

Limit cycles of a three-dimensional bio-reactor with inhibition responses

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Abstract By using a relation connecting the global stability and Hopf bifurcation, the existence of limit cycles in 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 obtained. We also correct the proof of the main result in a previous paper of the same model (Su et al., J. Math. Chem., 2007).

Keywords Global stability · Center manifold · Competition model · Limit cycles

1 Introduction

The purpose of this short article is to correct the mistake in the proof of the main result in paper [1] (Journal of Mathematical Chemistry, 2007), and then give an analytical proof of the existence of 3-D limit cycles in the 3-D bio-reactor model of exploitative competition of two predator organisms with inhibition responses for the same renewable organism with reproductive properties. The model studied in [1] takes the form:

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

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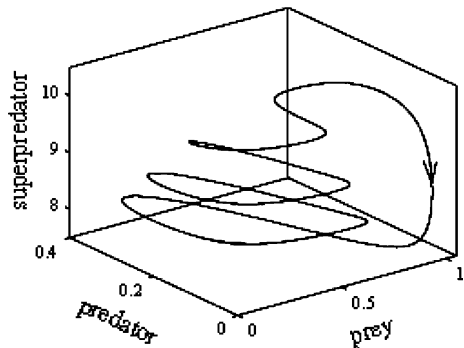
$$\frac{dx_2}{dt} = \left(\frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} - d_2 \right) x_2, \quad S(0) > 0, x_1(0) > 0, x_2(0) > 0. \tag{1}$$

This can be considered a generalization of the so-called Rosenzweig–MacArthur model of three level food chains [2]. It can also be considered as the 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 is the growth rate, and K , the carrying capacity of the renewable resource S . m_i, a_i and $d_i, i = 1, 2$, 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 $\frac{m_1 d_1 S}{(a_1 + S)(b_1 + S)}$ and $\frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)}$, respectively. δ_i is the yield constant for the predator x_i , which is assumed as 1 in our discussion. It is noticed that in the case of the Rosenzweig–MacArthur model, the functional response is in Michaelis–Menten type: $\frac{m_1 S}{a_1 + S}$ and $\frac{m_2 S}{a_2 + S}$, which are monotone, but in the inhibition type is non-monotone.

The relationship between dynamic complexity and mean yield of such exploited food chains was first studied by Rosenzweig in his famous paper, where he says “Man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance” [3]. It has been shown (May [4] and Gilpin [5]) that for low prey carrying capacities such food chains settle to a positive equilibrium, while for higher carrying capacities the asymptotic regime is cyclic. The positive equilibrium loses stability when the carrying capacity is increased and when it becomes unstable, the attractor becomes a stable limit cycle. It is also proved (in [4]) that the mean yield associated to the attractor of a food chain first increases and then decreases with prey carrying capacity and reaches its maximum for $K = K^*$, where K^* is the critical value of the carrying capacity separating stationary from cyclic regimes.

As to the cyclic regimes, it was shown that there are either low-frequency or high-frequency regimes. A low-frequency limit cycle obtained by a computer numerical simulation for Rosenzweig–MacArthur model is shown in Fig. 1, as an example ([2]).

Fig. 1 A limit cycle of low-frequency in Rosenzweig–MacArthur model



Since the behavior of solutions of the three-level food-chain bio-reactor model (1) is very complicated, even for the case of simple Michaelis–Menten type response, most of the results are derived by numerical simulation. Therefore, a further study is very necessary. Recently, [1] using a modified Lyapunov function and LaSalle’s invariant principle proved the global stability of the model. The 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. In the proof of their main result (Theorem 3, [1]), it is supposed to show that $\dot{V} \leq 0$, where

$$V(S, x_1, x_2) = x_1^\theta \int_{\lambda_1}^S \frac{(m_1 - a_1 - b_1)\xi - \xi^2 - a_1 b_1}{m_1 \xi} d\xi + \int_{h_1(\lambda_1)}^{x_1} \xi^{\theta-1} (\xi - h_1(\lambda_1)) d\xi + c x_1^\theta x_2. \quad (2)$$

In the process of differentiation of $V(S, x_1, x_2)$, both the parameter θ and c were assumed to be constants. Actually, in [1], it was chosen that $c = \Psi(\lambda_1) (> 0)$. Unfortunately, in that case the main formula (22) in the proof of [1] is not valid because $\Delta(S)$ takes the form:

$$\Delta(S) = \left(\theta d_1 (\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{m_2 d_2 (a_2 b_2 - S \lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right) \cdot \frac{S - \lambda_1}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)} (\Psi(\lambda_1) - (\lambda_1' - S)\Psi(S)), \quad (3)$$

which has a factor $\lambda_1' - S$ before $\psi(S)$ and which is not always ≤ 0 even though $\Psi(S)$ is increasing. Therefore, the proof of Theorem 3 of [1] is wrong.

Moreover, formula (16) in [1] has a sign problem which should be

$$(m_1 - a_1 - b_1)S - S^2 - a_1 b_1 = (S - \lambda_1)(\lambda_1' - S), \quad (4)$$

and there are mistakes in the expressions of V_3 , $\Delta(S)$, $\psi(S)$, $\psi'(S)$ and also in formulas (17–21) and (24).

The construction of a Lyapunov function in establishing the global stability of an equilibrium is not easy. However, once the Lyapunov function is obtained, then the global stability follows directly from the LaSalle’s invariant principle. The basic idea of [1] is correct and interesting if we can fix the proof by choose the parameter c as a variable not a constant and make sure that the Lyapunov–LaSalle’s principle also works for the food-chain bio-reactor with the non-monotonic inhibition responses.

As is well known, a mathematical proof instead of a computer simulation of the existence of limit cycles for a 3-D differential system is very hard. This is because the powerful tools in the plane system like Poincaré–Bendixson theorem cannot be applied directly to the cases of $n \geq 3$, in general. Some counterexamples can be found in D’Heedene [6] and Schweitzer [7]. In this paper, by applying the center manifold theorem [8, 9], we build a relationship between the global stability and the 3-D Hopf

bifurcation. Then the existence of limit cycles for the three-dimensional food-chain bio-reactor model is obtained consequently. The method used here can be extended to many other 3-D differential equation systems. Here we just provide another example. By comparing to prove the existence of 3-D limit cycles directly and analytically, our method is much simple.

The main results are presented in the next two sections.

2 Proof of Theorem 3 of [1]

Theorem A If $\lambda_1 < \lambda_2$, and if $S_1 \leq \lambda_1$, then $E_1(\lambda_1, h_1(\lambda_1), 0)$ is globally asymptotically stable.

Proof Let $V(S, x_1, x_2)$ be defined as in (2). The derivative of V along the trajectory of system (1) is

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

where θ is a constant, and $c = c(S)$, a function of S , c' is the derivative of $c(S)$. Denote

$$\dot{V}(S, x_1, x_2) = V_1 + V_2 + V_3 + V_4,$$

with

$$\begin{aligned} V_1 = & x_1^\theta \frac{(m_1 - a_1 - b_1)S - S^2 - a_1b_1}{(a_1 + S)(b_1 + S)} \left(\frac{\gamma}{m_1d_1K} (K - S)(a_1 + S)(b_1 + S) - h_1(\lambda_1) \right. \\ & \left. + \theta \int_{\lambda_1}^S \frac{(m_1 - a_1 - b_1)S - S^2 - a_1b_1}{m_1\xi} d\xi \right), \end{aligned}$$

$$\begin{aligned}
 V_2 &= cx_1^\theta x_2 \left(\frac{m_2 d_2 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)} - d_2 \right), \\
 V_3 &= x_1^\theta x_2 \left(-\frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1 S} \frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} \right. \\
 &\quad \left. + c\theta \left(\frac{m_1 d_1 S}{(a_1 + S)(b_1 + S)} - d_1 \right) \right. \\
 &\quad \left. + c \left(\frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} - \frac{m_2 d_2 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right) \right), \quad V_4 = c'(S)x_1^\theta x_2.
 \end{aligned}$$

It is easy to see that V_1 and V_2 are non-positive as shown in [1]. We only prove V_3 and V_4 non-positive. For that purpose, let

$$\begin{aligned}
 \Delta(S) &= \frac{-m_2 d_2}{(a_2 + S)(b_2 + S)} \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{m_1} \\
 &\quad + c\theta d_1 \frac{(m_1 - a_1 - b_1)S - S^2 - a_1 b_1}{(a_1 + S)(b_1 + S)} \\
 &\quad + c \left(\frac{m_2 d_2 S}{(a_2 + S)(b_2 + S)} - \frac{m_2 d_2 \lambda_1}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right). \quad (5)
 \end{aligned}$$

By (4), it follows that

$$\begin{aligned}
 \Delta(S) &= \frac{-m_2 d_2}{m_1(a_2 + S)(b_2 + S)} (S - \lambda_1)(\lambda_1' - S) + c\theta d_1 \frac{(S - \lambda_1)(\lambda_1' - S)}{(a_1 + S)(b_1 + S)} \\
 &\quad + c \frac{m_2 d_2 (S - \lambda_1)(a_2 b_2 - S \lambda_1)}{(a_2 + S)(b_2 + S)(a_2 + \lambda_1)(b_2 + \lambda_1)};
 \end{aligned}$$

and hence,

$$\begin{aligned}
 \Delta(S) &= \frac{S - \lambda_1}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)} \left(\frac{-m_2 d_2 (\lambda_1' - S)(a_1 + S)(b_1 + S)}{m_1} \right. \\
 &\quad \left. + c\theta d_1 (\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{cm_2 d_2 (a_2 b_2 - S \lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right). \quad (6)
 \end{aligned}$$

Define

$$\Psi(S) = \frac{\frac{m_2 d_2}{m_1} (a_1 + S)(b_1 + S)}{\theta d_1 (\lambda_1' - S)(a_2 + S)(b_2 + S) + \frac{m_2 d_2 (a_2 b_2 - S \lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)}}. \quad (7)$$

Following the same argument as in [1], we can show that $\Psi'(S) > 0$.

Since $a_2b_2 - S\lambda_1 > 0$, we can choose $c = (\lambda'_1 - S)\Psi(\lambda_1) > 0$. It follows that

$$\begin{aligned} \Delta(S) &= \left(\theta(\lambda'_1 - S)(a_2 + S)(b_2 + S) + \frac{m_1d_1(a_2b_2 - S\lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right) \\ &\quad \times \frac{(S - \lambda_1)}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)} (c - (\lambda'_1 - S)\Psi(S)) \\ &= \left(\theta(\lambda'_1 - S)(a_2 + S)(b_2 + S) + \frac{m_1d_1(a_2b_2 - S\lambda_1)(a_1 + S)(b_1 + S)}{(a_2 + \lambda_1)(b_2 + \lambda_1)} \right) \\ &\quad \times \frac{(S - \lambda_1)(\lambda'_1 - S)}{(a_2 + S)(a_1 + S)(b_2 + S)(b_1 + S)} (\psi(\lambda_1) - \Psi(S)) \\ &\leq 0, \end{aligned} \tag{8}$$

since $\Psi'(S) > 0$.

Therefore, $\Delta(S)$ is always negative if $S \neq \lambda_1$, and so is V_3 .

For V_4 , we have

$$V_4 = c'(S)x_1^\theta x_2 = -x_1^\theta x_2 \leq 0.$$

Therefore, $\dot{V}(S, x, y) = V_1 + V_2 + V_3 + V_4 \leq 0$.

Then using the LaSalle’s invariant principle, the same argument as in [1] will finish the proof of Theorem A. □

3 Existence of 3-D limit cycles

The following lemma is useful for the existence of limit cycles. Let μ be the bifurcation parameter, and rewrite system (1) in μ as follows:

$$\frac{dX}{dt} = f(X, \mu). \tag{9}$$

The global stability of an equilibrium is connected with the Hopf bifurcation by the center manifold theorem.

Theorem B Let W be an open set in R^3 , $O = (0, 0, 0) \in W$, and the analytic function f is defined as $f : W \times (-\mu_0, \mu_0) \rightarrow R^3$, 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 (9) 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 μ , $\mu > 0$ such that system (9) has an asymptotically stable closed orbit surrounding $(0, 0, 0)$.

The proof of Theorem B can be found in [8,9]. In order to use this result, we prove the next theorem.

Theorem 1 If $\lambda_1 < \lambda_2$ and $S_1 > \lambda_1$, E_1 is an unstable equilibrium of system (1).

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

$$(r - a_{33})(r^2 - a_{11}r - a_{12}a_{21}) = 0, \quad (10)$$

where

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

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

Assume the three roots of (10) as r_1, r_2 and r_3 . It follows that

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

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

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

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 1 is complete. \square

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

Theorem 2 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

Proof 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:

$$\begin{aligned} S_1' &= \varphi_1(S, x_1, x_2, \mu), \\ x_1' &= \varphi_2(S, x_1, x_2, \mu), \\ x_2' &= \varphi_3(S, x_1, x_2, \mu). \end{aligned} \tag{11}$$

Use the variable changes:

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

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

$$\frac{dX}{dt} = f(X, \mu), \tag{12}$$

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

Consider system (12) and its Jacobian at $\mu = 0$ and $(\bar{S}, \bar{x}_1, \bar{x}_2) = (0, 0, 0)$,

$$\begin{aligned} &J(f(O, 0)) \\ &= J(\bar{S}, \bar{x}_1, \bar{x}_2) \bigg|_{\substack{(\bar{S}, \bar{x}_1, \bar{x}_2) = (0, 0, 0) \\ \mu = 0}} = J(S, x_1, x_2) \bigg|_{\substack{(S, x_2, x_3) = (\lambda_1, h_1(\lambda_1), 0) \\ S_1 = \lambda_1}} \end{aligned}$$

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

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

By Theorem B when $\lambda_1 < \lambda_2$ and $S_1 \leq \lambda_1$, 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 $\bar{S}, \bar{x}_1, \bar{x}_2$ 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 (12) 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 $\mu, \mu > 0$, system (12) has an asymptotically stable closed orbit surrounding $(0, 0, 0)$. In other words, for $0 < S_1 - \lambda_1 \ll 1$, system (1) has an asymptotically stable closed orbit surrounding $E_1(\lambda_1, h(\lambda_1), 0)$. The proof of Theorem 2 is complete. \square

Theorem 3 If $\lambda_1 < \lambda_2$, system (1) has at least one limit cycle around the equilibrium E_1 .

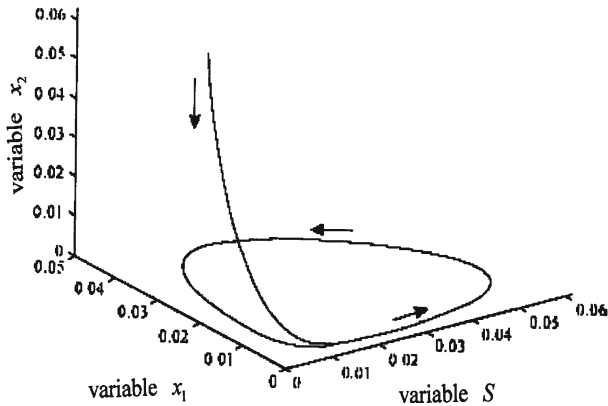


Fig. 2 Example of limit cycles of competition in bio-reactor

4 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 [10, 11]. 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.

Recently, a quite similar food chain model but with Monod functional response is published [12] with some numerical results. The limit cycles in the numerical simulation of [12] take the following forms which give us some idea about the locations and shapes of limit cycles in the model (1.1) (Fig. 2).

It is known to all that a limit cycle in 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 [13, 14]. Therefore, a further mathematical analysis of the food-chain bio-reactor is definitely necessary.

We also correct the mistakes in the proof of the main result in paper [1], which helps the readers to understand the competition in the bio-reactor system more precisely and clearly.

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