

A Mathematical Model Related To Chemostat With Variable Yields

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Abstract

In this paper, a three dimensional chemostat model with variable yields is studied. The properties of the steady state points, the local and global stability, the Hopf bifurcation and the positive invariant set for the system are investigated by qualitative analysis of differential equations.

Key words: · Continuous culture · Variable yield · Stability · Hopf bifurcation.

I. Introduction

Mathematical modeling is a branch of bioscience which is a process that makes a relation between biology and mathematics. The chemostat is both a laboratory device used in biological science, and a well established mathematical model that is important to fields as diverse as ecology, pharmacological compartmental modeling, chemical engineering and medicine. In ecology, it serves as the model of the simple lake where the populations compete for the available nutrient. The analysis of a big number of chemostat models can be found in the monograph Waltman and Smith [10].

Most of the models in chemostat assume that the yield coefficient is a constant. But the accumulation of experimental data suggests that a constant yield fails to explain the observed oscillatory behavior in the chemostat [3]. Cooke [1,2] suggested a linear function for the yield coefficient and declared that a limit cycle may exist in his model. Huang [11,12] and Pilyugin and Waltman [7] constructed the model with a general variable yield, and studied the multiple limit cycles and the hopf bifurcation for the model. However, all these model considered only one microorganism in the system. A three dimensional chemostat with two microorganisms which are both with linear yields was studied by [9]. In the model, the functional reaction functions were in the Monod type, and the yield coefficients were assumed linear function of the concentration of nutrient. The stability of the solution was obtained. Xucheng Huang and Lemin Zhu [5] studied a three dimensional chemostat with quadratic yields. A three dimensional continuous fermentation model with yield coefficients $\delta_1 = A + BS^3$ and $\delta_2 = C + DS^4$ was discussed in [6]. They studied the stability of the equilibrium points, the existence of limit cycles, the hopf bifurcation and the positive invariant set for their model.

In this paper, we study a three dimensional chemostat model of which one yield coefficient is linear and another yield coefficient is cubic functions of the concentration of nutrient. In section II, we formulate the chemostat model with two microorganisms which are with variable yield coefficients and illustrate the process of non-dimensionalization to simplify the system. In section III,

we study the steady state points with their stability, the positive invariant set, the existence of limit cycles, and the Hopf bifurcation in the two dimensional stable manifold of one microorganism when the other is going to vanish in the competition. In section IV, MATHEMATICA is used for numerical simulation to illustrate the key points of our model. Finally, conclusion of the paper is carried out in section V.

II. The Model

At time t , let $S(t)$ denote the concentration of nutrient in the vessel, $x(t)$ and $y(t)$ the concentration of two microorganism. The model takes the form

$$\begin{aligned} \frac{dS}{dt} &= (S_0 - S)Q - \frac{1}{\delta_1} \left(\frac{m_1 S}{k_1 + S} - L \right) x - \frac{1}{\delta_2} \frac{m_2 S}{k_2 + S} y \\ \frac{dx}{dt} &= x \left(\frac{m_1 S}{k_1 + S} - L - Q \right) \\ \frac{dy}{dt} &= y \left(\frac{m_2 S}{k_2 + S} - Q \right) \end{aligned} \quad (1)$$

$$S(0) > 0, \quad x(0) > 0, \quad y(0) > 0.$$

where S_0 is the input concentration of nutrient, Q is the washout rate, m_i , the maximal growth rates, k_i , the Michaelis-Menton constants, δ_i , the yield coefficients and L , is the intrinsic consumption rate for the first microorganism, which are all positive. This model is usually called the Monod model or the model with Michaelis Menten dynamics.

Here we investigate the system (1) with yield coefficients $\delta_1 = A + BS$, $\delta_2 = C + DS^3$, which means that the production of the microbial biomasses is very sensitive to the concentration of the nutrient.

In system (1) we have used the growth rate functions

$$F_i(S) = \frac{m_i S}{k_i + S}, \text{ where } i = 1, 2$$

which have the following common features:

- $F_i(0) = 0$
- $F_i(S)$ is an increasing function of S .
- $F_i(S)$ approaches a constant value as S approaches infinity.

Performing the standard scaling for the chemostat, let

$$\bar{S} = \frac{S}{S_0}, \quad \bar{x} = \frac{x}{S_0}, \quad \bar{y} = \frac{y}{S_0}, \quad T = Qt, \quad \bar{m}_i = \frac{m_i}{Q}, \quad \bar{k}_i = \frac{k_i}{S_0},$$

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$$\bar{L} = \frac{L}{Q}$$

then drop the bars and replace T with t , system (1) becomes

$$\begin{aligned} \frac{dS}{dt} &= (1 - S) - \frac{1}{A + BS_0S} \left(\frac{m_1S}{k_1 + S} - L \right) x - \frac{1}{C + DS_0^3S^3} \left(\frac{m_2S}{k_2 + S} \right) y \\ \frac{dx}{dt} &= \left(\frac{m_1S}{k_1 + S} - L - 1 \right) x \\ \frac{dy}{dt} &= \left(\frac{m_2S}{k_2 + S} - 1 \right) y \end{aligned} \tag{2}$$

The parameters have been scaled by the operating environment of the chemostat, which are determined by S_0 and Q . The variables are non-dimensional and the discussion is in $R_+^3 = \{(S, x, y) | 0 \leq S \leq 1, x \geq 0, y \geq 0\}$.

To be biologically meaningful, it is important to prove that the solutions of the model (2), with positive initial data, will remain positive for all time $t > 0$. The proof of the following lemma is similar to [8].

Lemma 1: The solutions $S(t), x(t), y(t)$ of (2) are positive for all $t > 0$ and for large $t, S(t) < 1$.

Lemma 2: For the system (2)

(i) if $m_1 < L + 1$, then $\frac{dx}{dt} < 0$ and $\lim_{t \rightarrow \infty} x(t) = 0$

(ii) if $m_2 < 1$, then $\frac{dy}{dt} < 0$ and $\lim_{t \rightarrow \infty} y(t) = 0$.

Proof: Let $F_1(S) = \frac{m_1S}{k_1 + S}$. Since $F_1'(S) > 0$ with $F_1(0) = 0$ and $m_1 = \lim_{S \rightarrow \infty} F_1(S)$, we have $L + 1 - m_1 > 0$. Thus there is $0 < \alpha = \min_{t \geq 0} \{(L + 1) - \max_{0 \leq S < \infty} |F_1(S)|\}$ such that $\frac{dx}{dt} < -\alpha x(t)$ for sufficiently large t by the second the equation of (2). This shows $x(t) < x(0) \exp[-\alpha t]$ and since $x(t) > 0$ for $t > 0$, so we have $\lim_{t \rightarrow \infty} x(t) = 0$. This completes the proof (i). Similarly, we can prove (ii).

III. Steady State Points and Their Stability Analysis

The system (2) has three steady state points in R_+^3 :

$$E_0 = (1, 0, 0),$$

$$E_1 = (\lambda_1, (1 - \lambda_1)(A + B\lambda_1 S_0), 0) \text{ and}$$

$$E_2 = (\lambda_2, 0, (1 - \lambda_2)(C + DS_0^3 \lambda_2^3))$$

where $\lambda_1 = \frac{k_1(L+1)}{m_1 - (L+1)}$ and $\lambda_2 = \frac{k_2}{m_2 - 1}$ are respectively unique solutions of

$$\frac{m_1S}{k_1 + S} - L - 1 = 0 \text{ and } \frac{m_2S}{k_2 + S} - 1 = 0.$$

E_0, E_1 and E_2 will exist if they have non-negative components. The steady state point E_0 always exists. The other E_i 's exist if $0 < \lambda_i < 1$ ($i = 1, 2$).

The parameter values λ_1, λ_2 represent the break-even concentration of the nutrient for the microorganism $x(t)$ and the microorganism $y(t)$ respectively and play an

important role in determining competitive ability. With the help of Lemma 1, we can prove the following lemma.

Lemma 3: (i) If $m_1 > L + 1$ and $\lambda_1 > 1$ then $\frac{dx}{dt} < 0$ and $\lim_{t \rightarrow \infty} x(t) = 0$; (ii) If $m_2 > 1$ and $\lambda_2 > 1$ then $\frac{dy}{dt} < 0$ and $\lim_{t \rightarrow \infty} y(t) = 0$.

So in order to avoid the microorganisms vanishing, we need to assume that

$$0 < \lambda_i < 1, \quad i = 1, 2$$

(which implies $m_1 > (k_1 + 1)(L + 1)$ and $m_2 > k_2 + 1$) (3)

Theorem 1: Let

$$D = \left\{ \begin{aligned} &(S, x, y) | 0 \leq S \leq l - x - y, \\ &0 \leq x \leq (A + BS_0\lambda_1)(1 - \lambda_1) + \varepsilon_0, \\ &0 \leq y \leq (C + DS_0^3\lambda_2^3)(1 - \lambda_2) + \varepsilon_0, \\ &0 < l < \infty, \varepsilon_0 > 0, \text{ constant} \end{aligned} \right\}.$$

Then D is positively invariant under the system (2). In other words, any trajectory initiated $(S, x, y) \in R_+^3$ enters into D as $t \rightarrow +\infty$.

Proof: By the first equation of (2), any trajectory in $D_1 = \{(S, x, y) | S < 0, x > 0, y > 0\}$ will cross the face $S = 0$ into R_+^3 . But the trajectory in $D \subset R_+^3$ will not cross $S = 0$ and go to D_1 .

Consider the face $W = S + x + y - l = 0$ ($0 < l < +\infty$) and it is easy to see that

$$\begin{aligned} \frac{dW}{dt} \Big|_{W=0} &= \left(\frac{dS}{dt} + \frac{dx}{dt} + \frac{dy}{dt} \right) \Big|_{S=l-x-y} \\ &= 1 - l - x \left(\frac{1}{A + BS_0(l-x-y)} - 1 \right) \left(\frac{m_1(l-x-y)}{k_1 + l-x-y} - L \right) - \\ &\quad y \left(\frac{1}{C + DS_0^3(l-x-y)^3} - 1 \right) \left(\frac{m_2(l-x-y)}{k_2 + l-x-y} \right). \end{aligned}$$

Since x, y are bounded and $A, B, C, D, S_0, m_i, k_i, i = 1, 2$ are all positive, $\frac{dW}{dt} \Big|_{W=0} < 0$ for sufficiently large l . Therefore, the trajectory of (2) will cross the face $W = 0$ into D from outside to inside. Moreover, both $x = 0$ and $y = 0$ are the solution faces of the system (2). Thus D is positively invariant under the system (2). The proof of Theorem 1 is completed.

Let

$$\begin{aligned} R_1 &= S_0 \frac{(1-\lambda_1)\{(k_1+\lambda_1)^2 - k_1 m_1 \lambda_1\} - \lambda_1(k_1 + \lambda_1)^2}{(k_1 + \lambda_1)^2 + (1 - \lambda_1)k_1 m_1} \\ R_2 &= S_0^3 \frac{(1-\lambda_2)\{3\lambda_2^2(k_2 + \lambda_2)^2 - k_2 m_2 \lambda_2^3\} - \lambda_2^3(k_2 + \lambda_2)^2}{(k_2 + \lambda_2)^2 + (1 - \lambda_2)k_2 m_2} \end{aligned} \tag{4}$$

III.A Local and Global Stability Analysis

The Jacobian matrix of the system (2) is

$$J(S, x, y) = \begin{bmatrix} T(S, x, y) & -\frac{1}{A + BS_0S} \left(\frac{m_1S}{k_1 + S} - L \right) & -\frac{1}{C + DS_0^3S^3} \left(\frac{m_2S}{k_2 + S} \right) \\ \frac{k_1 m_1 x}{(k_1 + S)^2} & \frac{m_1S}{k_1 + S} - L - 1 & 0 \\ \frac{k_2 m_2 y}{(k_2 + S)^2} & 0 & \frac{m_2S}{k_2 + S} - 1 \end{bmatrix}$$

where,

$$T(S, x, y) = -1 - \frac{x}{A+BS_0S} \frac{k_1 m_1}{(k_1+S)^2} + \frac{BS_0 x}{(A+BS_0S)^2} \left(\frac{m_1 S}{k_1+S} - L \right) - \frac{y}{C+DS_0^3 S^3} \frac{k_2 m_2}{(k_2+S)^2} + \frac{3DS_0^3 S^2 y}{(C+DS_0^3 S^3)^2} \left(\frac{m_2 S}{k_2+S} \right).$$

At E_0 , the eigenvalues of $J(E_0)$ are

$$-1, \frac{m_1}{k_1+1} - L - 1 \text{ and } \frac{m_2}{k_2+1} - 1.$$

Hence, E_0 is stable if $\lambda_1 > 1$ and $\lambda_2 > 1$.

At E_1 , the characteristics equation of $J(E_1)$ is

$$(r - a_1)(r^2 + b_1 r + c_1) = 0 \quad (5)$$

where

$$a_1 = \frac{m_2 \lambda_1}{k_2 + \lambda_1} - 1$$

$$b_1 = 1 + (1 - \lambda_1) \left\{ \frac{k_1 m_1}{(k_1 + \lambda_1)^2} - \frac{BS_0}{A + BS_0 \lambda_1} \right\}$$

$$c_1 = (1 - \lambda_1) \frac{k_1 m_1}{(k_1 + \lambda_1)^2} > 0.$$

Therefore, E_1 is stable iff the roots of (5) have negative real part. By Routh-Hurwitz criteria, the stability holds if and only if $a_1 < 0$ and $b_1 > 0$ or equivalently, $\lambda_1 < \lambda_2$ and $\frac{A}{B} > R_1$.

At E_2 , the characteristics equation of $J(E_2)$ is

$$(r - a_2)(r^2 + b_2 r + c_2) = 0 \quad (6)$$

where

$$a_2 = \frac{m_1 \lambda_2}{k_1 + \lambda_2} - L - 1$$

$$b_2 = 1 + (1 - \lambda_2) \left\{ \frac{k_2 m_2}{(k_2 + \lambda_2)^2} - \frac{3DS_0^3 \lambda_2^2}{C + DS_0^3 \lambda_2^3} \right\}$$

$$c_2 = (1 - \lambda_2) \frac{k_2 m_2}{(k_2 + \lambda_2)^2} > 0.$$

Therefore, E_2 is stable iff the roots of (6) have negative real part. By Routh-Hurwitz criteria, stability holds if and only if $a_2 < 0$ and $b_2 > 0$, or equivalently, $\lambda_2 < \lambda_1$ and $\frac{C}{D} > R_2$.

From the above stability analysis of the steady state points of system (2), we can summarize the results in the following theorem.

Theorem 2: The system (2) has three steady state points in R_+^3 : E_0 , E_1 and E_2 in which E_0 is stable if $\lambda_1 > 1$ and $\lambda_2 > 1$; unstable if $\lambda_1 < 1$ and $\lambda_2 < 1$. E_1 is stable if $A/B > R_1$ and $\lambda_1 < \lambda_2$; unstable if $A/B > R_1$ and $\lambda_1 > \lambda_2$, or $A/B < R_1$. E_2 is stable if $C/D > R_2$ and $\lambda_1 > \lambda_2$; unstable if $C/D > R_2$ and $\lambda_1 < \lambda_2$ or $C/D < R_2$.

Theorem 3: (a) If $\lambda_1 < \lambda_2$, and $A/B > R_1$, the steady state point E_1 is globally asymptotically stable in R_+^3 ; (b) If $\lambda_1 > \lambda_2$, and $C/D > R_2$, the steady state point E_2 is globally asymptotically stable, too.

Proof: Let

$$\theta = \left\{ \begin{array}{l} (S, x, y) | 0 \leq S \leq l - x - y, \\ 0 \leq x \leq (A + BS_0 \lambda_1)(1 - \lambda_1) + \varepsilon_0, \\ 0 \leq y \leq (C + DS_0^3 \lambda_2^3)(1 - \lambda_2) + \varepsilon_0, \\ 0 < l < \infty, \varepsilon_0 > 0 \end{array} \right\}$$

We first prove that θ is positively invariant set of (2).

Consider the face $S = 0$, and by equation (2),

$$\frac{dS}{dt} \Big|_{S=0} = 1 + \frac{Lx}{A} > 0.$$

Thus, any trajectory in $\{(S, x, y) | S < 0, x > 0, y > 0\}$ will go through $S = 0$ into R_+^3 , but the reverse is not true.

Consider the face $M = S + x + y - l = 0$ ($0 < l < +\infty$),

$$\frac{dM}{dt} \Big|_{M=0} = 1 - l - x \left(\frac{1}{A+BS_0(l-x-y)} - 1 \right) \left(\frac{m_1(l-x-y)}{k_1+l-x-y} - L \right) - y \left(\frac{1}{C+DS_0^3(l-x-y)^3} - 1 \right) \frac{m_2(l-x-y)}{k_2+l-x-y}.$$

Since x, y are bounded and all the parameters are positive, $\frac{dM}{dt} \Big|_{M=0} < 0$ for sufficiently large l . That is, any trajectory in R_+^3 will cross $M = S + x + y - l = 0$ into θ .

Moreover, because both $x = 0$ and $y = 0$ are the solutions of the system (2). Thus θ is positively invariant set of the system (2). In other words, any trajectory initiating in R_+^3 will go to θ when $t \rightarrow +\infty$. Therefore, both E_1 and E_2 are globally asymptotically stable. The proof of Theorem 3 is completed.

In the case when one of the microorganisms is going to vanish, some nonlinear oscillatory phenomena for the microorganism and the nutrient occur. In other words, in the corresponding stable manifold, a limit cycle exists. Regarding the dynamical system on the two dimensional faces $x = 0$ or $y = 0$, we have the following results.

For E_2 , we study the phase portrait in the solution plane $x = 0$. In this case the system (2) takes the form

$$\begin{aligned} \frac{dS}{dt} &= (1 - S) - \frac{1}{C + DS_0^3 S^3} \left(\frac{m_2 S}{k_2 + S} \right) y \\ \frac{dy}{dt} &= \left(\frac{m_2 S}{k_2 + S} - 1 \right) y \end{aligned} \quad (7)$$

We would like to point out that the system (7) is a special case of the simple chemostat system:

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{g(S)}{F(S)} y \\ \frac{dy}{dt} &= (g(S) - 1) y \end{aligned} \quad (8)$$

if letting $F(S) = C + DS_0^3 S^3$, $g(S) = \frac{m_2 S}{k_2 + S}$.

In the region $\{(S, y) | 0 \leq S \leq 1, y \geq 0\}$, the system (8) has two steady state points $(1, 0)$, and (S^*, y^*) if $g(1) > 1$, where $y^* = (1 - S^*)F(S^*)$, $S^* = g^{-1}(1)$.

It is easy to see that $(1, 0)$ is globally asymptotically stable if $g(1) < 1$, unstable if $g(1) > 1$. Denote

$$p = 1 + y * \left. \frac{d}{ds} \left(\frac{g}{F} \right) \right|_{S=S^*} \tag{9}$$

The following theorem is established [4].

Theorem 4: Assume $g(1) > 1$. If $p > 0$ then (S^*, y^*) is stable; if $p < 0$, it is unstable and there exists at least one limit cycle in (8) surrounding the equilibrium (S^*, y^*) .

Then, we have

Theorem 5: Assume (3) or $m_2 > k_2 + 1$. The system (7) has two steady state points: $M_1(1,0)$, which is unstable, and $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^3\lambda_2^3))$, which is stable if $C/D > R_2$, and unstable if $C/D < R_2$. In the case when M_2 is unstable, there exists at least one limit cycle in (7) surrounding M_2 .

In the face $y = 0$, the system (2) takes the form

$$\begin{aligned} \frac{ds}{dt} &= 1 - S - \frac{1}{A + BS_0S} \left(\frac{m_1S}{k_1 + S} - L \right) x \\ \frac{dx}{dt} &= \left(\frac{m_1S}{k_1 + S} - L - 1 \right) x \end{aligned} \tag{10}$$

which is also a special case of (8) with

$$F(S) = A + BS_0S, g(S) = \frac{m_1S}{k_1 + S} - L \text{ and } y = x \tag{11}$$

In $R_+^2 = \{(S, x) | 0 \leq S \leq 1, x \geq 0\}$, the system (10) has steady state points: $N_1(1,0)$ which is unstable, and $N_2(\lambda_1, (1 - \lambda_1)(A + BS_0S))$, if $g(1) > 1$.

Calculating p in (9) and R_1 will result the following theorem.

Theorem 6: Assume (3) or $m_1 > (k_1 + 1)(L + 1)$. If $A/B > R_1$, then N_2 is stable; If $A/B < R_1$, then N_2 is unstable and there exists at least one limit cycle in (10) surrounding N_2 .

Regarding the bifurcation on the two dimensional stable manifolds, the following theorem is valid.

Theorem 7: The system (10) undergoes a Hopf bifurcation at $A/B = R_1$ and so does the system (7) at $C/D = R_2$.

Proof: Let $J(N_2)$ be the Jacobian at N_2 . The corresponding characteristic equation is

$$r^2 + b_1r + c_1 = 0.$$

Let $A/B = \mu$. Denote b_1 , the coefficient of r in the above equation, as $tr(A/B)$, or $trJ(\mu)$, where,

$$trJ(\mu) = 1 + (1 - \lambda_1) \left(\frac{-S_0}{\mu + \lambda_1 S_0} + \frac{k_1 m_1}{(k_1 + \lambda_1)^2} \right).$$

Since

$$\left. \frac{d}{d\mu} trJ(\mu) \right|_{\mu=R_1} = (1 - \lambda_1) \frac{S_0}{(R_1 + \lambda_1 S_0)^2} > 0,$$

the function $trJ(\mu)$ is increasing at $\mu = R_1$.

Since

$$trJ(\mu) \begin{cases} < 0 & \text{if } \mu < R_1 \\ = 0 & \text{if } \mu = R_1 \\ < 0 & \text{if } \mu > R_1 \end{cases}$$

the phase structure of $N_2 = (\lambda_1, (1 - \lambda_1)(A + B\lambda_1 S_0))$ changes from unstable to stable at R_1 as the parameter μ increases. So (10) undergoes a Hopf bifurcation at $A/B = R_1$ by the definition.

Similarly, for the steady state point $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^3\lambda_2^3))$, we can prove the bifurcation theorem for the system (7) at $C/D = R_2$.

IV. Numerical Simulations

The numerical experiments performed on the system (2) using experimental data confirm our theoretical findings. For the parameter values $m_1 = 3.25, k_1 = 2, m_2 = 1.75, k_2 = 2.5, L = 0.5, A = 0.75, B = 5, C = 3.75, D = 2.25, S_0 = 0.4$, we have $\lambda_1 > 1, \lambda_2 > 1$ and the solution curves tend to E_0 (see Fig-1) representing the extinction of both microorganisms. For $m_1 = 3.25, k_1 = 0.2, m_2 = 2.5, k_2 = 0.3, L = 0.002, A = 0.04, B = 3, C = 0.0001, D = 0.2, S_0 = 0.4$, we have $A/B > R_1, \lambda_1 < \lambda_2$ and the solution curves tend to E_1 (see Fig-2) representing the extinction of second microorganism. For $m_1 = 3.5, k_1 = 0.4, m_2 = 3, k_2 = 0.2, L = 0.001, A = 0.0005, B = 0.3, C = 0.75, D = 3, S_0 = 0.4$, we have $C/D > R_2, \lambda_1 > \lambda_2$ and the solution curves tend to E_2 (see Fig-3) representing the extinction of first microorganism. For $m_1 = 3.25, k_1 = 0.2, L = 0.002, A = 0.0188496, B = 2, S_0 = 0.4$, figures 4-5 contain the solution curves and phase structure of N_2 of the system (10), resulting the system undergoes a Hopf bifurcation at $A/B = R_1$. The two plots in figures-6,7 have $A/B > R_1$ and the the system (10) is unstable through limit cycle oscillation. The two plots in figure-8, 9 have $A/B < R_1$ and all plotted trajectories tend to N_2 , resulting in a stable situation.

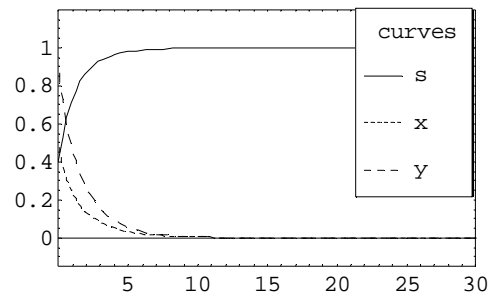


Fig. 1. Solution curves of (2) tend to E_0

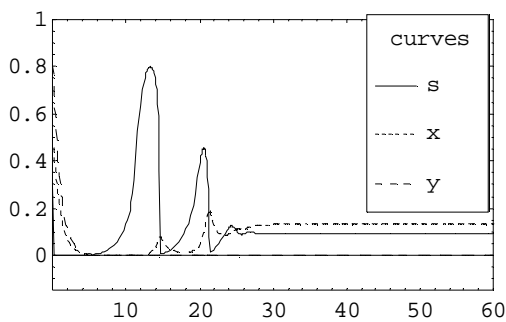


Fig. 2. Solution curves of (2) tend to E_1

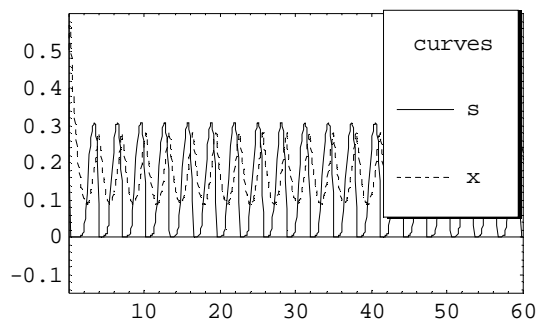


Fig. 6. Solution curves of system (10) when $A/B > R_1$

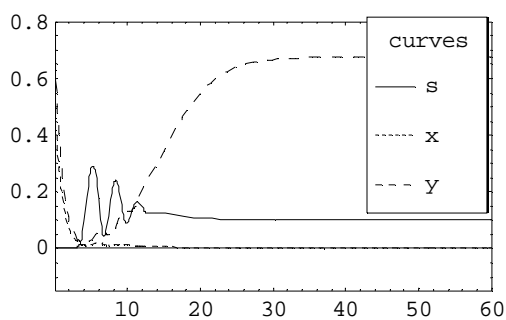


Fig. 3. Solution curves tend to E_2

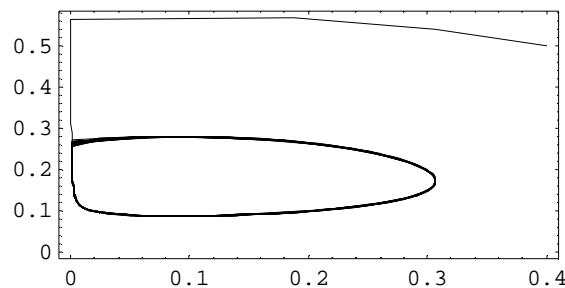


Fig. 7. System (10) is unstable when $A/B > R_1$

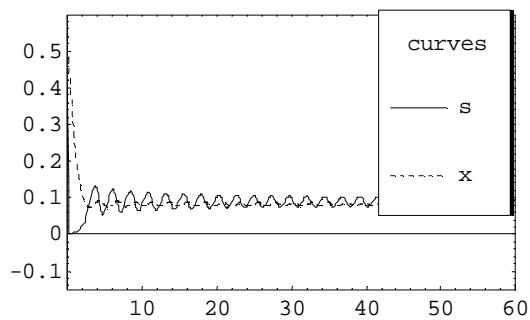


Fig. 4. Solution curves of system (10) when $A/B = R_1$

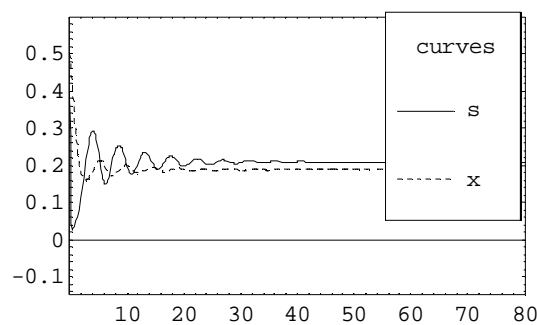


Fig. 8. Solution curves of system (10) when $A/B < R_1$

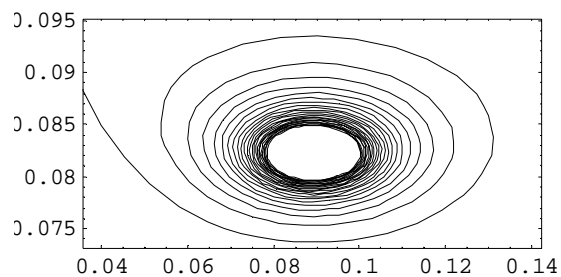


Fig. 5. System (10) undergoes a Hopf bifurcation at $A/B = R_1$

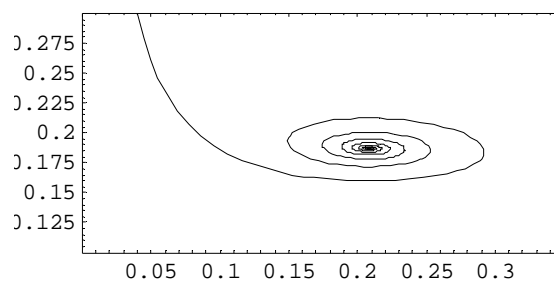


Fig. 9. System (10) is stable when $A/B < R_1$

V. Conclusion

In this paper, we considered a basic resource-based three dimensional chemostat model with variable yields. In this model, we assumed Monod type growth rate functions of which one yield coefficient is linear and another yield coefficient is cubic. The model (2) has three steady states. One is associated with extinction of both microorganisms, the other with survival of one microorganism. We studied the local stability of these steady states by using the Routh-Hurwitz criterion. We found that if the break-even concentration of one microorganism is larger than one then that microorganism dies out whether or not there is other competitor. If E_0 is the only steady state point, we showed that E_0 is LAS (this happens if both $\lambda_1 > 1$, $\lambda_2 > 1$). When E_0 , E_1 or E_2 are the steady state points, we found that E_1 is LAS (for $A/B > R_1$, $\lambda_1 < \lambda_2$) and E_2 is LAS (for $C/D > R_2$, $\lambda_1 > \lambda_2$), i.e., the microorganism that survives is the one with the lowest break-even concentration.

Thus, for a variable yield coefficients chemostat model, we found that the break-even concentrations λ_1 , λ_2 and parameters A, B, C, D in variable yields play an important role for the extinction and survival of the microorganisms, and the limit cycle oscillation of the system.

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