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Nonlinear Oscillations in a three-Dimensional Competition with Inhibition Responses in a Bio-Reactor

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Abstract: A three-dimensional bio-reactor model of exploitative competition of two predator organisms with inhibition responses for the same renewable organism with reproductive properties is considered. By using a Lyapunov function and the center manifold theorem the global stability, the existence of Hopf bifurcation and limit cycles are proved. This result is useful in understanding the nonlinear oscillation phenomena in bio-engineering.

Keywords: bio-reactor; center manifold theorem; Lyapunov function; Hopf bifurcation; limit cycles; nonlinear oscillation.

1. Introduction

The oscillation is an important phenomenon in many natural systems in biology, ecology, bio-chemistry and bio-engineering. A typical example is the cyclic behavior in bio-reactors. In this paper, we study the competition of two predators competes exploitatively for a single prey species in a bio-reactor. When the prey species is non-renewable, many results have been reported (see [1,2], for example). But there are not so many results reported for the case when the prey species is renewable with reproductive properties --- a more classic prey. Examples of competing for a renewable resource with some numerical simulations can be found in Hsu, Hubbell and Waltman [3,4], McGehee and Armstrong [5], and Koch [6]. In most of such models, it is assumed that the predators consume the nutrient (prey) and the consumed nutrient converted to growth is proportional to consumption. Nutrient uptake (consumption) is usually taken to be of the Monod (or Michaelis-Menten) form: $mxS/(a+S)$ [3,4]. But in reality, other prototypes of functional responses are also possible [2,7]. In population modeling, the global stability of the model is often established by constructing a Lyapunov function. Once the Lyapunov function is obtained, the global stability follows directly from the LaSalle's invariant principle [2,9,10]. Then from the global asymptotical stability the Hopf bifurcation follows by the center manifold theorem.

A limit cycle of a mathematical model is related to the nonlinear phenomena of the corresponding system. Thus, the study of limit cycles is helpful in understanding the oscillation of the nonlinear system. The existence of limit cycles is often follows from the Hopf bifurcation. It is known that to establish the existence of limit cycles in $n-$dimensional system for $n \geq 3$ is quite difficult. Because the powerful tools in the plane systems like Poincare-Bendixon theorem cannot be applied

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directly to the ones of $n \geq 3$ (see counter-examples [11,12]). Therefore, the method we use in this paper is also interesting in mathematical analysis.

The Michaelis- Menten type of response is monotonic, but the inhibition type is not. In the literature there are not so many results reported for the models with non-monotonic response functions. The study of the three-dimensional competition model with the non-monotonic inhibition response certainly has some interests in bio-mathematical modeling. In this paper, a three-dimensional bio-reactor model of exploitative competition of two predator organisms with inhibition responses for the same renewable organism with reproductive properties is considered. We shall use the Lyapunov function method and the center manifold theorem to prove the global stability, the existence of Hopf bifurcation and limit cycles.

We would like to mention that the Ardito-Ricciardi type Layapunov function for the system discussed in this paper was used before by Chiu and Hsu in the three-level food-chain model [17,18].

The model and our main results are presented in the next section, and the proofs are listed in the Appendix.

2. The Model and Main Theorems

The competition model of two predators competes exploitatively for a single prey species in chemostat with inhibition response and different death rates takes the form:

$$\begin{aligned}
&\frac{dS}{dt} = \gamma S(1-\frac{S}{K}) - \frac{m_1 d_1 S}{(a_1+S)(b_1+S)}\frac{x_1}{\delta_1} - \frac{m_2 d_2 S}{(a_2+S)(b_2+S)}\frac{x_2}{\delta_2},\\
&\frac{dx_1}{dt} = \left(\frac{m_1 d_1 S}{(a_1+S)(b_1+S)} - d_1\right)x_1,\\
&\frac{dx_2}{dt} = \left(\frac{m_2 d_2 S}{(a_2+S)(b_2+S)} - d_2\right)x_2,\\
&S(0)>0,\ x_1(0)>0,\ x_2(0)>0.
\end{aligned} \tag{1}$$

The meaning of the symbols is listed in the following table:

Table 1. Meaning of the symbols

Mathematical Symbol	Biological Meaning
$x_i,\ i=1,2$	two predators
S	prey species
γ	growth rate
K	carrying capacity of the renewable resource S
$a_i, b_i,\ i=1,2$	half saturation constants
$d_i,\ i=1,2$	death rate of predator x_i
$m_i,\ i=1,2$	maximum predation rate
$\delta_i,\ i=1,2$	yield constant for x_i

Notice that in model (1), the predators: x_i consumes the prey with functional response of inhibition type $\frac{m_i d_i S}{(a_i+S)(b_i+S)}$, $i=1,2.$ For simplicity, we will assume the yield constant $\delta_i = 1,\ i=1,2$ in the following discussion because, if not, a variable transformation can always make the constant yield as 1.

We shall use a corollary to the center manifold theorem to prove the existence of the

Hopf bifurcation and the limit cycles of the system.

Our discussion is on the set $R_+^3 = \{(S, x_1, x_2) | S \geq 0,\ x_1 \geq 0,\ x_2 \geq 0\}$ with the following basic assumptions for the parameters: for each $i = 1, 2$,

(B_1): $\sqrt{m_i} \geq \sqrt{a_i} + \sqrt{b_i}$;

(B_2): $m_i - a_i - b_i + \sqrt{(m_i - a_i - b_i)^2 - 4a_i b_i} > 2K$;

(B_3): $K > a_i + b_i$;

The purpose of these basic assumptions is to guarantee that our discussion is limited in the first quadrant due to biological reasons. For example, because of (B_2), only the usual three equilibrium points in R_+^3 : $E_0 : (K, 0, 0)$, $E_1 : (\lambda_1, h_1(\lambda_1), 0)$ and $E_1 : (\lambda_2, 0, h_2(\lambda_2))$ need to be considered.

It is easy to verify that the solutions of system (1) are bounded and positive for all $t > 0$, and $S(t) \leq K$ for t sufficient large [1,3,7].

For each $i = 1, 2$, λ_i and $\lambda_i^{'}$ are the solutions of the equation

$$\frac{m_i d_i S}{(a_i + S)(b_i + S)} - d_i = 0. \tag{2}$$

Then

$$\lambda_i = \frac{1}{2}\left(m_i - a_i - b_i - \sqrt{(m_i - a_i - b_i)^2 - 4a_i b_i}\right),$$
$$\lambda_i^{'} = \frac{1}{2}\left(m_i - a_i - b_i + \sqrt{(m_i - a_i - b_i)^2 - 4a_i b_i}\right). \tag{3}$$

By (B_2), $\lambda_i^{'} > K$, so there are only three equilibrium points in R_+^3 that we need to consider: $E_0 : (K, 0, 0)$, $E_1 : (\lambda_1, h_1(\lambda_1), 0)$ and $E_1 : (\lambda_2, 0, h_2(\lambda_2))$, where for each i, $h_i(S)$ is defined as

$$h_i(S) = \frac{\gamma}{m_i d_i}(1 - \frac{S}{K})(a_i + S)(b_i + S), \quad i = 1, 2. \tag{4}$$

It follows that λ_i , $i = 1, 2$, represent the "break-even" concentrations, the values of the nutrient where the derivatives of x_i, $i = 1, 2$ are zeros. And, $x_1 = h_1(S)$ is the prey isocline when $x_2 = 0$, and so is $x_2 = h_2(S)$ when x_1 is absent.

Regarding the prey isociline $x_1 = h_1(S)$, as shown in Figure 1, there exists an $S_1 \in (0, K)$, such that $h_1^{'}(S_1) = 0$, where

$$S_1 = \left(K - a_1 - b_1 + \sqrt{K^2 + a_1^2 + b_1^2 - a_1 b_1 + K a_1 + K b_1}\right)/3. \tag{5}$$

Also, there exists an $\overline{S}_1 \in (S_1, K)$ such that $h_1(\overline{S}_1) = h_1(0) = \gamma a_1 b_1 / m_1 d_1$.

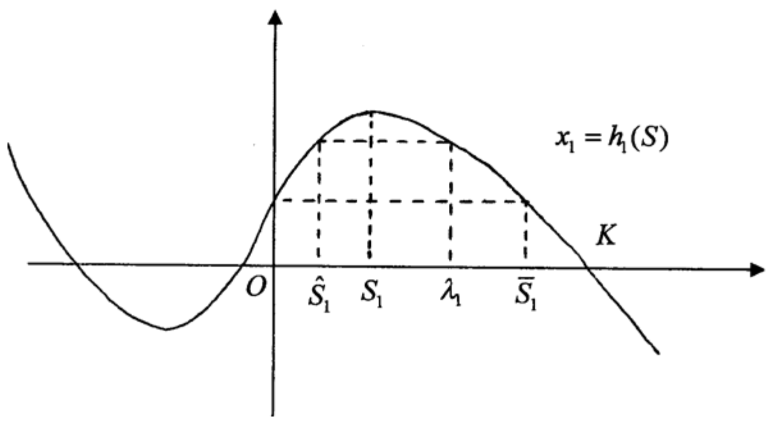

Figure 1. The prey isocline $x_1 = h_1(S)$ when $x_2 = 0$.

For the stability of the equilibrium E_1, we have

Theorem 1. If $\lambda_1 < \lambda_2$, and if $S_1 \le \lambda_1$, then E_1 is globally asymptotically stable; in other words, $(S(t), x_1(t), x_2(t)) \to (\lambda_1, h_1(\lambda_1), 0)$ as $t \to +\infty$.

The proof can be found in Appendix.

Now, let μ be the bifurcation parameter, and rewrite system (1) in μ as follows:

$$\frac{dX}{dt} = f(X, \mu). \tag{6}$$

The stability of an equilibrium and the Hopf bifurcation are connected by the center manifold theorem.

Theorem A. Let W be an open set in R^3, $O = (0,0,0) \in W$, and the analytic function f is defined as $f : W \times (-\mu_0, \mu_0) \to R^3$, where μ_0 is a small positive number. Denote the Jacobian of f at $(X, \mu) = (O, 0)$ as $J(f(O,0))$. Assume

(i) system (6) has (0,0,0) as its equilibrium point for any μ;

(ii) the eigenvalues of $J(f(O,0))$ are $\pm i\beta(\mu)|_{\mu=0} = \pm i\beta(0),\ \alpha(\mu)|_{\mu=0} = \alpha(0)$ which satisfy the conditions $\beta(0) > 0,\ \alpha(0) < 0.$

Then, if $(0,0,0)$ is asymptotically stable at $\mu = 0$, unstable on $\mu > 0$, there exists a sufficiently small $\mu,\ \mu > 0$ such that system (6) has an asymptotically stable closed orbit surrounding $(0,0,0)$.

The proof of Theorem A can be found in [13,14]. In order to use this theorem to establish the existence of bifurcation, we need the following theorem

Theorem 2. If $\lambda_1 < \lambda_2$ and $S_1 > \lambda_1$, E_1 is unstable.

Now, assume $\mu = S_1 - \lambda_1$ is a bifurcation parameter. We are going to prove the following theorem.

Theorem 3. If $\lambda_1 < \lambda_2$, then system (1) undergoes a Hopf bifurcation at $\mu = S_1 - \lambda_1 = 0$, and the periodic solution created by the Hopf bifurcation is asymptotically stable for $0 < S_1 - \lambda_1 << 1$.

Recently, a quite similar food chain model but with Monod functional response is published [16] with some numerical results. The limit cycles in the numerical simulation of [16] take the following forms which give us some idea about the locations and shapes of limit cycles in the model (1.1) (Figure 2).

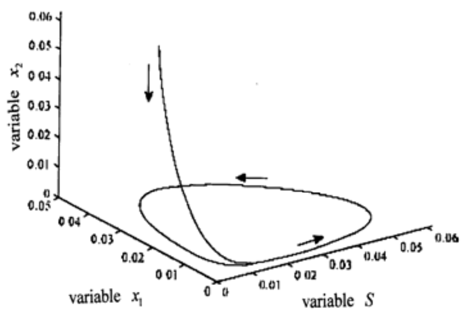

Figure 2. Example of limit cycles of competition in bio-reactor.

For the following discussion, we recall a result from our previous work [8]. Considering the system

$$\begin{aligned} \frac{dx}{dt} &= \phi(x)(F(x)-\pi(y)), \\ \frac{dy}{dt} &= \rho(y)(-r+\psi(x)+\xi(y)), \end{aligned} \tag{7}$$

in which the biological meanings of the functions and parameters in (7) are as in [8].

Let E be the equilibrium point of system (7). Assume the following assumptions are satisfied:

(H_1) $\phi,\psi,\pi,\xi \in C^1[0,\infty)$, $F \in C^1(0.\infty), F > 0$, $\phi(0)=\pi(0)=\rho(0)=\xi(0)=0$, and $\phi' \geq 0$ for all $x \geq 0$, and $\pi',\rho',\xi' \geq 0$ for all $y > 0$; Also, there exists an $\bar{x} \geq 0$ such that $\psi(\bar{x}) = r$, and for $x \neq \bar{x}$, $\psi'(x) > 0$; For $0 \leq x \leq k$, $\phi(x)$ is bounded by a linear function.

(H_2) The curve $\pi(y)-F(x)=0$ is defined for all $x > 0$, $\psi(x)+\xi(y)=r$ is for $y > 0$ and $r \geq 0$.

(H_3) There exists $k > \bar{x}$ such that $F(k) = 0$, $F'(k) < 0$, and $F(x) > 0$, for all $0 < x < k$; and for any $\bar{k} > k$, $F'(\bar{k}) \neq 0$ if $F(\bar{k}) = 0$.

It is proved in [8] that

Theorem B. If E is unstable, then the system (7) has at least one limit cycles around E.

The following result is for the case when $E_1 = (\lambda_1, h_1(\lambda), 0)$ is unstable. The projecting system of (1) onto the plane $x_2 = 0$ takes the form:

$$\begin{aligned} \frac{dS}{dt} &= \gamma S(1-\frac{S}{K}) - \frac{m_1 d_1 S}{(a_1+S)(b_1+S)}\frac{x_1}{\delta_1}, \\ \frac{dx_1}{dt} &= \left(\frac{m_1 d_1 S}{(a_1+S)(b_1+S)} - d_1\right)x_1, \\ S(0) &> 0,\ x_1(0) > 0. \end{aligned} \tag{8}$$

It follows that the point $E_1^{'} = (\lambda_1, h_1(\lambda_1))$ is the equilibrium of (8). It is easy to see that, $E_1^{'}$ is unstable since $S_1 > \lambda_1$. In other words, $E_1^{'}$ is on the two dimensional unstable manifold of E_1.

Consider S as x, and x_1 as y, then system (8) is reduced to a special case of system (7) with

$$\phi(S) = \frac{m_1 d_1 S}{(a_1+S)(b_1+S)}, F(S) = h_1(S) = \frac{r}{m_1 d_1}(1-\frac{S}{K})(a_1+S)(b_1+S),$$

$$\pi(x_1) = \frac{x_1}{\delta_1},\ \rho(x_1) = x_1, \xi(x_1) = 0,$$

$$r = d_1 \text{ and } \psi(S) = \frac{m_1 d_1 S}{(a_1+S)(b_1+S)}. \tag{9}$$

$$F(S) = h_1(S) = \frac{r}{m_1 d_1}(1-\frac{S}{K})(a_1+S)(b_1+S),$$

$$\rho(x_1) = x_1, \xi(x_1) = 0, r = d_1 \text{ and } \psi(S) = \frac{m_1 d_1 S}{(a_1+S)(b_1+S)}.$$

The basic assumptions $(H_1 - H_3)$ are satisfied, by Theorem C, for system (8), there exists at least a limit cycle around $E_1^{'}$. Therefore, we have

Theorem 4. If $\lambda_1 < \lambda_2$, system (1) has at least one limit cycle around the equilibrium E_1.

3. Discussion

Competition between species exploiting a common prey species is probably frequent occurrence in both nature and laboratory. However, not many theoretical work has been done on such systems [4,7,15]. Moreover, in most of the population models, the functional responses are chosen to be some monotonic functions such as Monod (or Michaelis-Menten) type. But in real world applications, it is not always the case. The one with non-monotonic inhibition response is, of course, worth a further study.

It looks to us the methods used in Section 2 for the equilibrium $E_1(\lambda_1, h_1(\lambda_1), 0)$ is also working for the equilibrium $E_2(\lambda_2, 0, h_2(\lambda_2))$. For example, if we define

$$S_2 = \left(K - a_2 - b_2 + \sqrt{K^2 + a_2^2 + b_2^2 - a_2 b_2 + Ka_2 + Kb_2}\right)/3 \tag{10}$$

Theorem A is also valid for $S_2 \le \lambda_2$. Moreover, in the proof of Theorem 1 in the Appendix, if we use $\lambda_1 \le \lambda_2$ instead of $\lambda_1 < \lambda_2$, it seems that the proof is still working. Therefore, an open problem arises what would happen if $\lambda_1 = \lambda_2$, the two predator species having same "break-even" concentration? Both survive? A further study of this phenomenon must be very interesting in the bio-mathematical modeling.

Some numerical simulation of limit cycles for the food chain model with Monod functional response can be found in [16]. As is well known, a limit cycle in a mathematical model corresponds to the nonlinear oscillation phenomena in the bio-reactor system. Thus the study of limit cycles of the model is useful in analyzing the behavior of the reactor. Actually, the reacting behavior of the food-chain bio-reactor system is very complicated. Computer simulation shows that it includes stationary, cyclic and chaotic coexistence [19.20]. Therefore, a further mathematical analysis of the food-chain is definitely necessary.

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Appendix

Before we prove Theorem 1, we need a useful lemma. At first we define an auxiliary function $F_1(S):(0,\lambda_1)\cup(\lambda_1,K)\to R$ as

$$F_1(S) = \frac{h_1(\lambda_1) - h_1(S)}{\int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)\xi - \lambda_1^2 - a_1 b_1}{m_1 \xi} d\xi}. \tag{11}$$

It follows that

$$\int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)\xi - \lambda_1^2 - a_1 b_1}{m_1 \xi} d\xi = \frac{m_1 - a_1 - b_1}{m_1}(S - \lambda_1)\left(1 - \lambda \frac{1}{\varsigma_1}\right),$$

where

$$\ln S - \ln \lambda_1 = \frac{1}{\varsigma_1}(S - \lambda_1), \text{ for some } \varsigma_1 \in (S, \lambda_1)\cup(\lambda_1, S).$$

Thus, it can be verified that

$$\int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)\xi - \xi^2 - a_1 b_1}{m_1 \xi} d\xi > 0, \text{ for } S \in (0,K),\ S \ne \lambda_1 \cdot \tag{12}$$

In fact, if $S \ge \lambda_1$, then $\varsigma_1 > \lambda_1$, and if $S < \lambda_1$, then $\varsigma_1 < \lambda_1$, therefore

$$\int_{\lambda_{1i}}^{S} \frac{(m_1 - a_1 - b_1)\xi - \lambda_1^2 - a_1 b_1}{m_1 \xi} d\xi = \frac{m_1 - a_1 - b_1}{m_1 \zeta_1}(S - \lambda_1)(\zeta_1 - \lambda_1) > 0.$$

The following result is necessary for the investigating of the stability of the equilibrium E_1.

As shown in Fig. 1, by the definition of $h_1(S)$, it is easy to see that there exists an $S_1 \in (0,K)$, such that $h_1'(S_1) = 0$, where

$$S_1 = \left(K - a_1 - b_1 + \sqrt{K^2 + a_1^2 + b_1^2 - a_1 b_1 + Ka_1 + Kb_1}\right)/3 \cdot \tag{13}$$

Moreover, there also exists $\overline{S}_1 \in (S_1, K)$ such that

$$h_1(\overline{S}_1) = h_1(0) = \gamma a_1 b_1 / m_1 d_1.$$

Lemma 1. If $S_1 \le \lambda_1$, then there exists a $\theta > 0$, such that

$$\max_{0 \le S \le \lambda_1} F_1(S) \le \theta \le \min_{\lambda_1 < S \le K} F_1(S). \quad (14)$$

Proof. We divide the proof into three different cases: (i) $S_1 < \lambda_1 \le \overline{S}_1$, (ii) $\overline{S}_1 \le \lambda_1$, and (iii) $\lambda_1 = S_1$. We shall find a θ such that (14) holds in each case.

The proof of (i): $S_1 < \lambda_1 \le \overline{S}_1$.

Consider the curve: $x_1 = h_1(S)$ in the $S - x_1$ plane, as it is shown in Fig. 1, it can be verified that there exists $\hat{S}_1 \in [0, S_1)$ such that $h_1(\hat{S}_1) = h_1(\lambda_1)$. By the definition of $F_1(S)$, we have

$$\lim_{S \to 0^+} F_1(S) = 0, \ F_1(\hat{S}_1) = 0,$$
$$\lim_{S \to \lambda_1^-} F_1(S) = -\infty, \ \lim_{S \to \lambda_1^+} F_1(S) = +\infty,$$

$$F_1(S) \begin{cases} > 0 \ \text{for } S \in (0, \hat{S}_1) \cup (\lambda_1, K], \\ < 0 \ \text{for } S \in (\hat{S}_1, \lambda_1). \end{cases}$$

Suppose

$$\max_{0 \le S \le \lambda_1} F_1(S) > \min_{\lambda_1 < S \le K} F_1(S).$$

Then there exists $\pi > 0$ such that the equation $F_1(S) - \pi = 0$ has three distinct roots, of which two are in $(0, \hat{S}_1)$ and one in $(\lambda_1, K]$. Let r_1, r_2, r_3 be the three roots, then $0 < r_1 < r_2 < \hat{S} < \lambda_1 < r_3 \le K$.

Consider the equation

$$H_1(S) = h_1(\lambda_1) - h_1(S) - \pi \int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)\xi - \lambda_1^2 - a_1 b_1}{m_1 \xi} d\xi = 0. \quad (15)$$

It has four roots: λ_1, and r_1, r_2, r_3 in $[0, K]$. By a simple calculation,

$$H_1'''(S) = \frac{6\gamma}{m_1 d_1 K} + \frac{2\pi(m_1 - a_1 - b_1)\lambda_1}{m_1 S^3} > 0 \cdot$$

From Rolle's Theorem, there exists $\zeta \in (0, K)$ such that $H_1'''(\zeta) = 0$. This contradiction implies the existence of $\theta > 0$ such that

$$\max_{0 \le S \le \lambda_1} F_1(S) \le \theta \le \min_{\lambda_1 < S \le K} F_1(S).$$

Since $F_1(S) < 0$ for $S \in (\hat{S}, \lambda_1)$, $\max_{0 \le S \le \lambda_1} F_1(S) < \max_{0 \le S \le \hat{S}} F_1(S)$. Obviously, this θ satisfies the hypothesis (14).

The proof of (ii): $\overline{S}_1 \le \lambda_1$.

In this case, we have,

$$\lim_{S \to 0^+} F_1(S) = 0, \ \lim_{S \to \lambda_1^-} F_1(S) = -\infty, \ \lim_{S \to \lambda_1^+} F_1(S) = +\infty,$$

and

$$F_1(S) \begin{cases} < 0 \ \text{for } S \in (0, \lambda_1), \\ > 0 \ \text{for } S \in (\lambda_1, K]. \end{cases}$$

It is easy to see that any $\theta \in (0, \min_{\lambda_1 < S \le K} F_1(S))$ will satisfy formula (14).

The proof of (iii): $\lambda_1 = S_1$.

It follows that

$$\lim_{S \to 0^+} F_1(S) = 0,$$
$$\lim_{S \to \lambda_1} F_1(S) = \frac{2\gamma\lambda_1 (3\lambda_1 - K + a_1 + b_1)}{d_1 K (m_1 - a_1 - b_1)} > 0$$

(by L'Hospital law), $F_1(S) \ge 0$ for $S \in (0, K]$, and $F_1(S)$ is continuous in $(0, K]$.

Let $S = \eta\lambda_1$, $\eta \in (0, K/\lambda_1)$, $\eta \ne 1$. Then

$$h_1(\eta\lambda_1) = \frac{\gamma}{m_1 d_1 K}(K - \eta\lambda_1)(a_1 + \eta\lambda_1)(b_1 + \eta\lambda_1),$$

and

$$F_1(\eta\lambda_1)=\frac{h_1(\lambda_1)-h(\eta\lambda_1)}{\frac{m_1-a_1-b_1}{m_1}\left((\eta\lambda_1-\lambda_i)-\lambda_1(\ln\eta\lambda_1-\ln\lambda_i)\right)}$$
$$=\frac{\delta_1\gamma\lambda_1\,(\eta-1)^2((\eta+2)\lambda_1+a_1+b_1-K)}{d_1K(m_1-a_1-b_1)(\eta\text{-}1\text{-}\ln\eta)},$$
$$\eta\in(0,K/\lambda_1),\ \eta\neq 1.$$

Consider the function

$$f_1(\eta)=(\eta-1)^2\left((\eta+2)\lambda_1+a_1+b_1-K\right)-\pi(m_1-a_1-b_1)(\eta-1-\ln\eta), \tag{16}$$

for $\eta\in(0,K/\lambda_1)$, and $\eta\neq 1$, where π is a positive constant which will be determined later. It is easy to see that

$$\lim_{\eta\to 0^+} f_1(\eta)=-\infty,\ f_1(1)=0,$$

and

$$f_1^{''}(\eta)=6\lambda_1\eta+2(a_1+b_1-K)-2\pi(m_1-a_1-b_1)/\eta^2.$$

Let $\eta=1$. We can choose

$$\pi=\pi_0\left(=\frac{2(3\lambda_1+a_1+b_1-K)}{m_1-a_1-b_1}>0\right). \tag{17}$$

such that $f_1^{''}(1)=0$. In other words, when π takes the value π_0, $\eta=1$ is an inflection point of the curve $y=f_1(\eta)$.

Since $\lambda_1=S_1$, $3\lambda_1+a_1+b_1-K>0$ and $\pi_0>0$.

Now by

$$f_1^{'''}(\eta)=6\lambda_1+\pi(m_1-a_1-b_1)/\eta^3>0,$$

for $\eta\in(0,K/\lambda_1)$, or $S\in(0,K)$. Therefore, $f_1^{''}(\eta)$ is increasing, and $f_1^{''}(\eta)>0$ on $\eta\in(1,K/\lambda_1)$. This implies that $f_1^{'}(\eta)$ is increasing on $\eta\in(1,K/\lambda_1)$, and $f_1^{'}(\eta)>f_1^{'}(1)=0$. In other words, $f_1(\eta)$ is increasing on $\eta\in(1,K/\lambda_1)$, and $f_1(\eta)>f_1(1)=0$, that is

$$\frac{(\eta-1)^2((\eta+2)\lambda_1+a_1+b_1-K)}{(m_1-a_1-b_1)(\eta-1-\ln\eta)}>\pi_0. \tag{18}$$

Thus,

$$F_1(S)=\frac{\delta_1\gamma\lambda_1\,(\eta-1)^2((\eta+2)\lambda_1+a_1+b_1-K)}{d_1K(m_1-a_1-b_1)(\eta-1-\ln\eta)}$$
$$>\frac{\delta_1\gamma\lambda_1}{d_1K}\pi_0=\frac{2\delta_1\gamma\lambda_1\,(3\lambda_1+a_1+b_1-K)}{d_1K(m_1-a_1-b_1)},$$
$$\forall S\in(\lambda_1,K).$$

Moreover, if $\eta\in(0,1)$, then $S\in(0,\lambda_1)$, and $f(\eta)<f(1)=0$, which implies

$$\frac{(\eta-1)^2((\eta+2)\lambda_1+a_1+b_1-K)}{(m_1-a_1-b_1)(\eta-1-\ln\eta)}<\pi_0,\quad \forall S\in(0,\lambda_1). \tag{19}$$

Thus,

$$F_1(S)<\frac{\delta_1\gamma\lambda_1}{d_1K}\pi_0=\frac{2\delta_1\gamma\lambda_1\,(3\lambda_1+a_1+b_1-K)}{d_1K(m_1-a_1-b_1)},\quad \forall S\in(0,\lambda_1).$$

Therefore, we always can choose

$$\theta=\frac{2\delta_1\gamma\lambda_1^2(3\lambda_1+a_1+b_1-K)}{d_1K(m_1-a_1-b_1)},$$

such that the hypothesis (14) is satisfied. We complete the proof of Lemma 1.

Proof of Theorem 1. Let

$$V(S,x_1,x_2)=x_1^{\theta}\int_{\lambda_1}^{S}\frac{(m_1-a_1-b_1)\xi-\xi^2-a_1b_1}{m_1\xi}d\xi+ \tag{20}$$
$$\int_{h_1(\lambda_1)}^{x_1}\xi^{\theta-1}(\xi-h_1(\lambda_1))d\xi+cx_1^{\theta}x_2,$$

$\theta,\ c\ (\geq 0)$ will be determined later. It is easy to see that $V(S,x_1,x_2)\in C^1(R_+^3,R)$, $R_+^3=\{(S,x_1,x_2)\,|\,S>0,x_1>0,x_2>0\}$, and $V(\lambda_1,h_1(\lambda_1),0)=0,\ V(S,x_1,x_2)>0$ for $(S,x,y)\in R_+^3/\{E_1\}$.

The derivative of V along the trajectory of system (1) is

$$\dot V(S,x_1,x_2)=$$
$$x_1^\theta\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{m_1S}\left(\gamma S\left(1-\frac{S}{K}\right)-\frac{m_1d_1S}{(a_1+S)(b_1+S)}x_1-\frac{m_2d_2S}{(a_2+S)(b_2+S)}x_2\right)$$
$$+\left(x_1^\theta-h_1(\lambda_1)x_1^{\theta-1}+\theta x_1^{\theta-1}\int_{\lambda_1}^S\frac{(m_1-a_1-b_1)\xi-\xi^2-a_1b_1}{m_1\xi}d\xi\right)\left(\frac{m_1d_1S}{(a_1+S)(b_1+S)}-d_1\right)x_1$$
$$+c\theta x_1^\theta\left(\frac{m_1d_1S}{(a_1+S)(b_1+S)}-d_1\right)x_2+cx_1^\theta\left(\frac{m_2d_2S}{(a_2+S)(b_2+S)}-d_2\right)x_2.$$

Denote

$$\dot V(S,x_1,x_2)=V_1+V_2+V_3,$$

where

$$V_1=x_1^\theta\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{(a_1+S)(b_1+S)}\left(\frac{\gamma}{m_1d_1K}(K-S)(a_1+S)(b_1+S)-h_1(\lambda_1)\right.$$
$$\left.+\theta\int_{\lambda_1}^S\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{m_1\xi}d\xi\right),$$
$$V_2=cx_1^\theta x_2\left(\frac{m_2d_2\lambda_1}{(a_2+\lambda_1)(b_2+\lambda_1)}-d_2\right),\ \text{and}$$
$$V_3=x_1^\theta x_2\left(-\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{m_1S}\frac{m_2d_2S}{(a_2+S)(b_2+S)}\right.$$
$$\left.+c\theta\left(\frac{m_1d_1S}{(a_1+S)(b_1+S)}-d_1\right)+c\left(\frac{m_2d_2S}{(a_2+S)(b_2+S)}-\frac{m_2d_2\lambda_1}{(a_2+\lambda_1)(b_2+\lambda_1)}\right)\right).$$

By Theorem 2, there exists $\theta>0$ such that (14) holds.

Notice that, $\lambda_1^{'}$ is as defined in (3),

$$(m_1-a_1-b_1)S-S^2-a_1b_1=(S-\lambda_1)(S-\lambda_1^{'}). \qquad (21)$$

If $S<\lambda_1$,

$$\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{(a_1+S)(b_1+S)}<0,$$

and

$$\frac{h_1(\lambda_1)-h_1(S)}{\int_{\lambda_1}^S\frac{(m_1-a_1-b_1)\xi-\xi^2-a_1b_1}{m_1\xi}d\xi}<\theta$$

Therefore,

$$h_1(S)-h_1(\lambda_1)>\theta\int_{\lambda_1}^S\frac{(m_1-a_1-b_1)\xi-\xi^2-a_1b_1}{m_1\xi}d\xi,$$

and thus $V_1\leq 0$. Similarly, if $S\geq\lambda_1$, we also have $V_1\leq 0$.

Also, since $\lambda_1<\lambda_2$, $V_2\leq 0$ for any $c\geq 0$. We now just need to show that there exists a $c\geq 0$, constant or a function of S, such that $V_3\leq 0$. In the case of c is a function of S, as we will see $c=(\lambda_1^{'}-S)\psi(\lambda_1)$, a negative term of $c^{'}x_1^\theta x_2=-\psi(\lambda_1)x_1^\theta x_2$ will be added into $V^{'}(S,x_1,x_2)$, which is still negative. We shall find the c in two cases: (i) $a_1\geq a_2$, or $b_1\geq b_2$ (ii) $a_1<a_2$ and $b_1<b_2$.

In the first case of $a_1\geq a_2$, or $b_1\geq b_2$, since $\lambda_1<\lambda_2$, by Markus theorem ([10,11]), we can follow the same argument of Theorem 3.4 in [11], for any number c, the solution of system (1) satisfies that

$$(S(t),x(t),y(t))\to(\lambda_1,h_1(\lambda_1),0)\ \text{as}\ t\to\infty.$$

This means that $E_1(\lambda_1,h_1(\lambda_1),0)$ is globally asymptotically stable. We just need to find a c for the second case of $a_1<a_2$ and $b_1<b_2$. Let

$$\Delta(S)=\frac{-m_2d_2}{(a_2+S)(b_2+S)}\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{m_1}+$$
$$c\theta d_1\frac{(m_1-a_1-b_1)S-S^2-a_1b_1}{(a_1+S)(b_1+S)}+ \qquad (22)$$
$$c\left(\frac{m_2d_2S}{(a_2+S)(b_2+S)}-\frac{m_2d_2\lambda_1}{(a_2+\lambda_1)(b_2+\lambda_1)}\right).$$

It follows that

$$\Delta(S)=\frac{-m_2d_2}{m_1(a_2+S)(b_2+S)}(S-\lambda_1)(\lambda_1^{'}-S)+c\theta d_1\frac{(S-\lambda_1)(\lambda_1^{'}-S)}{(a_1+S)(b_1+S)}$$
$$+c\frac{m_2d_2(S-\lambda_1)(a_2b_2-S\lambda_1)}{(a_2+S)(b_2+S)(a_2+\lambda_1)(b_2+\lambda_1)};$$

or,

$$\Delta(S) = \frac{S-\lambda_1}{(a_2+S)(a_1+S)(b_2+S)(b_1+S)} \left(\frac{-m_2 d_2 (\lambda_1^{'}-S)(a_1+S)(b_1+S)}{m_1} + c\theta d_1(\lambda_1^{'}-S)(a_2+S)(b_2+S) + \frac{c m_1 d_1 (a_2 b_2 - S\lambda_1)(a_1+S)(b_1+S)}{(a_2+\lambda_1)(b_2+\lambda_1)} \right). \tag{23}$$

Define

$$\Psi(S) = \frac{\frac{m_2 d_2}{m_1}(a_1+S)(b_1+S)}{\theta d_1(\lambda_1^{'}-S)(a_2+S)(b_2+S) + \frac{m_1 d_1 (a_2 b_2 - S\lambda_1)(a_1+S)(b_1+S)}{(a_2+\lambda_1)(b_2+\lambda_1)}}. \tag{24}$$

That is

$$\Psi(S) = \frac{m_2 d_2}{m_1 d_1} \frac{1}{\theta(\lambda_1^{'}-S)\left(1+\frac{a_2-a_1}{a_1+S}\right)\left(1+\frac{b_2-b_1}{b_1+S}\right) + \frac{m_1(a_2 b_2 - S\lambda_1)}{(a_2+\lambda_1)(b_2+\lambda_1)}}.$$

Since

$$\Psi^{'}(S) = \frac{m_2 d_2}{m_1 d_1} \frac{\Theta(S)}{-\left(\theta(\lambda_1^{'}-S)\left(1+\frac{a_2-a_1}{a_1+S}\right)\left(1+\frac{b_2-b_1}{b_1+S}\right) + \frac{m_1 d_1(a_2 b_2 - S\lambda_1)}{(a_2+\lambda_1)(b_2+\lambda_1)}\right)^2}, \tag{25}$$

where

$$\begin{aligned}\Theta(S) &= -\theta\left(1+\frac{a_2-a_1}{a_1+S}\right)\left(1+\frac{b_2-b_1}{b_1+S}\right) + \theta(\lambda_1^{'}-S)\left(-\frac{a_2-a_1}{(a_1+S)^2}\right)\left(1+\frac{b_2-b_1}{b_1+S}\right) \\ &\quad + \theta(\lambda_1^{'}-S)\left(1+\frac{a_2-a_1}{a_1+S}\right)\left(-\frac{b_2-b_1}{(b_1+S)^2}\right) - \frac{m_1 d_1 \lambda_1}{(a_2+\lambda_1)(b_2+\lambda_1)} \\ &< 0.\end{aligned} \tag{26}$$

It follows that $\Psi^{'}(S) > 0$, since $a_2 - a_1 > 0$ and $b_2 - b_1 > 0$.

By (B_2), $\lambda_2^{'} > K$, then $a_2 b_2 = \lambda_2 \lambda_2^{'} > \lambda_2 K$, or $a_2 b_2 - \lambda_2 K > 0$, which implies

$$a_2 b_2 - S\lambda_1 \ge a_2 b_2 - K\lambda_1 > a_2 b_2 - K\lambda_2 > 0.$$

Since $a_2 b_2 - \lambda_1^2 > 0$, we can choose $c = (\lambda_1^{'} - S)\Psi(\lambda_1) > 0$. It follows that

$$\begin{aligned}\Delta(S) &= \left(\theta d_1(\lambda_1^{'}-S)(a_2+S)(b_2+S) + \frac{m_1 d_1(a_2 b_2 - S\lambda_1)(a_1+S)(b_1+S)}{(a_2+\lambda_1)(b_2+\lambda_1)}\right) \\ &\quad \cdot \frac{(\lambda_1^{'}-S)(S-\lambda_1)}{(a_2+S)(a_1+S)(b_2+S)(b_1+S)}\left(\Psi(\lambda_1)-\Psi(S)\right) \\ &\le 0 \text{ (since } \Psi(S) \text{ increases).}\end{aligned} \tag{27}$$

Note that $\Delta(S)$ is always negative if $S \ne \lambda_1$.

Therefore, $\dot{V}(S,x,y) = V_1 + V_2 + V_3 \le 0.$

By the LaSalle's invariant principle, all trajectories tend to the largest invariant set in $\Lambda = \{(S,x,y) \mid V^{'} = 0\}$. This requires $S \equiv \lambda_1$ and $y \equiv 0$.

To make $\{S \mid S = \lambda_1\}$ invariant under the condition $y = 0$, it follows

$$S' = \gamma\lambda_1\left(1-\frac{\lambda_1}{K}\right) - \frac{m_1 d\ \lambda_1}{(a_1+\lambda_1)(b_1+\lambda_1)} x_1 = 0. \tag{28}$$

In other words,

$$x_1 = \frac{\gamma}{m_1 d_1}\left(1-\frac{\lambda_1}{K}\right)(a_1+\lambda_1)(b_1+\lambda_1) = h_1(\lambda_1).$$

Therefore $\{E_1\}$ is the only invariant set in Λ. We thus complete the proof of Theorem 1.

Proof of Theorem 2. Consider the Jocobian of system (1) at E_1, $J(E_1) = (a_{ij})$, $i, j = 1,2,3$. It follows that its characteristic equation is

$$(r - a_{33})(r^2 - a_{11} r - a_{12} a_{21}) = 0, \tag{29}$$

$$a_{11} = \gamma(1 - 2\lambda_1 / K) - \frac{m_1 d_1 (a_1 b_1 - \lambda_1^2)}{(a_1+\lambda_1)^2 (b_1+\lambda_1)^2} h_1(\lambda_1),\ a_{12} = \frac{-m_1 d_1 \lambda_1}{(a_1+\lambda_1)(b_1+\lambda_1)},$$

$$a_{21} = \frac{m_1 d_1 (a_1 b_1 - \lambda_1^2)}{(a_1+\lambda_1)^2 (b_1+\lambda_1)^2} h_1(\lambda_1),\ a_{33} = \frac{m_2 d_2 \lambda_1}{(a_1+\lambda_1)(b_1+\lambda_1)} - d_2.$$

Assume the three roots of (29) as r_1, r_2 and r_3. It follows that

$$r_1 + r_2 = a_{11},\ r_1 r_2 = -a_{12} a_{21} > 0 \text{ (since } a_1 b_1 > \lambda_1^2),$$
$$r_3 = a_{33} < 0 \text{ (since } \lambda_1 < \lambda_2).$$

Therefore, if

$$a_{11}\begin{cases} >0, & r_1 \text{ and } r_2 \text{ have positive real part, } E_1 \text{ is unstable;} \\ <0, & r_1 \text{ and } r_2 \text{ have negative real part, } E_1 \text{ is stable.} \end{cases}$$

Notice that

$$a_{11} = \gamma(1-2\lambda_1/K) - \frac{m_1 d_1 (a_1 b_1 - \lambda_1^2)}{(a_1+\lambda_1)^2 (b_1+\lambda_1)^2}\frac{\gamma}{m_1 d_1}\left(1-\frac{\lambda_1}{K}\right)(a_1+\lambda_1)(b_1+\lambda_1)$$
$$= \frac{\gamma\lambda_1}{K(a_1+\lambda_1)(b_1+\lambda_1)}\left(-3\lambda_1^2 + 2(K-a_1-b_1)\lambda_1 + K(a_1+b_1) - a_1 b_1\right).$$

Since S_1 is the only point such that $h_1'(S_1)=0$ on $(0,K]$, it follows that if $S_1<\lambda_1$, $a_{11}<0$ and E_1 is stable; if $S_1>\lambda_1$, $a_{11}>0$ and E_1 is unstable but with a one-dimensional stable manifold. The proof of Theorem 2 is complete.

Proof of Theorem 3. Since $\lambda_1 = \mu - S_1$, $m_1 = \frac{(a_1+\lambda_1)(b_1+\lambda_1)}{\lambda_1}$, system (1) can be written in μ as follows:

$$S_1' = \varphi_1(S, x_1, x_2, \mu),$$
$$x_1' = \varphi_1(S, x_1, x_2, \mu),$$
$$x_2' = \varphi_1(S, x_1, x_2, \mu).$$

Use the variable changes:

$$\overline{S} = S - \lambda_1,\ \overline{x}_1 = x_1 - h_1(\lambda_1),\ \overline{x}_2 = x_2,$$

system (1) in variables $\overline{S}$, $\overline{x}_1$, $\overline{x}_2$ is

$$\frac{dX}{dt} = f(X,\mu), \tag{30}$$

whose Jacobian is denoted as $J(\overline{S},\overline{x}_1,\overline{x}_2)$.

Consider system (30) and its Jacobian at $\mu=0$ and $(\overline{S},\overline{x}_1,\overline{x}_2)=(0,0,0)$,

$$J(f(O,0)) = J(\overline{S},\overline{x}_1,\overline{x}_2)\Big|_{\substack{(\overline{S},\overline{x}_1,\overline{x}_2)=(0,0,0)\\ \mu=0}} = J(S,x_1,x_2)\Big|_{\substack{(S,x_2,x_3)=(\lambda_1,h_1(\lambda_1),0)\\ S_1=\lambda_1}}.$$

Its characteristic equation has the eigenvalues: $\pm i\beta(0)$ and $\alpha(0)$, where

$$\beta(0) = \sqrt{\frac{m_1^2 d_1^2 \lambda_1 (a_1 b_1 - \lambda_1^2)}{(a_1+\lambda_1)^3 (b_1+\lambda_1)^3}} > 0,$$
$$\alpha(0) = \frac{m_2 d_2 \lambda_1}{(a_2+\lambda_1)(b_2+\lambda_1)} - d_2 < 0 \text{ (since } \lambda_1 < \lambda_2).$$

By Theorem A when $\lambda_1<\lambda_2$ and $S_1 \le \lambda_1$, the equilibrium E_1 is globally asymptotically stable, and by Theorem 1, when $S_1>\lambda_1$, it is unstable. Therefore, the hypotheses of Theorem B are satisfied. Actually, we have

(1) The equilibrium of system (1): $O=(0,0,0)$ in the $\overline{S},\overline{x}_1,\overline{x}_2$ coordinate, or $E_1=(\lambda_1,h(\lambda_1),0)$ in S,x_1,x_2, is globally asymptotically stable if $\mu=0$;
(2) and, it is unstable if $\mu>0$.

Therefore, system (8) undergoes a Hopf bifurcation at $\mu=0$, and so does system (1) at $S_1=\lambda_1$. From Theorem B it follows that, for a sufficient small μ, $\mu>0$, system (30) has an asymptotically stable closed orbit surrounding $(0,0,0)$. In other words, for $0<S_1-\lambda_1<<1$, system (1) has an asymptotically stable closed orbit surrounding $E_1(\lambda_1,h(\lambda_1),0)$. The proof of Theorem 3 is complete.

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