Global stability of a three-dimensional bio-reactor with inhibition responses

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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 constructing a modified Lyapunov function and using LaSalle's invariant principle, it is shown that the lower "break-even" concentration predator organism survives in the competition.

KEY WORDS: global stability, competition, break-even, Lyapunov function, invariant principle

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1. Introduction

The asymptotically behavior is an important topic in modeling the bio-reactor in which two populations of micro-organisms compete exploitatively for a single substrate. In the case of a non-reproducing and growth-limiting substrate, many results have been reported (see, for example, [1–3]). However, in addition to a constant input of limiting nutrient, a renewable resource with reproductive properties – a more classic prey, should also be considered in the system [4]. Examples of competing for a renewable resource with some numerical simulations can be found in the literature (see McGehee and Armstrong [5], Koch [6], and Hsu et al. [4]). Usually, in the study of competition for a renewable substrate, organisms consume the nutrient and the consumed nutrient converted to

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growth is proportional to consumption. Nutrient uptake (consumption) is usually taken to be of the Monod (or Michaelis–Menten) form: $mxS/(a+S)$, where m is called the maximal growth rate and a is the Michaelis–Menten constant [4]. But in reality, other prototypes of functional responses are also possible [2, 3, 7]. In this paper, we consider such a competition with inhibition responses and different death rates [7] in the following form:

$$
\begin{aligned}
\frac{\mathrm{d}S}{\mathrm{d}t} &= \gamma S\left(1 - \frac{S}{K}\right) - \frac{m_1 \mathrm{d}_1 S}{(a_1 + S)(b_1 + S)}\frac{x_1}{\delta_1} - \frac{m_2 \mathrm{d}_2 S}{(a_2 + S)(b_2 + S)}\frac{x_2}{\delta_2}, \\
\frac{\mathrm{d}x_1}{\mathrm{d}t} &= \left(\frac{m_1 \mathrm{d}_1 S}{(a_1 + S)(b_1 + S)} - \mathrm{d}_1\right)x_1, \\
\frac{\mathrm{d}x_2}{\mathrm{d}t} &= \left(\frac{m_2 \mathrm{d}_2 S}{(a_2 + S)(b_2 + S)} - \mathrm{d}_2\right)x_2, \\
S(0) &> 0,\ x_1(0) > 0,\ x_2(0) > 0.
\end{aligned}
\tag{1}
$$

This system can be considered as predator-prey system consisting two predators x_1 and x_2, and a single prey species S, the renewable resource in the reaction vessel at time t. The parameters, γ and K are the growth rate and carrying capacity of the renewable resource S; m_i, a_i and $\mathrm{d}_i, i = 1, 2$, are maximum predation rates, half saturation constants, and death rate of predators. The predators: x_1 and x_2 consume the prey with functional response of inhibition type $\frac{m_1 \mathrm{d}_1 S}{(a_1+S)(b_1+S)}$ and $\frac{m_2 \mathrm{d}_2 S}{(a_2+S)(b_2+S)}$, respectively. δ_i is the yield constant for the predator x_i. For simplicity, we will assume $\delta_i = 1, i = 1, 2$ in the following discussion because if not the case, a variable transformation can always make the constant yield as 1. It is easy to see that the Michaelis–Menten type of response is a monotone function, but the inhibition type is non-monotone. Since not many results have been reported for the models with inhibition responses, a further mathematical analysis for system (1) is important.

We shall use a modified Lyapunov function and LaSalle's invariant principle to prove the global stability of the model. Our results show that in the competition of two predator organisms for a single prey organism with inhibition responses and with different death rates of the predator species, the lower "break-even" predator organism survives in the competition.

Constructing a Lyapunov function to establish the global stability of a equilibrium is not easy. However, once the Lyapunov function is obtained, then the global stability follows directly from the LaSalle's invariant principle. This method is suitable for a large number of population models. The model with inhibition responses studied in this paper is another good example in the application of the Lyapunov–LaSalle's principle for the global stability. One thing we would like to mention that in the proofs of Theorems 2 and 3, even if the "break-even" concentrations are equal, the proofs may still go through. So it is possible that both organisms survive in the competition. This phenomenon is definitely worth a further investigation.

Our main results are presented in the next section.

2. Main theorems and proofs

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 $i = 1, 2$,

(B1): $\sqrt{m_i} \geq \sqrt{a_i} + \sqrt{b_i}$;

(B2): $m_i - a_i - b_i + \sqrt{(m_i - a_i - b_i)^2 - 4a_i b_i} > 2K$;

(B3): $K_i > a_i + b_i$;

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, 4, 8].

For $i = 1, 2$, define λ_i as the solution 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 (B2), $\lambda_i' > K$, so there are only three equilibrium points in R_+^3 that we need to considered: $E_0 : (K, 0, 0)$, $E_1 : (\lambda_1, h_1(\lambda_1), 0)$, and $E_1 : (\lambda_2, 0, h_2(\lambda_2))$, where for each i, $h_i(S)$ is defined as

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

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.

Before we present our main theorem, we introduce the following definition and some known results (see [2, 3, 9]).

Definition 1. Consider the system of differential equations

$$\frac{dX}{dt} = f(X), \tag{5}$$

where $f : \Omega \subseteq R^n \to R^n$ is continuous. V is called a Lyapunov function on $G \subset \Omega$ for system (2.1), if

(i) V is continuous on G;

(ii) if V is not continuous at a point $\bar{X} \in \bar{G}$ (the closure of G), then

$$\lim_{\substack{X \to \bar{X} \\ X \in G}} V(X) = \infty;$$

(iii) $V' = \text{grad}V \cdot f \leq 0$ on G.

Theorem 1. (LaSalle's Invariance Principle) Assume that V is a Lyapunov function of (2.1) on G. Define $\Delta = \{X \in \bar{G} \cap \Omega : \dot{V}(X) = 0\}$. Suppose M is the largest invariant set in Δ. Then every bounded trajectory of (5) that remains in G approaches the set M as $t \to +\infty$.

Following the idea in constructing Lyapunov functions of population models [9], we first introduce an auxiliary function $F_i(S) : (0, \lambda_i) \cup (\lambda_i, K) \to R_+^3$ as

$$F_i(S) = \frac{h_i(\lambda_i) - h_i(S)}{\int_{\lambda_i}^{S} \frac{(m_i - a_i - b_i)\xi - \xi^2 - a_i b_i}{m_i \xi} d\xi}. \tag{6}$$

It follows that

$$\int_{\lambda_i}^{S} \frac{(m_i - a_i - b_i)\xi - \xi^2 - a_i b_i}{m_i \xi} d\xi$$

$$= \frac{m_i - a_i - b_i}{m_i}(S - \lambda_i) - \frac{1}{2m_i}(S^2 - \lambda_i^2) - \frac{a_i b_i}{m_i}(\ln S - \ln \lambda_i)$$

$$= (S - \lambda_i)\left(\frac{m_i - a_i - b_i}{m_i} - \frac{S + \lambda_i}{2m_i} - \frac{a_i b_i}{m_i}\frac{1}{\varsigma_i}\right),$$

where

$$\ln S - \ln \lambda_i = \frac{1}{\varsigma_i}(S - \lambda_i), \text{ for some } \varsigma_i \in (S, \lambda_i) \cup (\lambda_i, S), \quad i = 1, 2.$$

It can be verified that

$$\int_{\lambda_i}^{S} \frac{(m_i - a_i - b_i)\xi - \xi^2 - a_i b_i}{m_i \xi} d\xi > 0, \qquad \text{for } S \in (0, K), \quad S \neq \lambda_i. \tag{7}$$

In fact, if $S \geqslant \lambda_i$, then $\varsigma_i > \lambda_i$,

$$\int_{\lambda_i}^{S} \frac{(m_i - a_i - b_i)\xi - \xi^2 - a_i b_i}{m_i \xi} d\xi$$

$$> (S - \lambda_i)\left(\frac{m_i - a_i - b_i}{m_i} - \frac{\lambda_i + \lambda_i}{2m_i} - \frac{a_i b_i}{m_i}\frac{1}{\lambda_i}\right)$$

$$= (S - \lambda_i)\frac{m_i \lambda_i - (a_i + b_i)\lambda_i - \lambda_i^2 - a_i b_i}{m_i \lambda_i}$$

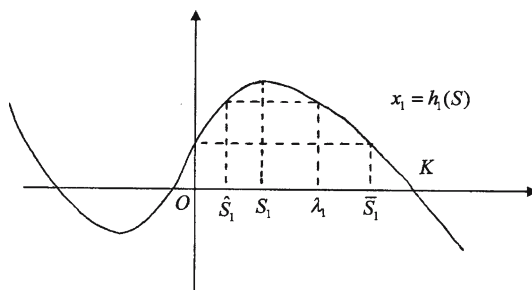$$= 0 \text{ (by the definition of } \lambda_i, i = 1, 2).$$

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

Similarly, (6) is also true for $S < \lambda_i$.

For simplicity, we are now presenting our results just for the case of $i = 1$ because the ones for $i = 2$ are exactly same. The following theorem is necessary for the investigating of the stability of the equilibrium E_1.

As shown in figure 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

$$S_1 = \left(k_1 - a_1 - b_1 + \sqrt{k_1^2 + a_1^2 + b_1^2 - a_1 b_1 + K a_1 + K b_1} \right) / 3. \tag{8}$$

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

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

Theorem 2. If $S_1 \leq \lambda_1$, then there exists a $\theta > 0$, such that

$$\max_{0 \leq S \leq \lambda_1} F_1(S) \leq \theta \leq \min_{\lambda_1 < S \leq K} F_1(S). \tag{9}$$

Proof. We divide the proof into three different cases: (i) $S_1 < \lambda_1 \leq \bar{S}_1$, (ii) $\bar{S}_1 \leq \lambda_1$, and (iii) $\lambda_1 = S_1$. We shall find a θ such that (9) holds in each case.
The proof of (i): $S_1 < \lambda_1 \leq \bar{S}_1$.

Consider the curve: $x_1 = h_1(S)$ in the $S - x_1$ plane, as it is shown in figure 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

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

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 $0 < r_1 < r_2 < \hat{S} < \lambda_1 < r_3 \leq K$.

Consider the equation

$$H_1(S) = h_1(\lambda_1) - h_1(S) - \pi \left(\frac{m_1 - d_1}{m_1}(S - \lambda_1) - \frac{S^2 - \lambda_1^2}{2m_1} - \frac{a_1 b_1}{m_1} \ln \frac{S}{\lambda_1} \right) = 0.$$

(10)

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

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

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

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

Since $F_1(S) < 0$ for $S \in (\hat{S}, \lambda_1)$, $\max\limits_{0 \leq S \leq \lambda_1} F_1(S) < \max\limits_{0 \leq S \leq \hat{S}} F_1(S)$. Obviously, this θ satisfies the hypothesis (9).

The proof of (ii): $\bar{S}_1 \leq \lambda_1$.

In this case, we have, $\lim\limits_{S \to 0^+} F_1(S) = 0$, $\lim\limits_{S \to \lambda_1^-} F_1(S) = -\infty$, $\lim\limits_{S \to \lambda_1^+} F_1(S) = +\infty$, 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 $\theta \in (0, \min\limits_{\lambda_1 < S \leq K} F_1(S))$ will satisfy formula (9).

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

It follows that $\lim\limits_{S \to 0^+} F_1(S) = 0$, $\lim\limits_{S \to \lambda_1} F_1(S) = \frac{2\gamma \lambda_1^2 (K - a_1 - b_1 - 3\lambda_1)}{d_1 K (a_1 b_1 - \lambda_1^2)}$ (by L'Hospital law), $F_1(S) \geqslant 0$ for $S \in (0, K]$, and $F_1(S)$ is continuous in $(0, K)$.

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

$$\begin{aligned} F_1(\eta \lambda_1) &= \frac{h_1(\lambda_1) - h(\eta \lambda_1)}{(\eta \lambda_1 - \lambda_1)\left(\frac{m_1 - a_1 - b_1}{m_1} - \frac{\eta \lambda_1 + \lambda_1}{m_1}\right) - \frac{a_1 b_1}{m_1} \ln \eta} \\ &= \frac{2\gamma \lambda_1^2 (\eta - 1)^2 ((\eta + 2)\lambda_1 + a_1 + b_1 - K)}{d_1 K (2a_1 b_1 (\eta - 1 - \ln \eta) - (\eta - 1)^2 \lambda_1^2)}, \quad \eta \in (0, K/\lambda_1), \eta \neq 1. \end{aligned}$$

Consider the function

$$f_1(\eta) = (\eta - 1)^2 \left((\eta + 2)\lambda_1^2 + a_1 + b_1 - K \right)$$
$$- \pi \left(2a_1b_1(\eta - 1 - \ln \eta) - (\eta - 1)^2\lambda_1^2 \right), \tag{11}$$

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

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

$$f_1'(\eta) = 3\lambda_1(\eta^2 - 1) + 2\pi a_1 b_1 \frac{\eta - 1}{\eta} + 2(\eta - 1)(a_1 + b_1 - K + \lambda_1^2\pi).$$

Moreover,

$$f_1''(\eta) = 6\lambda_1\eta - 2\pi a_1b_1/\eta^2 + 2(a_1 + b_1 - K + \lambda_1^2\pi).$$

Let $\eta = 1$. We can choose

$$\pi = \pi_0 = \frac{3\lambda_1 + a_1 + b_1 - K}{a_1b_1 - \lambda_1^2}, \tag{12}$$

Such that $f_1''(1) = 0$. In other words, when π takes the value of 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 by the definition of λ_1,

$$m_1 - a_1 - b_1 = 2\lambda_1 + \sqrt{(m_1 - a_1 - b_1)^2 - 4a_1b_1} > 2\lambda_1,$$

thus

$$a_1b_1 - \lambda_1^2 = (m_1 - a_1 - b_1)\lambda_1 - 2\lambda_1^2 > 0,$$

and $\pi_0 > 0$.

Now by

$$f_1'''(\eta) = 6\lambda_1 + 4\pi a_1b_1/\eta^3 > 0, \quad \text{for } \eta \in (0, K/\lambda_1), \quad \text{or} \quad S \in (0, K)$$

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

$$\frac{(\eta - 1)^2((\eta + 2)\lambda_1 + a_1 + b_1 - K)}{2a_1b_1(\eta - 1 - \ln \eta) - (\eta - 1)^2\lambda_1^2} > \pi_0. \tag{13}$$

Thus,

$$
\begin{aligned}
F_1(S) &= \frac{2\gamma\lambda_1^2(\eta-1)^2((\eta+2)\lambda_1 + a_1 + b_1 - K)}{d_1 K(2a_1 b_1(\eta - 1 - \ln \eta) - (\eta - 1)^2\lambda_1^2)} \\
&> \frac{2\gamma\lambda_1^2}{d_1 K}\pi_0 = \frac{2\gamma\lambda_1^2(3\lambda_1 + a_1 + b_1 - K)}{d_1 K(a_1 b_1 - \lambda_1^2)}, \quad \forall S \in (\lambda_1, K).
\end{aligned}
$$

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

$$
\frac{(\eta-1)^2((\eta+2)\lambda_1 + a_1 + b_1 - K)}{2a_1 b_1(\eta - 1 - \ln \eta) - (\eta - 1)^2\lambda_1^2} < \pi_0, \quad \forall S \in (0, \lambda_1). \tag{14}
$$

Thus,

$$
F_1(S) < \frac{2\gamma\lambda_1^2}{d_1 K}\pi_0 = \frac{2\gamma\lambda_1^2(3\lambda_1 + a_1 + b_1 - K)}{d_1 K(a_1 b_1 - \lambda_1^2)}, \quad \forall S \in (0, \lambda_1).
$$

Therefore, we always can choose

$$
\theta = \frac{2\gamma\lambda_1^2(3\lambda_1 + a_1 + b_1 - K)}{d_1 K(a_1 b_1 - \lambda_1^2)},
$$

such that the hypothesis (9) is satisfied. We complete the proof of Theorem 2.
Now we are in a position to prove the stability theorem.

Theorem 3. If $\lambda_1 < \lambda_2$, and if $S_1 \leq \lambda_1$, 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 $t \to +\infty$.

Proof. Let

$$
\begin{aligned}
V(S, x_1, x_2) = x_1^\theta \int_{\lambda_1}^S \frac{(m_1 - a_1 - b_1)\xi - \xi^2 - a_1 b_1}{m_1 \xi} d\xi \\
+ \int_{h_1(\lambda_1)}^{x_1} \xi^{\theta-1}(\xi - h_1(\lambda_1))d\xi + cx_1^\theta x_2, \tag{15}
\end{aligned}
$$

$\theta, c(\geqslant 0)$ will be determined later. It is easy to see that $V(S, x_1, x_2) \in C^1(R_+^3, R)$, $R_+^3 = \{(S, x_1, x_2) \mid S > 0, x_1 > 0, x_2 > 0\}$, 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

$$\dot{V}(S, x_1, x_2) = x_1^\theta \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1 S}$$

$$\times \left(\gamma S \left(1 - \frac{S}{K} \right) - \frac{m_1 d_1 S}{(a_1 + S)(b_1 + S)} x_1 - \frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} x_2 \right)$$

$$+ \left(x_1^\theta - h_1(\lambda_1) x_1^{\theta-1} + \theta x_1^{\theta-1} \int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)\xi - \xi^2 - a_1 b_1}{m_1 \xi} d\xi \right)$$

$$\times \left(\frac{m_1 d_1 S}{(a_1 + S)(b_1 + S)} - d_1 \right) x_1 + c\theta x_1^\theta \left(\frac{m_1 d_1 S}{(a_1 + S)(b_1 + S)} - d_1 \right) x_2$$

$$+ c x_1^\theta \left(\frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} - d_2 \right) x_2.$$

Denote

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

where

$$V_1 = x_1^\theta \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{(a_1 + S)(b_1 + S)} \left(\frac{\gamma}{m_1 d_1 K} (K - S)(a_1 + S)(b_1 + S) - h_1(\lambda_1) \right.$$

$$\left. + \theta \int_{\lambda_1}^{S} \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1 \xi} d\xi \right),$$

$$V_2 = c x_1^\theta x_2 \left(\frac{m_2 d_2 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)} - d_2 \right), \quad \text{and}$$

$$V_3 = x_1^\theta x_2 \left(-\frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1 S} \frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} \right.$$

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

By Theorem 2, there exists $\theta > 0$ such that (9) holds.

Notice that, λ_1' is as defined in (3),

$$(m_1 - a_1 - b_1)S - S^2 - a_1 b_1 = (S - \lambda_1)(S - \lambda_1'). \tag{16}$$

If $S < \lambda_1$,

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

and

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

Therefore,

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

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

Also, since $\lambda_1 < \lambda_2$, $V_2 < 0$. We now just need to show that there exists a c such that $V_3 \leq 0$. We shall find the c in two cases: (i) $a_1 \geqslant a_2$, or $b_1 \geqslant b_2$ (ii) $a_1 < a_2$ and $b_1 < b_2$.

In the first case of $a_1 \geqslant a_2$, or $b_1 \geqslant b_2$, 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

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

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

$$\begin{aligned}
\Delta(S) = {}& \frac{-m_2 \mathrm{d}_2}{(a_2 + S)(b_2 + S)} \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1} \\
& + c\theta \mathrm{d}_1 \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1} \\
& + c\left(\frac{m_2 \mathrm{d}_2 S}{(a_2 + S)(b_2 + S)} - \frac{m_2 \mathrm{d}_2 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right).
\end{aligned} \tag{17}$$

It follows that

$$\begin{aligned}
\Delta(S) = {}& \frac{-m_2 \mathrm{d}_2}{m_1(a_2 + S)(b_2 + S)}(S - \lambda_1)(\lambda_1' - S) + c\theta \frac{(S - \lambda_1)(\lambda_1' - S)}{(a_1 + S)(b_1 + S)} \\
& + c\frac{m_2 \mathrm{d}_1(S - \lambda_1)(a_2 b_2 - S\lambda_1)}{(a_2 + S)(b_2 + S)(a_2 + \lambda_1)(b_2 + \lambda_1)};
\end{aligned}$$

or,

$$\begin{aligned}
\Delta(S) = {}& \frac{S - \lambda_1}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)} \left(\frac{-m_2 \mathrm{d}_2(\lambda_1' - S)(a_1 + S)(b_1 + S)}{m_1} \right. \\
& \left. + c\theta(\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{cm_1 \mathrm{d}_1(a_2 b_2 - S\lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right).
\end{aligned} \tag{18}$$

Define

$$\Psi(S) = \frac{\frac{m_2 d_2}{m_1}(a_1 + S)(b_1 + S)}{\theta(\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{m_1 d_1(a_2 b_2 - S\lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)}}. \tag{19}$$

That is

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

Since

$$\Psi'(S) = \frac{m_2 d_2 / m_1 \Theta(S)}{-\left(\theta(\lambda_1' - S)\left(1 + \frac{a_2 - a_1}{a_1 + S}\right)\left(1 + \frac{b_2 - b_1}{b_1 + S}\right) + \frac{m_1 d_1(a_2 b_2 - S\lambda_1)}{(a_2 + \lambda_1)(b_2 + \lambda_1)}\right)^2}, \tag{20}$$

where

$$\Theta(S) = -\theta\left(1 + \frac{a_2 - a_1}{a_1 + S}\right)\left(1 + \frac{b_2 - b_1}{b_1 + S}\right) + \theta(\lambda_1' - S)\left(-\frac{a_2 - a_1}{(a_1 + S)^2}\right)\left(1 + \frac{b_2 - b_1}{b_1 + S}\right)$$
$$+ \theta(\lambda_1' - S)\left(1 + \frac{a_2 - a_1}{a_1 + S}\right)\left(-\frac{b_2 - b_1}{(b_1 + S)^2}\right) - \frac{m_1 d_1 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)}$$
$$< 0. \tag{21}$$

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

By (B2), $\lambda_2' > K$, then $a_2 b_2 = \lambda_2 \lambda_2' > \lambda_2 K$, or $a_2 b_2 - \lambda_2 K > 0$, which implies

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

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

$$\Delta(S) = \left(\theta(\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{m_1 d_1(a_2 b_2 - S\lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)}\right)$$
$$\cdot \frac{S - \lambda_1}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)}(\Psi(\lambda_1) - \Psi(S))$$
$$\leq 0 \text{ (since } \Psi(S) \text{ increases).} \tag{22}$$

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

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

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

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

$$S' = \gamma \lambda_1 \left(1 - \frac{\lambda_1}{K}\right) - \frac{m_1 d \lambda_1}{(a_1 + \lambda_1)(b_1 + \lambda_1)} x_1 = 0. \tag{23}$$

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.

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, 8, 11]. Moreover, in most of the population models, the functional responses are chosen to be some monotone functions such as Monod (or Michaelis–Menten) function. But in real world applications, it is not always the case. The one with non-monotone inhibition response is, of course, worth a further study.

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

$$S_2 = \left(k_2 - a_2 - b_2 + \sqrt{k_2^2 + a_2^2 + b_2^2 - a_2 b_2 + K a_2 + K b_2}\right) \Big/ 3, \qquad (24)$$

Theorem 2 is also valid for $S_2 \leq \lambda_2$. Moreover, in the proof of Theorem 3, if we use $\lambda_1 \leq \lambda_2$ instead of $\lambda_1 < \lambda_2$, then step by step the proof is still working. Therefore, I would like to make a guess that if $\lambda_1 = \lambda_2$, the two predator organisms having same "break-even" concentration, both organisms will survive. Therefore, to study the nonlinear oscillation between the two predator organisms and the prey organism must be very interesting.

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