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The 3-D bifurcation in a chemostat with nth and mth yields

Xuncheng Huang and **Yuping Zhou**
Yangzhou Polytechnic University, 20 Mountain Tiger Road, 2-403 Yangzhou 225002, CHINA
e-mail: xh311@yahoo.com

SUMMARY

The structure of solutions of the three dimensional chemostat competition system with the yield functions $\delta_1=A_1+B_1S^n$ and $\delta_2=A_2+B_2S^m$, is analysed. The stability of equilibrium points and the three dimensional Hopf bifurcation of the system are discussed. The conditions of the existence of limit cycles on the two dimensional stable manifold when one microorganism vanishes are obtained. Some examples are used to show the applicability of the results.

***Key words**: chemostat, variable yield, equilibrium point, 3-D bifurcation.*

1. INTRODUCTION

The chemostat, sometimes also referred to as bioreactor, serves as a basic model in the continuous culture vessel. It often serves as a starting model of the open system in biology ecology, and also it is used in modelling the waste water treatment and in the mammalian large intestine (see, for instance, [14]). Many of these models and references can be found in [1]. Usually, a chemostat consists of three vessels: the culture vessel, the feed bottle, and the overflow vessel. The feed bottle contains medium with all of the nutrients needed for growth which is pumped at a constant rate into the culture vessel. The culture vessel is charged with one or more microorganisms which compete for the nutrient. The contents of the culture vessel are pumped into the overflow vessel at a constant rate to keep the volume of the reactor constant. The basic assumptions are that the culture vessel is well stirred, and the temperature, pH, etc., are kept constant.

Let $S(t)$ denote the concentration of nutrient in the culture vessel, $x_i(t)$, $i=1,2$, denote the concentration of two microorganisms. Let S^0 denote the input concentration of nutrient, and D, the dilution rate (flow rate/volume), m_i, the maximal growth rates, k_i, the Michaelis-Menton constants, and δ_i, $i=1,2$, the yield coefficients, which are all positive. This is usually called the Monod model or the model with Michaelis-Menten dynamics. The model takes the form:

$$\begin{aligned}
\frac{dS}{dt} &= (S^0-S)D-\frac{1}{\delta_1}x_1\frac{m_1S}{k_1+S}-\frac{1}{\delta_2}x_2\frac{m_2S}{k_2+S}\\
\frac{dx_1}{dt} &= x_1\left(\frac{m_1S}{k_1+S}-D\right)\\
\frac{dx_2}{dt} &= x_2\left(\frac{m_2S}{k_2+S}-D\right)\\
S(0) &= S^0>0,\quad x_1(0),\ x_2(0)>0.
\end{aligned}\tag{1}$$

Most of the models in the chemostat assume that the yield coefficient is a constant [1, 5-7]. But the accumulation of experimental data indicates that a constant yield fails to explain the observed oscillatory behavior in the vessel (see Dorofeev, et al. [2,7]). Therefore, to modify the model becomes necessary. Crooke [3,4] suggested a linear function for the yield coefficient and declared a limit cycle may exist in his model. Huang (1990 [8]), and Pilyugin and Waltman (2003 [7]) constructed a model with a general yield function, and studied the limit cycles and their relative positions. However, all the above models considered only one microorganism in the vessel. In Ref. [16], a three dimensional chemostat with two microorganisms was studied. In the model the functional reaction functions were in the Monod type, and the yield coefficients were assumed to be $\delta_i=A_i+BS,\ i=1,2$. Also, in Ref. [17] the yield coefficients were assumed as $\delta_1=A+BS^2$, and $\delta_2=const$. Some properties of the equilibrium points were discussed there [16,17]. Ref. [7] gave a numerical example with $\delta_1=1+50S^3$, and $\delta_2=120$ and it obtained five limit cycles through a bifurcation numerically. Recently, Ref. [19] studied the chemostat with quadratic yields: $\delta_1=A+BS^2$, and $\delta_2=C+DS^2$, and proved the conditions of the existence of two limit cycles in the model.

In this paper, we study a three dimensional chemostat of which both the yield coefficients are functions of the nutrient in the general forms: $\delta_1=A+BS^n$, and $\delta_2=C+DS^m$. The model is useful in modelling the case when the microorganism is very sensitive to the nutrient. We shall analyze analytically the equilibrium points, global stability and the Hopf bifurcation of the three dimensional system. It is easy to see that the model in this paper includes almost all the previous results as special cases (for example, see those in Refs. [3, 4,16-19]). Our model and the main theorems with proofs are in Section 2.

It is always of interest in both theory and applications to study the existence and properties of periodic solutions of the n-dimensional autonomous differential system for $n\geq 3$. The situation of $n\geq 3$ is much complicated than the one in the plane. This is because some powerful tools in the plane system like Poincare-Bendixson theorem cannot be applied directly in the cases of $n\geq 3$. We use the Hopf bifurcation method directly to the three dimensional system to show the existence of limit cycles. Not many of the results for $n\geq 3$ are reported in the literature [13]. Some examples are applied to illustrate our theorems in Section 3, which will help us to understand our results.

2. THE MODEL AND MAIN THEOREMS

Performing the standard scaling for the continuous fermentation, let:

$$\bar{S}=\frac{S}{S^0},\ \bar{x}=\frac{x}{S^0},\ \bar{y}=\frac{y}{S^0},\ \tau=Dt,$$
$$\bar{m}_i=\frac{m_i}{D},\ \bar{k}_i=\frac{k_i}{S_0},\ \bar{L}=\frac{L}{D},$$

and then drop the bars, and replace τ with t, $B_1(S^0)^n$ with B_1, $B_2(S^0)^m$ with B_2, the system (1) becomes:

$$\begin{aligned}
\frac{dS}{dt}&=1-S-\frac{x_1}{A_1+B_1S^n}\frac{m_1S}{k_1+S}-\frac{x_2}{A_2+B_2S^m}\frac{m_2S}{k_2+S}\\
\frac{dx_1}{dt}&=\left(\frac{m_1S}{k_1+S}-1\right)x_1\\
\frac{dx_2}{dt}&=\left(\frac{m_2S}{k_2+S}-1\right)x_2.
\end{aligned}\tag{2}$$

The parameters have been scaled by the operating environment of the continuous fermentation, determined by S^0 and D. The variables are non-dimensional and the discussion is in:

$$R_+^3=\left\{\left(S,x_1,x_2\right)\ \middle|\ 0\leq S\leq 1,\ x_1\geq 0,\ x_2\geq 0\right\}$$

Let $\lambda_1=\dfrac{k_1}{m_1-1},\quad \lambda_2=\dfrac{k_2}{m_2-1}$.

It is easy to see that:

$$\begin{aligned}
&(i)\ \text{if}\ \ 0<m_i<1,\ i=1,2,\ \text{then}\ \frac{dx_1}{dt}<0,\ \frac{dx_2}{dt}<0\ \text{and}\\
&\qquad lim_{t\to+\infty}x_1(t)=lim_{t\to+\infty}x_2(t)=0;\\
&(ii)\ \text{if}\ \ \lambda_1\geq 1,\ \text{then}\ \frac{dx_1}{dt}<0\ \text{and}\ lim_{t\to+\infty}x_1(t)=0;\\
&(iii)\ \text{if}\ \ \lambda_2\geq 1,\ \text{then}\ \frac{dx_2}{dt}<0\ \text{and}\ lim_{t\to+\infty}x_2(t)=0.
\end{aligned}\tag{3}$$

So in order to avoid the microorganisms vanishing, we need to assume that: $0<\lambda_i<1,\ i=1,2$ (which imply $m_i>1,\ i=1,2$).

Let:

$$R_1\equiv\frac{(1-\lambda_1)[n\lambda_1^{n-1}(k_1+\lambda_1)^2-\lambda_1^n m_1k_1]-\lambda_1^n(k_1+\lambda_1)^2}{(k_1+\lambda_1)^2+m_1k_1(1-\lambda_1)},\tag{4}$$

$$R_2\equiv\frac{(1-\lambda_2)[m\lambda_2^{m-1}(k_2+\lambda_2)^2-\lambda_2^m m_2k_2]-\lambda_2^m(k_2+\lambda_2)^2}{(k_2+\lambda_2)^2+m_2k_2(1-\lambda_2)}.\tag{5}$$

Theorem 1. The system (2) has three equilibrium points in R_+^3:

$$E_0\left(1,0,0\right),\ E_1\left(\lambda_1,(A_1+B_1\lambda_1^n)(1-\lambda_1),0\right)$$
$$\text{and}\ E_2\left(\lambda_2,0,(A_2+B_2\lambda_2^m)(1-\lambda_2)\right)$$

in which is E_0 unstable (saddle); E_1 is asymptotically stable if $\frac{A_1}{B_1} > R_1$ and $\lambda_1<\lambda_2$, unstable if either inequality is reversed; E_2 is asymptotically stable if $\frac{A_2}{B_2} > R_2$ and $\lambda_1>\lambda_2$, unstable if either inequality is reversed.

Proof. We only prove the cases for E_1 and E_2. From the Jacobians of the system (2) at E_1 and E_2, the corresponding characteristic equations take the form:

$$(r - a_i)(r^2 + b_i r + c_i)=0, \quad i=1,2 \tag{6}$$

where:

$$\begin{aligned} a_1 &= \frac{m_2\lambda_1}{k_2+\lambda_1} - 1 \\ b_1 &= 1 + (1-\lambda_1)\left(\frac{-nB_1\lambda_1^{n-1}}{A_1+B_1\lambda_1^{n3}} + \frac{m_1k_1}{(k_1+\lambda_1)^2}\right) \\ c_1 &= (1-\lambda_1)\frac{m_1k_1}{(k_1+\lambda_1)^2} \qquad (\text{which is} > 0); \end{aligned} \tag{7}$$

$$\begin{aligned} a_2 &= \frac{m_1\lambda_2}{k_1+\lambda_2} - 1 \\ b_2 &= 1 + (1-\lambda_2)\left(\frac{-mB_2\lambda_2^{m-1}}{A_2+B_2\lambda_2^{m}} + \frac{m_2k_2}{(k_2+\lambda_2)^2}\right) \\ c_2 &= (1-\lambda_2)\frac{m_2k_2}{(k_2+\lambda_2)^2} \qquad (\text{which is} > 0). \end{aligned} \tag{8}$$

When $\frac{A_1}{B_1} > R_1,\ b_1 > 0$, the roots of $r^2 + b_1 r + c_1=0$ have negative real parts. The stability of E_1 is determined by the sign of a_1. Thus E_1 is stable if $a_1<0$, (or $\lambda_1<\lambda_2$), unstable if $\lambda_1>\lambda_2$. When $\frac{A_2}{B_2} > R_2,\ b_2 > 0$ the roots of $r^2 + b_1 r + c_1=0$ have positive real parts, E_1 is unstable.

Similarly, when $\frac{A_2}{B_2} > R_2,\ b_2 > 0$, the roots of the equation $r^2 + b_2 r + c_2=0$ have negative real parts. The stability of E_2 is determined by the sign of $a_2 = \frac{m_1\lambda_2}{k_1+\lambda_2} - 1$. Thus, if (or if $\lambda_1>\lambda_2$), E_2 is stable; it is unstable if $\lambda_1<\lambda_2$. When $\frac{A_2}{B_2} < R_2,\ b_2 < 0$, E_2 is always unstable. The proof of Theorem 1 is completed.

Theorem 2. (i) If $\lambda_1<\lambda_2$, and $\frac{A_1}{B_1} > R_1$, the equilibrium point E_1 is globally asymptotically stable in R_+^3; (ii) if $\lambda_1>\lambda_2$, and $\frac{A_2}{B_2} > R_2$, the equilibrium point E_2 is globally asymptotically stable.

Proof. Let:

$$\begin{aligned} \Omega = \{ & (S, x_1, x_2) \mid 0 \le S \le l - x_1 - x_2, \\ & 0 \le x_1 \le (1-\lambda_1)(A_1 + B_1\lambda_1^n) + \varepsilon_0, \\ & 0 \le x_2 \le (1-\lambda_2)(A_2 + B_2\lambda_2^m) + \varepsilon_0, \\ & 0 < l < +\infty,\ \varepsilon_0 > 0 \}. \end{aligned} \tag{9}$$

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

Consider on the face $S=0$ and, by system (2), $\left.\frac{dS}{dt}\right|_{S=0} = 1 > 0$. Thus, any trajectory inwill go through into R_+^3 but the reverse is not true. For the face $M=S+x_1+x_2-l=0$ $(0<l<+\infty)$:

$$\begin{aligned} \left.\frac{dM}{dt}\right|_{M=0} &= 1 - l - \\ & - x_1\left(\frac{1}{A_1+B_1(l-x_1-x_2)^n} - 1\right)\frac{m_1(l-x_1-x_2)}{k_1+(l-x_1-x_2)} - \\ & - x_2\left(\frac{1}{A_2+B_2(l-x_1-x_2)^m} - 1\right)\frac{m_2(l-x_1-x_2)}{k_2+(l-x_1-x_2)}. \end{aligned} \tag{10}$$

Since both x_1 and x_2 are bounded and all the parameters are positive, $\left.\frac{dM}{dt}\right|_{M=0} < 0$ if l is sufficiently larger. That is, any trajectory in R_+^3 will cross the plane $M=S+x_1+x_2-l=0$ into Ω. Moreover, because $x_1=0$, $x_2=0$ both are the solutions of system (2), Ω is a positively invariant set of system (2). In other words, any trajectory initiating in R_+^3 will go to Ω when $t\to+\infty$. Therefore, both E_1 and E_2 are globally asymptotically stable. We thus complete the proof of Theorem 2.

It follows from Theorem 2 that:

(i) if $\lambda_1<\lambda_2$, and $\frac{A_1}{B_1} > R_1$, then, for any trajectory in R_+^3,

$$lim_{t\to+\infty} S(t) = \lambda_1,$$
$$lim_{t\to+\infty} x_1(t) = (1-\lambda_1)(A_1 + B_1\lambda_1^n),$$
$$lim_{t\to+\infty} x_2(t) = 0$$ and:

(ii) if $\lambda_1 > \lambda_2$, and $\frac{A_2}{B_2} > R_2$, then, for any trajectory in R^3_+,

$$lim_{t\to+\infty} S(t) = \lambda_2,$$
$$lim_{t\to+\infty} x_1(t) = 0,$$
$$lim_{t\to+\infty} x_2(t) = (1-\lambda_2)(A_2 + B_2\lambda_2^m).$$

Before we prove the theorem of the Hopf bifurcation for the three dimensional system, we must first study the stability of E_1 when $\frac{A_1}{B_1} = R_1$, and E_2 when $\frac{A_2}{B_2} = R_2$, by using the LaSalle corollary to the Liapunov stability theorem. Since our Liapunov function is not necessarily continuous on the closure of the region, we shall use the extension that was used by Wolkowicz and Lu [15]. The extension states that V is a Liapunov function for a system $\frac{dX}{dt} = f(X)$ in a region if:

(i) V is continuous on G;

(ii) V is not continuous at a point $\bar{X} \in \bar{G}$ implies that $lim_{\substack{X\to\bar{X} \\ X\in G}} V(X) = \infty$;

(iii) $V` = \nabla V \cdot f \le 0$ on G.

It is different from Theorem 2 that the condition of $\frac{A_1}{B_1} > R_1$ or $\frac{A_2}{B_2} > R_2$ is no longer needed in the following theorem.

Theorem 3. Assume $A_i \ge 1$, $i=1,2$. (i) If $\lambda_1 < \lambda_2$, then the equilibrium point E_1 of (2) is always globally asymptotically stable in R^3_+; (ii) if $\lambda_1 > \lambda_2$, then E_2 is globally asymptotically stable.

Proof. We prove the case of (i) first. Let:

$$V(S,x_1,x_2) = \int_{\lambda_1}^{S} \frac{\eta - \lambda_1}{\eta} d\eta + c_1 \int_{x_1^*}^{x_1} \frac{\eta - x_1^*}{\eta} d\eta + c_2 x_2 \quad (11)$$

where $x_1^* = (1-\lambda_1)\cdot(A_1 + B_1\lambda_1^n)$, and c_1, c_2 are determined late. Then:

$$\begin{aligned} V' &= \frac{S-\lambda_1}{S}\left(1 - S - \frac{x_1}{A_1 + B_1S^n}\frac{m_1S}{k_1+S} - \frac{x_2}{A_2+B_2S^m}\frac{m_2S}{k_2+S}\right) + \\ &+ c_1\frac{x_1 - x_1^*}{x_1}x_1\left(\frac{m_1S}{k_1+S} - 1\right) + c_2x_2\left(\frac{m_2S}{k_2+S} - 1\right) = \\ &= \frac{S-\lambda_1}{S}\left(1 - S - \frac{x_1}{A_1+B_1S^n}\frac{m_1S}{k_1+S}\right) + \\ &+ c_1(x_1 - x_1^*)(\frac{m_1S}{k_1+S} - 1) + c_2x_2\left(\frac{m_2\lambda_1}{k_2+\lambda_1} - 1\right) + \\ &+ x_2\left(c_2(\frac{m_2S}{k_2+S} - \frac{m_2\lambda_1}{k_2+\lambda_1}) - \frac{S-\lambda_1}{S}\frac{1}{A_2+B_2S^m}\frac{m_2S}{k_2+S}\right) \\ &\equiv V_1 + V_2 + V_3. \end{aligned}$$

It follows that:

$$\begin{aligned} V_1 &\equiv \frac{S-\lambda_1}{S}(1-S) - c_1(1-\lambda_1)(A_1 + B_1\lambda_1^n)(\frac{m_1S}{k_1+S} - 1) + \\ &+ \left(-\frac{S-\lambda_1}{S}\frac{x_1}{A_1+B_1S^n}\frac{m_1S}{k_1+S} + c_1x_1(\frac{m_1S}{k_1+S} - 1)\right) \\ &= V_{11} + V_{12}. \end{aligned}$$

Note that:

$$\frac{m_1S}{k_1+S} - 1 = \frac{(m_1-1)(S-\lambda_1)}{k_1+S}.$$

We have:

$$\begin{aligned} V_{12} &\equiv -(S-\lambda_1)\frac{x_1}{A_1+B_1S^n}\frac{m_1}{k_1+S} + c_1x_1(\frac{m_1S}{k_1+S} - 1) \\ &= -(S-\lambda_1)\frac{x_1}{A_1+B_1S^n}\frac{m_1}{k_1+S} + c_1x_1\frac{m_1-1}{k_1+S}(S-\lambda_1) \\ &= \frac{x_1(S-\lambda_1)}{(k_1+S)(A_1+B_1S^n)}\Big(c_1(m_1-1)(A_1+B_1S^n) - m_1\Big). \end{aligned} \quad (12)$$

In order to have $V_{12} \le 0$, we determine c_1 as it follows:

(1) if $S \le \lambda_1$, choose $c_1 = \frac{m_1}{m_1 - 1}$ such that:

$c_1(m_1-1)(A_1+B_1S^n) \ge c_1(m_1-1) = m_1$, and $V_{12} \le 0$.

Then, we have:

$$\begin{aligned} V_{11} &= \frac{S-\lambda_1}{S}(1-S) - \frac{m_1}{m_1-1}(1-\lambda_1)(A_1+B_1\lambda_1^n)\frac{(m_1-1)(S-\lambda_1)}{k_1+S} \\ &\le (S-\lambda_1)\left(\frac{1-S}{S} - (1-\lambda_1)\frac{m_1}{k_1+S}\frac{k_1+\lambda_1}{m_1\lambda_1}\right) \\ &= -(S-\lambda_1)^2\frac{S\lambda_1 + k_1}{S(k_1+S)\lambda_1} \le 0. \end{aligned}$$

(2) if $S>\lambda_1$, choose $c_1=\frac{m_1}{(m_1-1)(A_1+B_1\lambda_1^n)}$ such that:

$$c_1(m_1-1)(A_1+B_1S^n)\geq c_1(m_1-1)(A_1+B_1\lambda_1^n)=m_1,$$

hence $V_{11}\leq 0$.

Also, since $m_1\lambda_1=k_1+\lambda_1$, one has:

$$\begin{aligned}V_{11}&\equiv\frac{S-\lambda_1}{S}(1-S)-\\&-\frac{m_1}{(m_1-1)(A_1+B_1\lambda_1^n)}(1-\lambda_1)(A_1+B_1\lambda_1^n)\frac{(m_1-1)(S-\lambda_1)}{k_1+S}=\\&=(S-\lambda_1)\left(\frac{1-S}{S}-(1-\lambda_1)\frac{m_1}{k_1+S}\frac{k_1+\lambda_1}{m_1\lambda_1}\right)\\&=(S-\lambda_1)\frac{-(\lambda_1S+k_1)(S-\lambda_1)}{S(k_1+S)\lambda_1}\\&=-(S-\lambda_1)^2\frac{\lambda_1S+k_1}{S(k_1+S)\lambda}\\&\leq 0,\quad (\text{the equal sign holds only when } S=\lambda_1).\end{aligned}$$

Thus $V_1\leq 0$.

Furthermore, since $\lambda_1<\lambda_2$,

$$V_2\equiv c_2x_2\left(\frac{m_2\lambda_1}{k_2+\lambda_1}-1\right)\leq c_2x_2\left(\frac{m_2\lambda_2}{k_2+\lambda_2}-1\right)=0,$$

$(\text{since } c_2>0 \text{ and } x_2\geq 0)$.

Now we shall choose c_2 so that $V_3=0$:

$$\begin{aligned}V_3&\equiv x_2\left(\frac{c_2m_2k_2(S-\lambda_1)}{(k_2+S)(k_2+\lambda_1)}-\frac{m_2(S-\lambda_1)}{(A_2+B_2\lambda_1^m)(k_2+S)}\right)\\&=\frac{x_2m_2(S-\lambda_1)}{k_2+S}\left(\frac{c_2k_2}{k_2+\lambda_1}-\frac{1}{A_2+B_2\lambda_1^m}\right).\end{aligned}$$

V_3 is less or equal to 0 if it determines c_2 as it follows:

$$c_2=\frac{k_2+\lambda_1}{k_2(A_2+B_2)}\quad \text{if } S\geq\lambda_1 \text{ since } S\leq 1;$$

$$c_2=\frac{k_2+\lambda_1}{k_2A_2}\quad \text{if } S<\lambda_1 \text{ since } S\geq 0.$$

Therefore:

$$V`=V_1+V_2+V_3\leq 0 \tag{13}$$

and by the LaSally corollary, all trajectories tend to the largest invariant set in $\Delta=\{(S,x_1,x_2)\,|\,V'=0\}$. This requires $S\equiv\lambda_1$ and $X_2\equiv 0$.

To make $\{S\,|\,S=\lambda_1\}$ invariant, under the condition $x_2=0$, it requires:

$$S'=1-\lambda_1-x_1\frac{1}{A_1+B_1\lambda_1^n}=0 \tag{14}$$

which implies $x_1=(1-\lambda_1)(A_1+B_1\lambda_1^n)$. Therefore $\{E_1\}$ is the unique invariant set in Δ. We thus complete the proof of the theorem 3-(i). A similar argument will prove Theorem 3-(ii).

The teorem 3 indicates that the stability of the equilibrium points E_1 and E_2 are now established for $\frac{A_1}{B_1}=R_1$, and $\frac{A_2}{B_2}=R_2$, respectively. We are now in a position to prove the three dimensional Hopf bifurcation theorem for the system (2). We first introduce the following Lemma (Theorem 1, p. 254 [13]).

Lemma 1. Let W be an open set in R^3, $(0,0,0)\in W$. Let $f:W\times(-\mu_0,\mu_0)\to R^3$ be an analytic function on $W\times(-\mu_0,\mu_0)$ where μ_0 is a small positive number. Denote the Jacobian of f at $(X,\mu)=((0,0,0),0)$ as $J(f(0,0))$ and assume that:

(i) the system:

$$\frac{dX}{dt}=f(X,\mu) \tag*{$(15)_\mu$}$$

has $(0,0,0)$ as its equilibrium point for any μ;

(ii) the eigenvalues of $J(f(0,0))$ are:

$\pm i\beta(\mu)|_{\mu=0}=\pm i\beta(0),\ \delta(\mu)|_{\mu=0}=\delta(0)$

with $\beta(0)>0$, $\delta(0)<0$.

Then if $(0,0,0)$ is asymptotically stable at $\mu=0$, there exists a sufficiently small μ, $\mu>0$ such that the system $(15)_\mu$ has an asymptotically stable closed orbit surrounding $(0,0,0)$.

The proof of the Lemma 1 is based on the Liapunov second method which can be found in Ref. [13] or any advanced level books on bifurcations [20].

Theorem 4. (i) If $\lambda_1<\lambda_2$, the system (2) undergoes a Hopf bifurcation at $R_1=\frac{A_1}{B_1}$, and the periodic solution created by the Hopf bifurcation is asymptotically stable for $0<R_1-\frac{A_1}{B_1}<<1$; (ii) If $\lambda_2<\lambda_1$, the system (2) undergoes a Hopf bifurcation at $R_2=\frac{A_2}{B_2}$, and the periodic solution created by the Hopf bifurcation is asymptotically stable for $0<R_1-\frac{A_1}{B_1}<<1$;

Proof. Make the variable change:

$\overline{S}=S-\lambda_1,\ \overline{x}_1=x_1-(1-\lambda_1)(A_1+B_1\lambda_1^n),\ \overline{x}_2=x_2,$ and denote the Jacobian of the system (2) in variables $\overline{S}$, $\overline{x}_1$, $\overline{x}_2$ as $J(\overline{S},\overline{x}_1,\overline{x}_2)$.

Choose $\mu = R_1 - \frac{A_1}{B_1}$, R_1 as in Eq. (4), as the Hopf bifurcation parameter, and consider the system (2) in variables $\overline{S}$, $\overline{x}_1$, $\overline{x}_2$ as $\frac{dX}{dt} = f(X,\mu)$ in Eq. $(15)_\mu$. Then:

$$J(f(0,0)) = J(\overline{S},\overline{x}_1,\overline{x}_2)\Big|_{\substack{(\overline{S},\overline{x}_1,\overline{x}_2)=(0,0,0)\\ \mu=0}} =$$

$$= J(S,x_1,x_2)\Big|_{\substack{(S,x_1,x_2)=(\lambda_1,(1-\lambda_1)(A_1+B_1\lambda_1^n),0)\\ \mu=0}}$$

The corresponding characteristic equation is:

$$\left(r - \frac{m_2\lambda_1}{k_2+\lambda_1} + 1\right)\left(r^2 + (1-\lambda_1)\frac{m_1k_1}{(k_1+\lambda_1)^2}\right) = 0. \quad (16)$$

The eigenvalues of Eq. (16) are $\pm i\beta(0)$ and $\delta(0)$, where:

$$\beta(0) = \frac{1}{k_1+\lambda_1}\sqrt{(1-\lambda_1)m_1k_1} > 0,$$
$$\delta(0) = \frac{m_2\lambda_1}{k_2+\lambda_1} - 1 < \frac{m_2\lambda_1}{k_2+\lambda_1} - \frac{m_2\lambda_2}{k_2+\lambda_2} < 0, \quad (17)$$
$$(since\ \lambda_1 < \lambda_2),$$

and the hypotheses of the Lemma 1 are satisfied. From Theorems 3 and 2, it follows that:

1) The equilibrium of the system (2): $(0,0,0)$ in the coordinate system, or $(\lambda_1, (1-\lambda_1)(A_1+B_1\lambda_1^n), 0)$ in $\overline{S}$, $\overline{x}_1$, $\overline{x}_2$, is asymptotically stable;
2) $(0,0,0)$ in $\overline{S}$, $\overline{x}_1$, $\overline{x}_2$, or in $(\lambda_1, (1-\lambda_1)(A_1+B_1\lambda_1^n), 0)$, is unstable if $\mu>0$.

Therefore, the system $(15)_\mu$, (or (2)), undergoes a Hopf bifurcation at $\mu>0$ (or, $R_1 = \frac{A_1}{B_1}$). Lemma 1 implies that for a sufficient small μ, $\mu>0$, the system $(15)_\mu$ has an asymptotically stable closed orbit surrounding $(0,0,0)$, that is, for $0 < R_1 - \frac{A_1}{B_1} << 1$, the system (2) has an asymptotically stable closed orbit surrounding $E_1(\lambda_1, (1-\lambda_1)(A_1+B_1\lambda_1^n), 0)$. Theorem 4-(i) is obtained.

A similar argument can prove Theorem 4-(ii).

Regarding the behavior of the trajectories near the equilibrium points, we have the following results.

For E_1, in the solution plane of $x_2=0$ the system (2) is reduced to:

$$\frac{dS}{dt} = 1 - S - \frac{x_1}{A_1+B_1S^n}\frac{m_1S}{k_1+S}$$
$$\frac{dx_1}{dt} = \left(\frac{m_1S}{k_1+S} - 1\right)x_1. \quad (18)$$

This is a special case of the following system ([8])

$$\frac{dx}{dt} = x\left(g(y)-1\right)$$
$$\frac{dy}{dt} = 1 - y - \frac{g(y)}{F(y)}x, \quad (19)$$

with $y=S$, $g(y) = \frac{m_1S}{k_1+S}$, $F(y) = A_1 + B_1S^n$, and $x=x_1$.

The system (19) has two equilibrium pints $(0,1)$, and (x^*,y^*), where:

$x^*=(1-y^*)F(y^*)$, $y^*=g^{-1}(1)$

with the condition $g(1)>1$.

It is easy to see that $(0,1)$ is a saddle. Denote:

$$p = 1 + x^*\frac{d}{dy}\left(\frac{g}{F}\right)\Big|_{y=y^*} \quad (20)$$

The following theorem is proved in Ref. [8].

Lemma 2. Assume $g(1)>1$. If $p>0$ then (x^*,y^*) is stable; if $p<0$, it is unstable and there exists at least one limit cycle in Eqs. (19) surrounding the equilibrium (x^*,y^*).

Thus, by Lemma 2, one has:

Theorem 5. Assume $m_1>k_1+1$. The system (18) has two equilibrium points: $M_1(1,0)$, which is a saddle, and $M_2(\lambda_1, (1-\lambda_1)(A_1+B_1\lambda_1^n))$, which is stable if $\frac{A_1}{B_1} > R_1$, and unstable if $\frac{A_1}{B_1} < R_1$. In the case when M_2 is unstable, there is at least one limit cycle in system (18) surrounding M_2.

For E_2, in the face $x_1=0$ we have the similar result for the two dimensional system:

$$\frac{dS}{dt} = 1 - S - \frac{x_2}{A_2+B_2S^m}\frac{m_2S}{k_2+S}$$
$$\frac{dx_2}{dt} = \left(\frac{m_2S}{k_2+S} - 1\right)x_2. \quad (21)$$

Theorem 6. Assume $m_2>k_2+1$. The system (21) has two equilibrium points: $N_1(1,0)$, which is a saddle, and $N_2(\lambda_1, (1-\lambda_1)(A_1+B_1\lambda_1^n))$, which is stable if $\frac{A_2}{B_2} > R_2$, and unstable if $\frac{A_2}{B_2} < R_2$. In the case when N_2 is unstable, there is at least one limit cycle in system (21) surrounding N_2.

3. EXAMPLES

Example 1. Consider:

$$\begin{aligned}
&\frac{dS}{dt}=1-S-\frac{x}{1+50S^3}\,\frac{2S}{0.7+S}-\frac{y}{120}\,\frac{9.85S}{6.5+S}\\
&\frac{dx}{dt}=x(\frac{2S}{0.7+S}-1)\\
&\frac{dy}{dt}=y(\frac{9.85S}{6.5+S}-1),\\
&S(0)=0.4,\; x(0)=2.0,\; y(0)=0.
\end{aligned} \tag{22}$$

The system (22) has shown numerically that multiple limit cycles exist [7]. It follows that $\lambda_1=0.7$, $\lambda_2=0.73$, $\frac{A_1}{B_1}=\frac{1}{50}=0.2$, and by formula (4):

$$\begin{aligned}
R_1&=\frac{(1-\lambda_1)\left(3\lambda_1^2(k_1+\lambda)_1^{\;2}-m_1k_1\lambda_1^3\right)-\lambda_1^3(k_1+\lambda_1)^2}{(k_1+\lambda_1)^2+(1-\lambda_1)m_1k_1}=\\
&=\frac{(1-0.7)\left(3(0.7^2)(0.7+0.7)^2-2(0.7)0.7^3\right)-0.7^3(0.7+0.7)^2}{(0.7+0.7)^2+(1-0.7)2(0.7)}=\\
&=\frac{0.048}{2.4}=0.02.
\end{aligned} \tag{23}$$

From Theorem 4, the system (22) undergoes a Hopf bifurcation and there exist limit cycles surrounding the equilibrium ($0.7,5.445,0$). This is an analytic proof of the numerical result shown in Ref. [7].

Example 2. Consider the system (2) with $\delta_1=A+BS^2$ and $\delta_2=C+DS^2$. In Ref. [19] the stability and the existences of two limit cycles were studied but the bifurcation for the three dimensional system is not considered. Following Theorem 4, we have:

Theorem 7. The system (2) with the yields $\delta_1=A+BS^2$ and $\delta_2=C+DS^2$ undergoes a Hopf bifurcation at $\frac{A}{B}=R_1$ if $\lambda_1<\lambda_2$, where R_1 is calculated by formula (4) for $n=2$.

We would like to mention that the corresponding two dimensional chemostat, that is, $x_2\equiv 0$ in Example 2, was studied in Ref. [18]. However, the discussion of the conditions for the Hopf bifurcation in the two dimensional case required that one more condition $g_3<0$ (Theorem 2, p. 389, [18]) is needed to guarantee the bifurcation. Since the formula [18] for g_3 is:

$$g_3=\frac{1}{2}\left(\frac{7}{6}a_1b_1-\frac{23}{12}a_1a_2-\frac{23}{12}b_1b_2+\frac{5}{3}a_2b_2+\frac{1}{4}b_4+\frac{3}{4}a_3\right) \tag{24}$$

and a_i, $i=1,2,3$, b_j, $j=1,2,3,4$ are involved some original variables, which is impossible to be valued. Because in their proof [18], before using the Friedrich method, a variable transformation:

$$\begin{aligned}
\bar{S}&=m_1-(L+1)\\
\bar{x}_1&=\frac{\sqrt{m_1k_1}}{\sqrt{x_1\left(A+BS_0^2\lambda_1^2\right)}}\cdot x_1\\
\bar{t}&=\sqrt{m_1k_1\left(A+BS_0^2\lambda_1^2\right)x_1}\cdot t
\end{aligned}$$

was made, which resulted in that the coefficients a_1, a_1, a_3, a_4, b_2, b_3, b_4, b_5 all have old variable x_1 such that the calculation for g_3 was impossible in this way and is definitely wrong.

We would like to conclude our article with the following remark.

Remark.The structure of the solutions of the systems (2) with the yields $\delta_1=A+BS^n$, $\delta_2=A+BS^m$ has quite similar property as in the case of any particular n and m (see Refs. [3, 4, 7, 8, 15-19]). Hence, a further study for the yields:

$$\delta_1=a_0+a_1S+a_2S^2+...+a_nS^n,$$
$$\delta_2=b_0+b_1S+b_2S^2+...+b_mS^m$$

may be very interesting.

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3-D BIFURKACIJA U BIOREAKTORU S N-TIM I M-TIM PRIRASTIMA

SAŽETAK

U ovom radu analizirana je konstrukcija rješenja trodimenzionalnog bioreaktorskog kompeticijskog sustava s funkcijama prirasta $\delta_1=A_1+B_1S^n$ i $d_2=A_2+B_2S^m$. Prodiskutirana je stabilnost točaka ravnoteže i trodimenzionalna Hopf-ova bifurkacija sustava. Definirani su uvjeti postojanja graničnih krugova na dvodimenzionalnoj stabilnoj plohi kad nestane jedan mikroorganizam. Primjenjljivost rezultata pokazana je na nekoliko riješenih primjera.

Ključne riječi: *bioreaktor, prirast varijable, točka ravnoteže, 3-D bifurkacija.*