_{12} \gamma_2}{\left(\gamma_2+\int_0^{+\infty} \beta(a) \overline{N}_2(a) da\right)^2}-\beta_1\right] \\ 0 & 0 & \frac{\tau \alpha_{21} \overline{N}_1\left(\gamma_1+\overline{N}_1\right)}{\left(\gamma_1+\overline{N}_1\right)^2} \\ 0 & 0 & 0 \end{array}\right) \int_0^{+\infty} \beta(a)\left(\begin{array}{c} N_1 \\ \left(\begin{array}{c} 0_{\mathbb{R}} \\ N_2 \end{array}\right) \end{array}\right) da .
\end{aligned}
$$

Then

$$
A=L+DF(\overline{x})=\widehat{L}+B
$$

By applying the results of Liu et al. [11], we obtain the following result.

Lemma 3.2 *For $\lambda \in \Omega$, $\lambda \in \rho(\widehat{L})$ and*

$$
(\lambda I-\widehat{L})^{-1}\left(\begin{array}{c} \alpha_1 \\ \left(\begin{array}{c} \alpha_2 \\ \psi \end{array}\right) \end{array}\right)=\left(\begin{array}{c} \beta \\ \left(\begin{array}{c} 0 \\ \varphi \end{array}\right) \end{array}\right)
$$

where

$$\left(\begin{array}{c}\alpha_1\\ \left(\begin{array}{c}\alpha_2\\ \psi\end{array}\right)\end{array}\right)\in X,\ \left(\begin{array}{c}\beta\\ \left(\begin{array}{c}0\\ \varphi\end{array}\right)\end{array}\right)\in D(L),$$

$$\beta=\frac{\alpha_1}{\lambda+\delta}$$

and

$$\varphi(a)=e^{-\int_0^a(\lambda+\tau d_2)dl}\alpha_2+\int_0^a e^{-\int_s^a(\lambda+\tau d_2)dl}\psi(s)ds.$$

Moreover, $\widehat{L}$ *is a Hille-Yosida operator, and*

$$\|(\lambda I-\widehat{L})^{-n}\|\leq\frac{1}{(\mathrm{Re}(\lambda)+\upsilon)^n},\ \forall\ \lambda\ \textit{with}\ \mathrm{Re}(\lambda)>-\upsilon,\ \forall\ n\geq 1. \tag{3.7}$$

Define the part of $\widehat{L}$ in $\overline{D(L)}$ by $\widehat{L}_0$,

$$\widehat{L}_0:D(\widehat{L}_0)\subset X\to X.$$

For $x\in D(\widehat{L}_0)=\{x\in D(L):\widehat{L}x\in\overline{D(L)}\}$, we have $\widehat{L}_0x=\widehat{L}x$. Then we get for $\left(\begin{array}{c}\beta\\ \left(\begin{array}{c}0\\ \varphi\end{array}\right)\end{array}\right)\in D(\widehat{L}_0)$,

$$\widehat{L}_0\left(\begin{array}{c}\beta\\ \left(\begin{array}{c}0\\ \varphi\end{array}\right)\end{array}\right)=\left(\begin{array}{c}-\delta\beta\\ \left(\begin{array}{c}0\\ \overline{L}_0\varphi\end{array}\right)\end{array}\right),$$

where $\overline{L}_0\varphi=-\varphi'-\tau d_2\varphi$ with

$$D(\overline{L}_0)=\{\varphi\in W^{1,1}((0,+\infty),\mathbb{R}):\varphi(0)=0\}.$$

Since $A=L+DF(\overline{x})=\widehat{L}+B$ and $B:\overline{D(L)}\subset X\longrightarrow X$ is a compact bounded linear operator. From (3.7), we obtain

$$\|T_{\widehat{L}_0}(t)\|\leq e^{-\upsilon t},\ \forall\ t\geq 0.$$

Thus we have

$$\omega_{0,\mathrm{ess}}(\widehat{L}_0)\leq\omega_0(\widehat{L}_0)\leq-\upsilon.$$

By applying the perturbation results in Thieme [27] or Ducrot, Liu and Magal [5], we obtain

$$\omega_{0,\mathrm{ess}}(A_0)\leq-\upsilon<0.$$

Hence we obtain the following proposition.

Proposition 3.3 *The linear operator* A *is a Hille-Yosida operator, and its part* A_0 *in* $\overline{D(A)}$ *satisfies*

$$\omega_{0,\mathrm{ess}}(A_0)<0.$$

Let $\lambda \in \Omega$. Since $\lambda I - \widehat{L}$ is invertible, it follows that $\lambda I - \left(\widehat{L} + B\right)$ is invertible if and only if $I - B\left(\lambda I - \widehat{L}\right)^{-1}$ is invertible. Moreover, when $I - B\left(\lambda I - \widehat{L}\right)^{-1}$ is invertible we have

$$\left(\lambda I - (\widehat{L} + B)\right)^{-1} = \left(\lambda I - \widehat{L}\right)^{-1}\left(I - B(\lambda I - \widehat{L})^{-1}\right)^{-1}.$$

Consider

$$(I - B(\lambda I - \widehat{L})^{-1})\begin{pmatrix}\alpha_1\\ \alpha_2\\ \psi\end{pmatrix} = \begin{pmatrix}\gamma_1\\ \gamma_2\\ \varphi\end{pmatrix}.$$

We have

$$\begin{cases}\left(1 - \frac{\delta - \tau d_1 \overline{N}_1}{\lambda + \delta}\right)\alpha_1 - \left(\tau \overline{N}_1\left[\frac{\alpha_{12}\gamma_2}{\left(\gamma_2 + \int_0^{+\infty}\beta(a)\overline{N}_2(a)da\right)^2} - \beta_1\right]\int_0^{+\infty}\beta(a)e^{-\int_0^a(\lambda + \tau d_2)dl}da\right)\alpha_2\\ = \gamma_1 - \int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\psi(s)dsda,\\ \left(1 - \tau\frac{\alpha_{21}\overline{N}_1}{\gamma_1 + \overline{N}_1}\int_0^{+\infty}\beta(a)e^{-\int_0^a(\lambda + \tau d_2)dl}da\right)\alpha_2 - \frac{\tau\alpha_{21}\int_0^{+\infty}\beta(a)\overline{N}_2(a)da\gamma_1}{\left(\gamma_1 + \overline{N}_1\right)^2(\lambda + \delta)}\alpha_1\\ = \gamma_2 + \tau\frac{\alpha_{21}\overline{N}_1}{\gamma_1 + \overline{N}_1}\int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\psi(s)dsda,\\ \psi = \varphi.\end{cases}.$$

Then we obtain the system

$$\begin{cases}\Delta(\lambda)\begin{pmatrix}\alpha_1\\ \alpha_2\end{pmatrix} = \begin{pmatrix}\gamma_1 - \int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\psi(s)dsda\\ \gamma_2 + \frac{\tau\alpha_{21}\overline{N}_1}{\gamma_1 + \overline{N}_1}\int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\psi(s)dsda\end{pmatrix},\\ \psi = \varphi,\end{cases}$$

where

$$\Delta(\lambda) = \begin{pmatrix}1 - \frac{\delta - \tau d_1\overline{N}_1}{\lambda + \delta} & -\tau\overline{N}_1\begin{pmatrix}\frac{\alpha_{12}\gamma_2}{\left(\gamma_2 + \int_0^{+\infty}\beta(a)\overline{N}_2(a)da\right)^2}\\ -\beta_1\end{pmatrix}\int_0^{+\infty}\beta(a)e^{-(\lambda + \tau d_2)a}da\\ -\frac{\tau\alpha_{21}\gamma_1\int_0^{+\infty}\beta(a)\overline{N}_2(a)da}{\left(\gamma_1 + \overline{N}_1\right)^2(\lambda + \delta)} & 1 - \frac{\tau\alpha_{21}\overline{N}_1}{\gamma_1 + \overline{N}_1}\int_0^{+\infty}\beta(a)e^{-(\lambda + \tau d_2)a}da\end{pmatrix}. \tag{3.8}$$

Whenever $\Delta(\lambda)$ is invertible, we have

$$\begin{pmatrix}\alpha_1\\ \alpha_2\end{pmatrix} = \Delta(\lambda)^{-1}\begin{pmatrix}\gamma_1 - \int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\varphi(s)dsda\\ \gamma_2 + \frac{\tau\alpha_{21}\overline{N}_1}{\gamma_1 + \overline{N}_1}\int_0^{+\infty}\beta(a)\int_0^a e^{-\int_s^a(\lambda + \tau d_2)dl}\varphi(s)dsda\end{pmatrix}.$$

From the above discussion, we obtain the following lemma.

Lemma 3.4 *The following results hold.*

(i) $\sigma(A) \cap \Omega = \sigma_P(A) \cap \Omega = \{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\}$.

(ii) If $\lambda \in \rho(A) \cap \Omega$, we have the following formula for the resolvent

$$(\lambda I - A)^{-1} \begin{pmatrix} \gamma_1 \\ \gamma_2 \\ \varphi \end{pmatrix} = \begin{pmatrix} \beta \\ \begin{pmatrix} 0 \\ \phi \end{pmatrix} \end{pmatrix}, \tag{3.9}$$

where

$$\beta := \frac{\alpha_1}{\lambda + \delta} \text{ and } \phi(a) := e^{-\int_0^a (\lambda + \tau d_2) dl} \alpha_2 + \int_0^a e^{-\int_s^a (\lambda + \tau d_2) dl} \varphi(s) ds$$

with

$$\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} := \Delta(\lambda)^{-1} \begin{pmatrix} \gamma_1 - \int_0^{+\infty} \beta(a) \int_0^a e^{-\int_s^a (\lambda + \tau d_2) dl} \varphi(s) ds da \\ \gamma_2 + \tau \frac{\alpha_{21} \overline{N}_1}{\gamma_1 + \overline{N}_1} \int_0^{+\infty} \beta(a) \int_0^a e^{-\int_s^a (\lambda + \tau d_2) dl} \varphi(s) ds da \end{pmatrix}$$

and $\Delta(\lambda)$ defined in (3.8).

Proof. Assume that $\lambda \in \Omega$ and $\det(\Delta(\lambda)) \neq 0$. Then $I - B(\lambda I - \widehat{L})^{-1}$ is invertible, and

$$(I - B(\lambda I - \widehat{L})^{-1})^{-1} \begin{pmatrix} \gamma_1 \\ \gamma_2 \\ \varphi \end{pmatrix} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \psi \end{pmatrix},$$

where

$$\begin{cases} \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = \Delta(\lambda)^{-1} \begin{pmatrix} \gamma_1 - \int_0^{+\infty} \beta(a) \int_0^a e^{-\int_s^a (\lambda + \tau d_2) dl} \varphi(s) ds da \\ \gamma_2 + \tau \frac{\alpha_{21} \overline{N}_1}{\gamma_1 + \overline{N}_1} \int_0^{+\infty} \beta(a) \int_0^a e^{-\int_s^a (\lambda + \tau d_2) dl} \varphi(s) ds da \end{pmatrix}, \\ \psi = \varphi. \end{cases}$$

Then we obtain (3.9), and we have $\{\lambda \in \Omega : \det(\Delta(\lambda)) \neq 0\} \subset \rho(A) \cap \Omega$, and $\sigma(A) \cap \Omega \subset \{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\}$. Assume $\lambda \in \Omega$ and $\det(\Delta(\lambda)) = 0$. We claim that we can find $\begin{pmatrix} N_1 \\ \begin{pmatrix} 0_{\mathbb{R}} \\ N_2 \end{pmatrix} \end{pmatrix} \in D(L) \setminus \{0\}$ such that

$$(\widehat{L} + B) \begin{pmatrix} N_1 \\ \begin{pmatrix} 0_{\mathbb{R}} \\ N_2 \end{pmatrix} \end{pmatrix} = \lambda \begin{pmatrix} N_1 \\ \begin{pmatrix} 0_{\mathbb{R}} \\ N_2 \end{pmatrix} \end{pmatrix} \tag{3.10}$$

if and only if we can find $\begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \psi \end{pmatrix} \in X \setminus \{0\}$ satisfying

$$[I - B(\lambda I - \widehat{L})^{-1}] \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \psi \end{pmatrix} = 0.$$

From the above argument this is equivalent to find $\begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \psi \end{pmatrix} \neq 0$ satisfying

$$\begin{cases} \Delta(\lambda) \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = 0, \\ \psi = 0, \end{cases}$$

which means that we can find a solution of (3.10) if and only if we can find $\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} \neq 0$ such that $\Delta(\lambda) \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = 0$. But by assumption $\det(\Delta(\lambda)) = 0$, there exists $\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} \neq 0$ such that $\Delta(\lambda) \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = 0$. So we can find $\begin{pmatrix} N_1 \\ \begin{pmatrix} 0_{\mathbb{R}} \\ N_2 \end{pmatrix} \end{pmatrix} \in D(A) \setminus \{0\}$ satisfying (3.10), and $\lambda \in \sigma_P(A)$. Hence we have $\{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\} \subset \sigma_P(A)$ and (i) follows. ■

Under the Assumption 1.1 and the condition $\alpha_{21} > \frac{d_1\gamma_1 + r}{R_0 r}$, it follows from (3.8) that

$$\det \Delta(\lambda) = \frac{\lambda^2 + \tau p_1 \lambda + \tau^2 p_2 + \left(\tau^2 p_3 + \tau p_4 \lambda\right) e^{-\lambda}}{(\lambda + \delta)(\lambda + \tau d_2)} =: \frac{f(\lambda)}{\widehat{f}(\lambda)} = 0,$$

where

$$\begin{aligned}
p_1 &= d_2 + d_1 \overline{N}_1, \\
p_2 &= d_1 \overline{N}_1 d_2, \\
p_3 &= -\frac{R_0 d_2 \alpha_{21} \overline{N}_1}{\gamma_1 + \overline{N}_1} d_1 \overline{N}_1 \\
&\quad - \left(\frac{\alpha_{12}\gamma_2 \overline{N}_1}{\left(\gamma_2 + \int_1^{+\infty} \beta^* \overline{N}_2(a)da\right)^2} - \beta_1 \overline{N}_1 \right) \frac{R_0 d_2 \gamma_1 \alpha_{21} \int_1^{+\infty} \beta^* \overline{N}_2(a)da}{\left(\gamma_1 + \overline{N}_1\right)^2}, \\
p_4 &= -\frac{R_0 d_2 \alpha_{21} \overline{N}_1}{\gamma_1 + \overline{N}_1}.
\end{aligned} \tag{3.11}$$

Let

$$\lambda = \tau\zeta.$$

Then we get

$$f(\lambda) = f(\tau\zeta) := \tau^2 g(\zeta) = \tau^2 \left(\zeta^2 + p_1\zeta + p_2 + (p_3 + p_4\zeta) e^{-\zeta\tau}\right).$$

It is easy to see that

$$\{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\} = \{\tau\zeta \in \Omega : g(\zeta) = 0\}.$$

3.5 The existence of a Hopf bifurcation

Let $\zeta = i\omega\,(\omega > 0)$ be a purely imaginary root of $g(\zeta) = 0$. Then we obtain

$$-\omega^2 + ip_1\omega + p_2 + p_3e^{-i\omega\tau} + ip_4\omega e^{-i\omega\tau} = 0,$$

where $p_i(i = 1, 2, 3, 4)$ are defined in (3.11). Separating the real and imaginary parts in the above equation, we obtain

$$\begin{cases} -\omega^2 + p_2 = -p_4\omega\sin(\omega\tau) - p_3\cos(\omega\tau), \\ p_1\omega = p_3\sin(\omega\tau) - p_4\omega\cos(\omega\tau). \end{cases} \tag{3.12}$$

Thus we have

$$\left(p_2 - \omega^2\right)^2 + \left(p_1\omega\right)^2 = p_3^2 + p_4^2\omega^2, \tag{3.13}$$

i.e.

$$\omega^4 + (p_1^2 - 2p_2 - p_4^2)\omega^2 + p_2^2 - p_3^2 = 0. \tag{3.14}$$

Set $\sigma = \omega^2$, (3.14) becomes

$$\sigma^2 + (p_1^2 - 2p_2 - p_4^2)\sigma + p_2^2 - p_3^2 = 0. \tag{3.15}$$

When $p_2^2 - p_3^2 < 0$, it is easy to know that Eq.(3.15) has only one positive real root

$$\sigma_0 = \frac{-(p_1^2 - 2p_2 - p_4^2) + \sqrt{(p_1^2 - 2p_2 - p_4^2)^2 - 4\,(p_2^2 - p_3^2)}}{2}.$$

So Eq.(3.14) has only one positive real root $\omega_0 = \sqrt{\sigma_0}$. From (3.12), we know that $g(\zeta) = 0$ with $\tau = \tau_k, k = 0, 1, 2, \cdots$ has a pair of purely imaginary roots $\pm i\omega_0$, where

$$\tau_k = \begin{cases} \dfrac{1}{\omega_0}[2k\pi + \arccos\dfrac{(p_3 - p_1p_4)\,\omega_0^2 - p_2p_3}{p_3^2 + p_4^2\omega_0^2}], & \text{if } \Theta \geq 0, \\ \dfrac{1}{\omega_0}[2(k+1)\pi - \arccos\dfrac{(p_3 - p_1p_4)\,\omega_0^2 - p_2p_3}{p_3^2 + p_4^2\omega_0^2}], & \text{if } \Theta < 0 \end{cases} \tag{3.16}$$

for $k = 0, 1, 2, \cdots$ and with

$$\Theta := \frac{p_1p_3\omega_0 + p_4\omega_0(\omega_0^2 - p_2)}{p_3^2 + p_4^2\omega_0^2}. \tag{3.17}$$

Lemma 3.5 *Let Assumption 1.1 be satisfied. Assume that* $\alpha_{21} > \frac{d_1\gamma_1 + r}{R_0 r}$ *and* $p_2^2 - p_3^2 < 0$. *Then*

$$\left.\frac{dg(\zeta)}{d\zeta}\right|_{\zeta = i\omega_0} \neq 0.$$

Therefore $\zeta = i\omega_0$ *is a simple root of* $g(\zeta) = 0$.

Proof. By the expression of $g(\zeta)=0$, we have

$$\left.\frac{dg(\zeta)}{d\zeta}\right|_{\zeta=i\omega_0} = i2\omega_0 + p_1 + p_4 e^{-i\omega_0\tau} - p_3\tau e^{-i\omega_0\tau} - ip_4\omega_0\tau e^{-i\omega_0\tau}$$

and

$$-\left(2\zeta + p_1 + p_4 e^{-\zeta\tau} - \tau\left(p_3 + p_4\zeta\right)e^{-\zeta\tau}\right)\frac{d\zeta(\tau)}{d\tau} = \zeta\left(p_3 + p_4\zeta\right)e^{-\zeta\tau}.$$

Thus if $\left.\dfrac{dg(\zeta)}{d\zeta}\right|_{\zeta=i\omega_0} = 0$, then

$$i\omega_0\left(p_3 + p_4 i\omega_0\right)e^{-i\omega_0\tau} = 0.$$

Since $\omega_0 > 0$,

$$p_3 + p_4 i\omega_0 = 0$$

which implies

$$p_3 = p_4 = 0.$$

However, $p_4 < 0$. Hence

$$\left.\frac{dg(\zeta)}{d\zeta}\right|_{\zeta=i\omega_0} \neq 0.$$

This completes the proof. ■

Lemma 3.6 *Let Assumption 1.1 be satisfied. Assume that* $\alpha_{21} > \frac{d_1\gamma_1 + r}{R_0 r}$ *and* $p_2^2 - p_3^2 < 0$. *Denote the root* $\zeta(\tau) = \alpha(\tau) + i\omega(\tau)$ *of* $g(\zeta) = 0$ *satisfying* $\alpha(\tau_k) = 0$, $\omega(\tau_k) = \omega_0$, *where* τ_k *is defined in (3.16). Then*

$$\alpha'(\tau_k) = \left.\frac{d\mathrm{Re}(\zeta)}{d\tau}\right|_{\tau=\tau_k} > 0.$$

Proof. For convenience, we study $\dfrac{d\tau}{d\zeta}$ instead of $\dfrac{d\zeta}{d\tau}$. From the expression of $g(\zeta) = 0$, we obtain

$$\left.\frac{d\tau}{d\zeta}\right|_{\zeta=i\omega_0} = \left.\left(-\frac{\tau}{\zeta} + \frac{p_4}{\zeta\left(p_3 + p_4\zeta\right)} - \frac{2\zeta + p_1}{\zeta\left(\zeta^2 + p_1\zeta + p_2\right)}\right)\right|_{\zeta=i\omega_0}.$$

By using (3.13), we have

$$\begin{aligned}\mathrm{Re}\left.\frac{d\tau}{d\zeta}\right|_{\zeta=i\omega_0} &= \frac{-p_4^2}{p_3^2 + p_4^2\omega_0^2} + \frac{2\omega_0^2 + \left(p_1^2 - 2p_2\right)}{p_1^2\omega_0^2 + (p_2 - \omega_0^2)^2}\\ &= \frac{2\omega_0^2 + p_1^2 - 2p_2 - p_4^2}{p_3^2 + p_4^2\omega_0^2}.\end{aligned}$$

Since

$$\omega_0^2 = \frac{-(p_1^2 - 2p_2 - p_4^2) + \sqrt{\left(p_4^2 - p_1^2 + 2p_2\right)^2 - 4\left(p_2^2 - p_3^2\right)}}{2},$$

we obtain

$$\begin{aligned} sign\Big(\frac{d\mathrm{Re}(\zeta)}{d\tau}\Big|_{\tau=\tau_k}\Big) &= sign\Big(\mathrm{Re}\Big(\frac{d\tau}{d\zeta}\Big|_{\zeta=i\omega_0}\Big)\Big) \\ &= sign\left(\frac{2\omega_0^2 + p_1^2 - 2p_2 - p_4^2}{p_3^2 + p_4^2\omega_0^2}\right) > 0. \end{aligned}$$

The lemma is proven. ∎

From the above discussion about $g(\zeta) = 0$, we know that for any $k \in N_0$, there exists τ_k such that the characteristic equation has two simple complex roots $\lambda(\tau) = \tau\zeta(\tau) = \tau\alpha(\tau) \pm i\tau\omega(\tau)$ that cross the imaginary axis transversely at $\tau = \tau_k$:

$$\tau_k\alpha(\tau_k) = 0, \quad \tau_k\omega(\tau_k) = \tau_k\omega_0,$$

$$sign\Big(\frac{d\mathrm{Re}(\lambda)}{d\tau}\Big|_{\tau=\tau_k}\Big) = \mathrm{Re}\zeta(\tau)|_{\tau=\tau_k} + \tau\left|\frac{d\mathrm{Re}(\zeta)}{d\tau}\right|_{\tau=\tau_k} > 0.$$

Summarizing the above results, we obtain the following conclusion.

Lemma 3.7 *Let Assumption 1.1 be satisfied. Assume that $\alpha_{21} > \frac{d_1\gamma_1 + r}{R_0 r}$, then there exists a unique positive equilibrium for system (1.1) given by*

$$\overline{N}_1 = \frac{\gamma_1}{\alpha_{21}R_0 - 1}, \overline{N}_2(a) = \overline{N}_2(0)e^{-d_2 a}$$

with

$$\overline{N}_2(0) := \left(\frac{\alpha_{21}\overline{N}_1\left(\ \left(\alpha_{12} - \beta_1\gamma_2 - d_1\overline{N}_1 + r\right) + \sqrt{\Delta}\ \right)}{2\beta_1\left(\gamma_1 + \overline{N}_1\right)}\right)$$

and

$$\Delta := \left(\alpha_{12} - \beta_1\gamma_2 - d_1\overline{N}_1 + r\right)^2 + 4\beta_1\gamma_2\left(r - d_1\overline{N}_1\right).$$

Assume in addition that

$$p_1 + p_4 > 0, p_2 + p_3 > 0 \text{ and } p_2 - p_3 < 0,$$

where $p_i (i = 1, 2, 3, 4)$ are defined in (3.11). Then we have the following alternatives:

(i) If $\tau \in [0, \tau_0)$ then the positive equilibrium of (1.1) is asymptotically stable.

(ii) If $\tau > \tau_0$, the positive equilibrium of (1.1) is unstable.

By Theorem 2.4, the above results can be summarized as the following Hopf bifurcation theorem for system (1.1).

Theorem 3.8 *Let Assumption 1.1 be satisfied. Assume that* $\alpha_{21} > \frac{d_1\gamma_1+r}{R_0 r}$ *and* $p_2^2 - p_3^2 < 0$*. Then there exists a sequence* $\{\tau_k\}_{k\geq 0} \subset (0,+\infty)$ *(defined by (3.16)), such that the consumer-resource interaction model (1.1) undergoes a Hopf bifurcation at the positive equilibrium* $(\overline{N}_1, \overline{N}_2)$ *whenever* τ *passes through* τ_k*. In particular, when* $\tau = \tau_k$*, a non-trivial periodic orbit bifurcates from the positive equilibrium* $(\overline{N}_1, \overline{N}_2)$*.*

We would like to mention that the stability of the bifurcated periodic solutions can be determined by using the normal form theory developed in our recent work Liu et al. [12].

4 Numerical Simulations and Discussions

Recently, Wang and DeAngelis [29] considered a specific uni-directional consumer-resource mutualism model in which the consumer species has both positive and negative effects on the resource species, while the resource has only a positive effect on the consumer, such as a predator-prey system in which the prey is able to kill or consume predator eggs or larvae.

In this article we generalized the ODE model of (2.1) of Wang and DeAngelis [29] to an age-structured model coupled by an ODE and a PDE, which describes uni-directional consumer-resource mutualism interactions with one species acting as a consumer and the other as a material and/or energy resource. Examples of such uni-directional consumer-resource mutualisms include the predator-prey systems in which the prey is able to kill or consume predator eggs or larvae, and the insect pollinator and the host plant relationship in which the plants provide food, seeds, nectar and other resources for the pollinators while the pollinators have both positive and negative effects on the plants. By carrying out local analysis and bifurcation analysis of the model, we discussed the stability of the positive equilibrium and found that under some conditions a non-trivial periodic solution through Hopf bifurcation appears when the maturation period of the consumer species τ passes through critical values $\tau = \tau_k$.

In the following, we provide some numerical simulations to illustrate the stability of the positive equilibrium and the existence of a Hopf bifurcation for system (1.1).

In the following, we choose parameters $r = 4$, $\alpha_{21} = \alpha_{12} = \beta_1 = d_1 = 0.5$, $d_2 = 1.0$, $\gamma_1 = \gamma_2 = 0.5$, and

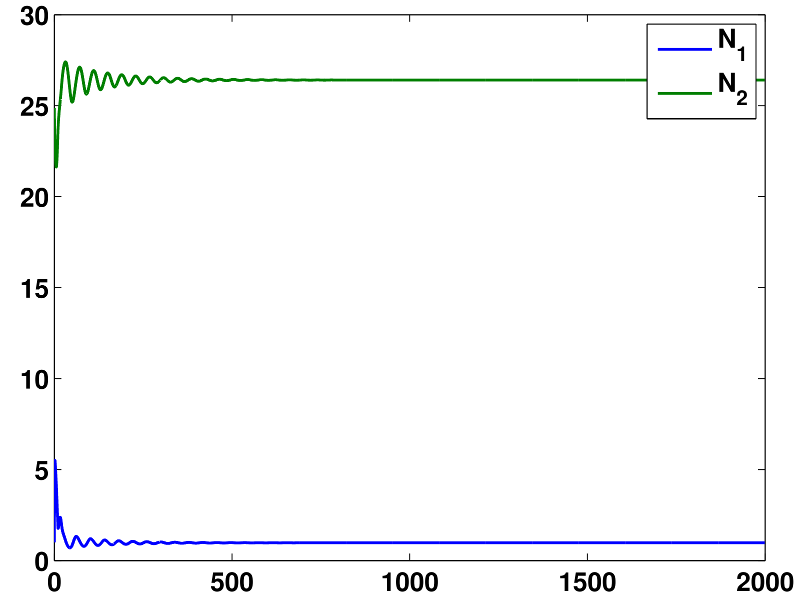
$$\beta(a) := \begin{cases} 3d_2 e^{d_2\tau}, \text{ if } a \geq \tau, \\ 0, \text{ if } a \in (0,\tau). \end{cases} \tag{4.1}$$

With these parameters value we obtain numerically that τ_0 is approximately equal to 12.55. Under the same initial values

$$N_1(0) = 1, N_2(0,a) = 5e^{-0.2a},$$

we choose $\tau = 10$ in Figure 1 and $\tau = 50$ in Figure 2, respectively, and obtain graphs $N_1(t)$ and $N_2(t,a)$ by using Matlab.

(a)



(b)

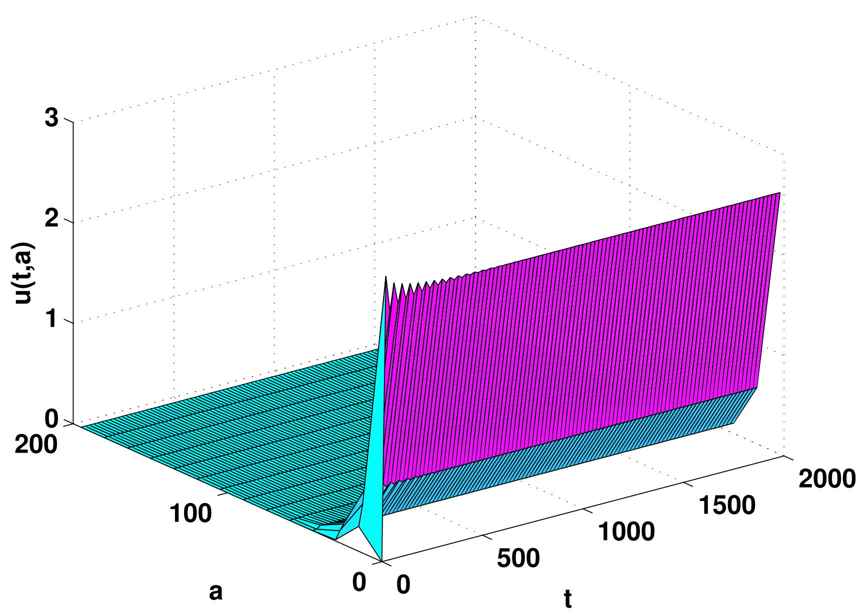
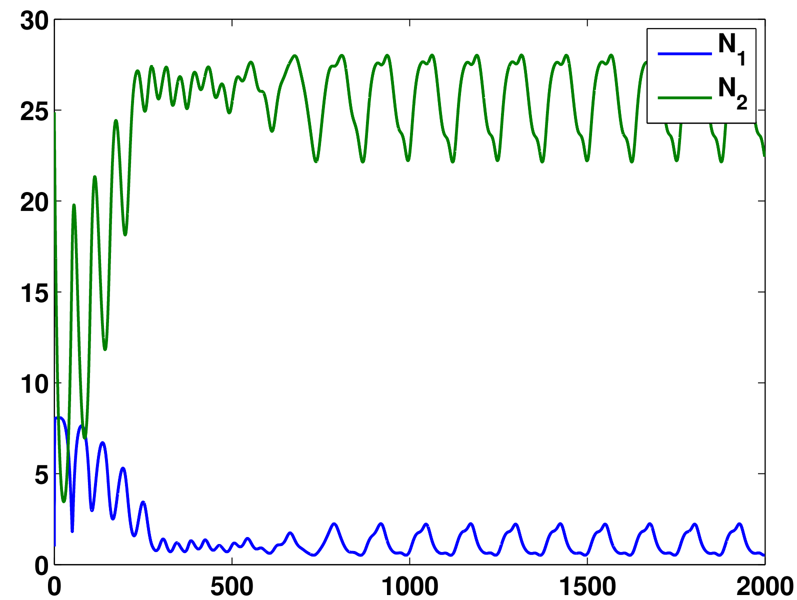


Figure 1: Numerical simulations of system (1.1) with $\tau = 10$. (a) Time series of $N_1(t)$ (blue curve) and $\int_0^{+\infty} N_2(t,a)da$ (green curve) which converge to their equilibrium values. (b) The age distribution and time series of $N_2(t,a)$.

(a)



(b)

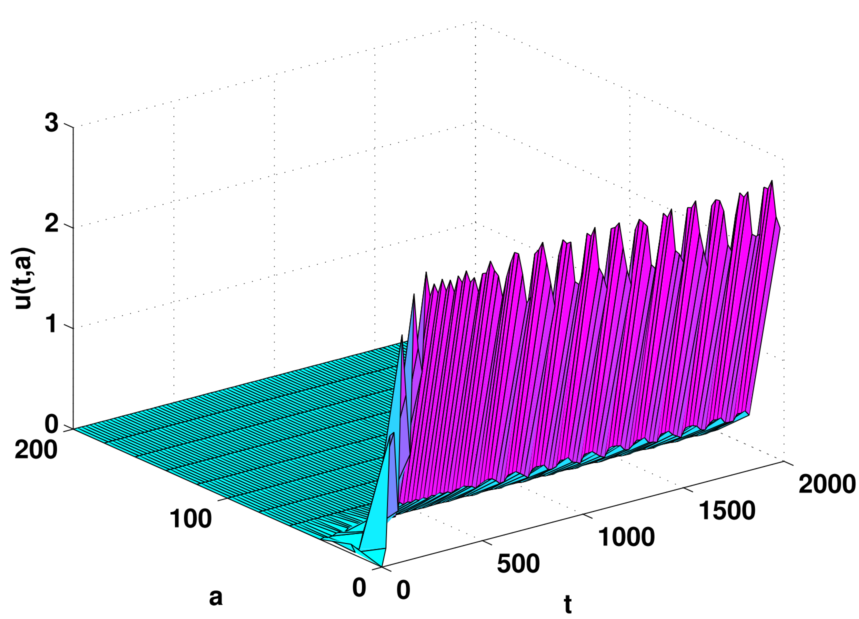


Figure 2: Numerical simulations of system (1.1) with $\tau = 50$. (a) Time series of $N_1(t)$ (blue curve) and $\int_0^{+\infty} N_2(t,a)da$ (green curve) which are oscillatory about their equilibrium values. (b) The age distribution of $N_2(t,a)$ which is periodic in time.

Fig. 1 and 2 demonstrate that the positive equilibrium $(\overline{N}_1, \overline{N}_2)$ of system (1.1) is asymptotically stable when the maturation period is less than its first critical value and system (1.1) undergoes a Hopf bifurcation and a non-trivial periodic solution bifurcates from the positive equilibrium when the maturation period passes through the critical value. Notice that the ordinary differential equation version of model (1.1) does not exhibit oscillatory behavior (Wang and DeAngelis [29]). It is well-known that periodic oscillations via limit cycles are common in predator-prey systems (May [19]). The existence of periodic solutions in system (1.1) via bifurcation demonstrates that the age-structured models has more dynamic possibilities than the unstructured model. It is shown that both consume and resource species are more likely to coexist in oscillatory modes when the maturation period of the consumer species is long enough.

It has been observed that Hopf bifurcation occurs in age-structured models (see Cushing [3], Magal and Ruan [17], and the references cited therein). Recently, by re-writing age-structured systems as nondensely defined Cauchy problems, we established a Hopf bifurcation theorem for a general class of age-structured models (Liu et al. [11]). Due to the complexity of analysis and computations, applications of this general Hopf bifurcation theorem mainly focus on single species age-structured models. In this article we applied the techniques and results to a uni-directional consume-resource mutualism model coupled of one ordinary differential equation and one age-structured equation. We would like to point out that, due to the form of the age-dependent maturation function $\beta(a)$, system (1.1) could be handled by reducing it to a system of delay differential equations. Nevertheless, we would like to use our recent results and techniques to treat this model in the age-structured model setting and believe that similar results hold for more general forms of age-dependent maturation functions. Moreover, such a model structure is similar to the classical predator-prey interaction systems, but is different. The nonlinear dynamics of age-structured predator-prey population models have been studied by many researchers, see for example, Cushing [2, 3], Cushing and Saleem [4], Gurtin and Levine [6], Levine [9], Li [10], Saleem [25], and Venturino [28], and various interesting asymptotical behaviors including bifurcation have been observed. It will be very interesting to apply the general Hopf bifurcation theorem in Liu et al. [11] to study Hopf bifurcations in predator-prey population models when both predator and prey species are age-structured.

Acknowledgement. We thank the reviewers for their valuable comments and suggestions which helped us to improve the presentation of the paper..

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