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ORIGINAL PAPER

Bifurcation in the stable manifold of the bioreactor with *n*th and *m*th order polynomial yields

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Abstract The three dimensional chemostat with *n*th and *m*th order polynomial yields, instead of the particular one such as $A + BS$, $A + BS^2$, $A + BS^3$, $A + BS^4$, $A + BS^2 + CS^3$ and $A + BS^n$, is proposed. The existence of limit cycles in the two-dimensional stable manifold, the Hopf bifurcation and the stability of the periodic solution created by the bifurcation are proved.

Keywords Chemostat · Polynomial yields · Stable manifold · Limit cycles · Hopf bifurcation

1 Introduction

Bioreactors often serve as laboratory models that are used to manufacture products by microorganisms [7,15]. In most of the bioreactor models, the yield coefficients are assumed to be constants. However, this assumption failed to explain the oscillatory behavior in the culture vessel observed in the experiments (see [2,14]). Some authors suggested that the stoichiometric yield coefficient to be a function of substrate concentration and such hypothesis was analyzed in a series of theoretical studies in chemical engineering literature [1,4,5]. The studies showed that if the yield coefficient increases non-linearly with substrate concentration, then in a suitable parameter range, the stable rest state may undergo a Hopf bifurcation and have a limit cycle. The yield coefficient depends on the substrate concentration is now well established in experimental literature (see, for instance [2,6,8–14]).

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In [2,12,14] the modeling approach developed in [1,4,5] has been modified and the yield coefficients are assumed to be a function of the substrate concentration. The properties of the equilibrium points, and the existence of limit cycles have been discussed. A three dimensional chemostat with two microorganisms which are both with linear yields was studied by Song and Li [16]. In the model the functional reaction functions were of the Monod type, and the yield coefficients were assumed linear functions of the concentration of nutrient. In a recent paper [13], the authors assumed that one of the two yield coefficients was a simple quadratic function and discussed the stability of the solution. We are going to generalize the yield functions in [12,13,16] to the nth and mth order polynomials and extend the functional reactions from the Monod type to general nondecreasing functions, and we study the equilibrium points, the globally asymptotically stability of the solutions, the existence of limit cycles in the two-dimensional stable manifold, the Hopf bifurcation, and the stability of the periodic solution created by the bifurcation for the system.

A polynomial with degree bigger than 1 is one of the simplest nonlinear functions in mathematics. Based on the strong support from the lab experiments, several authors have used some simple polynomials with degrees 2, 3, 4, or even n as the yield functions in the literature [2,12–14,16]. For example, Pilyugin and Waltman provided a numeric example with the yields of the first microorganism $\delta_1(S) = 1 + 50S^3$ and the second $\delta_2(S) = 120$, and obtained multiple limit cycles in computer simulating (see Fig. 1, and page 161, Fig. 4 [14]). These limit cycles are obtained for different values of the bifurcation parameters.

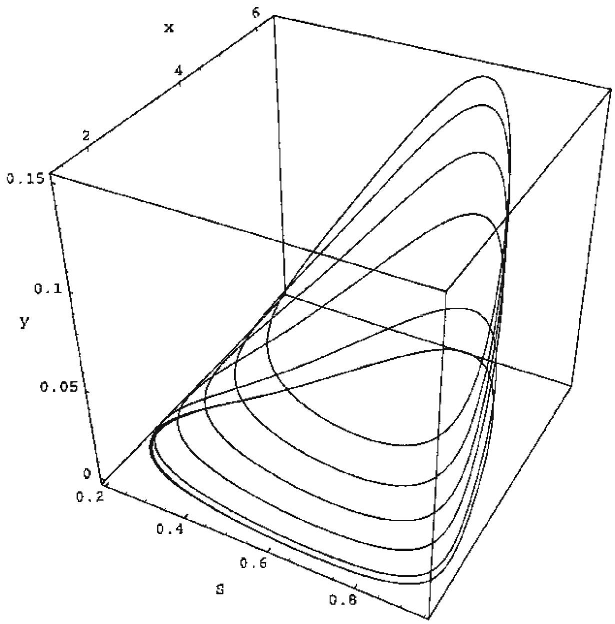

Fig. 1 The Existence of more limit cycles in the chemostat with the cubic yield $\delta_1(S) = 1 + 50S^3$ and constant yield $\delta_2 = 120$

It is easy to see that the above numerical example is a special case of our system (2) with $A_0 = 1, A_3 = 50, B_0 = 120$, and $A_i = 0, i = 1, 2, 4, \dots, n, B_i = 0, i = 1, 2, \dots, m$. Another example with $\delta_1(S) = A_0 + A_n S^n$, and $\delta_2(S) =$ const. can be found in the paper of Arino et al. [2]. For particular, some numerical simulation with $\delta_1(S) = 1 + c_1 S^4$, c_1 varies and $\delta_2(S) = 120$ is given in [2]. Therefore, in this paper, we propose a general mode with the nth and mth order polynomial yields, instead of the particular ones such as $A + BS, A + BS^2, A + BS^3, A + BS^4, A + BS^2 + CS^3$ and $A + BS^n$. This generalization is supported strongly by the literature [2,12–14,16], and a thorough mathematical analysis for the model is, of course, interesting.

2 The model

Let $S(t)$ denote the concentration of nutrient in the vessel at time t, $x(t)$ and $y(t)$, the concentration of the two microorganisms. The model of two microorganisms takes the form (see [2,12,14], for instance):

$$\begin{aligned}
\frac{dS}{dt} &= (S_0 - S)Q - \frac{1}{\delta_1} g_1(S)x - \frac{1}{\delta_2} g_2(S)y, \\
\frac{dx}{dt} &= x\left(g_1(S) - Q\right), \\
\frac{dy}{dt} &= y(g_2(S) - Q), \\
S(0) &= S_0 > 0, x(0), y(0) \geq 0,
\end{aligned} \tag{1}$$

where S_0 is the input concentration of nutrient, Q is the washout rate, $g_i(S), i = 1, 2$ are the growth rates of microorganisms, and $\frac{1}{\delta_i}, i = 1, 2,$ are the yield coefficients, in which $\delta_i = \delta_i(S), i = 1, 2,$ are functions of S. All these parameters are positive. Usually, $g_i(S)$ takes the form of $\frac{m_i S}{k_i + S}, i = 1, 2.$

System (1) with the yield coefficients $\delta_i(S) = A_i + S, g_i(S) = \frac{m_i S}{k_i + S}, i = 1, 2,$ and $\delta_1(S) = A + BS^2, \delta_2(S) =$ const., $g_i(S) = \frac{m_i S}{k_i + S}, i = 1, 2$ was studied in [13,16], and with $\delta_1(S) = 1 + 50S^3, \delta_2(S) = 120$ was studied in [14], and $\delta_1(S) = 1 + 50S^4, \delta_2(S) = 120$ in [2], respectively. Here we investigate system (1) with $\delta_1(S) = A_0 + A_1 S + \cdots + A_n S^n, \delta_2(S) = B_0 + B_1 S + \cdots + B_m S^m$, and $g_i(S), i = 1, 2,$ the two general functions with the assumptions that $g_i(0) = 0, g_i' > 0, i = 1, 2$. For the yield coefficients, we assume that $A_i \geq 0, i = 0, 1, 2, \dots, n, B_j \geq 0, j = 0, 1, 2, \dots, m$ with at least, one of A_i and one of B_j positive. This model is for the case when the production of the microbial biomasses is more sensitive to the concentration of the nutrient in the vessel than the cases in [12,13,16,19].

Performing the standard scaling for the chemostat, let

$$\bar{S} = \frac{S}{S_0}, \bar{x} = \frac{x}{S_0}, \bar{y} = \frac{y}{S_0}, \tau = Qt, \bar{g}_i(\bar{S}) = \frac{g_i(\bar{S}S_0)}{Q}, \ i = 1, 2,$$

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

$$
\begin{aligned}
\frac{dS}{dt} &= 1 - S - \frac{x}{A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n} g_1(S) \\
&\quad - \frac{y}{B_0 + B_1 S_0 S + \cdots + B_m S_0^m S^m} g_2(S), \\
\frac{dx}{dt} &= x\left(g_1(S) - 1\right), \\
\frac{dy}{dt} &= y(g_2(S) - 1).
\end{aligned} \tag{2}
$$

Here, 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

$$
\{(S, x, y) \mid 0 \leq S \leq 1, \quad x \geq 0, \quad y \geq 0\}.
$$

Due to the biological background, it is assumed that all these coefficients $A_i, i = 0, 1, \ldots, n$ and $B_i, i = 0, 1, \ldots, m$ are non-negative but not all zeros.

Let $\lambda_i = g_i^{-1}(1), i = 1, 2$. We have [3],

Lemma 1 *For system (2),*

$$
\begin{aligned}
&(i) \quad \text{if } g_1(S) < 1, \text{ then } \frac{dx}{dt} < 0, \text{ and } \lim_{t\to\infty} x(t) = 0; \\
&(ii) \text{ if } g_2(S) < 1, \text{ then } \frac{dy}{dt} < 0, \text{ and } \lim_{t\to\infty} y(t) = 0.
\end{aligned}
$$

(Note that $g_i(S) < 1$ on $0 \leq S \leq 1$ implies that $g_i(1) < g_i(\lambda_i)$, and then $\lambda_i > 1$.)

Proof Let $\hat{x}(t)$ be the solution of

$$
\begin{aligned}
\frac{d\hat{x}(t)}{dt} &= (g_1(1) - 1)\hat{x}(t), \\
\hat{x}(t_0) &= x(t_0).
\end{aligned}
$$

It follows that $0 < x(t) \leq \hat{x}(t)$; then $\lim_{t\to\infty} \hat{x}(t) = \lim_{t\to\infty} x(t_0)e^{(g(1)-1)t} = 0$, since $g_1(1) - 1 < 0$. Therefore, $\lim_{t\to\infty} x(t) = 0$. Similarly, $\lim_{t\to\infty} y(t) = 0$.

In the case of $\lambda_1 = 1$, consider the system

$$
\begin{aligned}
\frac{d\hat{x}(t)}{dt} &= (g_1(S) - 1)\hat{x}(t), \\
\hat{x}(t_0) &= x(t_0).
\end{aligned}
$$

The same argument as above can show that $\lim_{t\to\infty} x(t) = 0$ on $0 \leq S < 1$. By the continuity of the solution on the variable S, we still have $\lim_{t\to\infty} x(t) = 0$. Therefore, in order to avoid the microorganisms vanishing, we need to assume $0 < \lambda_i < 1, i = 1, 2$. □

System (2) has the following three possible equilibrium points:

$E_0(1,0,0)$, $E_1(\lambda_1, (1-\lambda_1)(A_0 + A_1 S_0 \lambda_1 + \cdots + A_n S_0^n \lambda_1^n), 0)$ if $0 < \lambda_1 < 1$, and $E_2(\lambda_2, 0, (1-\lambda_2)(B_0 + B_1 S_0 \lambda_2 + \cdots + B_m S_0^m \lambda_2^m))$ if $0 < \lambda_2 < 1$.

Denote

$$Q_1 \equiv (A_1 + A_2 S_0 \lambda_1 + \cdots + A_n S_0^{n-1} \lambda_1^{n-1}) S_0,$$
$$Q_2 \equiv (B_1 + B_2 S_0 \lambda_2 + \cdots + B_m S_0^{m-1} \lambda_2^{m-1}) S_0,$$

and

$$R_1 = \frac{1 - 2\lambda_1 + \lambda_1(1-\lambda_1)\left(\frac{A_2 S_0 + 2A_3 S_0^2 \lambda_1 + \cdots + (n-1) A_n S_0^{n-1} \lambda_1^{n-2}}{A_1 + A_2 S_0 \lambda_1 + \cdots + A_n S_0^{n-1} \lambda_1^{n-1}} - g_1'(\lambda_1)\right)}{1 + (1-\lambda_1)\, g_1'(\lambda_1)},$$
$$R_2 = \frac{1 - 2\lambda_2 + \lambda_2(1-\lambda_2)\left(\frac{B_2 S_0 + 2B_3 S_2^2 \lambda_2 + \cdots + (m-1) B_m S_0^{m-1} \lambda_2^{m-2}}{B_1 + B_2 S_0 \lambda_2 + \cdots + B_m S_0^{m-1} \lambda_2^{m-1}} - g_2'(\lambda_2)\right)}{1 + (1-\lambda_2)\, g_2'(\lambda_2)}.$$

Our main results are in the next section.

3 Main theorems and proofs

For the property of the equilibrium points, we have

Theorem 1 *(i) E_0 is always an equilibrium point. It is globally asymptotically stable if $\lambda_i > 1$, or $g_i(1) < 1$, $i = 1, 2$. It is unstable if either inequality is reversed.*

(ii) E_1 exists if and only if $0 < \lambda_1 < 1$, or $g_1(1) > 1$. If it exists, it is possible to have a two-dimensional stable manifold (the plane $x = 0$), and is locally asymptotically stable if $\frac{A_0}{Q_1} > R_1$ and $\lambda_1 < \lambda_2$, and unstable if either inequality is reversed.

(iii) E_2 exists if and only if $0 < \lambda_2 < 1$, or $g_2(1) > 1$. If it exists, it is possible to have a two-dimensional stable manifold (the plane $y = 0$), and is locally stable if $\frac{B_0}{Q_2} > R_2$ and $\lambda_1 > \lambda_2$, and unstable if either inequality is reversed.

Proof The Jacobian matrix of (2) takes the form

$$J(S, x, y) = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix}, \tag{3}$$

where

$$j_{11} = -1 - \frac{x}{(A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n)^2} \times (g_1'(S)(A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n)$$

$$
\begin{aligned}
&- g_1(S)(A_1S_0 + 2A_2S_0^2S + \cdots + nA_nS_0^nS^{n-1}))\\
&- \frac{y}{(B_0 + B_1S_0S + \cdots + B_mS_0^mS^m)^2}(g_2'(S)\\
&\times(B_0 + B_1S_0S + \cdots + B_mS_0^mS^m)\\
&- g_2(S)(B_1S_0 + 2B_2S_0^2S + \cdots + mB_mS_0^mS^{m-1})),\\
j_{12} &= -\frac{g_1(S)}{A_0 + A_1S_0S + \cdots + A_nS_0^nS^n},\\
j_{13} &= -\frac{g_2(S)}{B_0 + B_1S_0S + \cdots + B_mS_0^mS^m},\\
j_{21} &= xg_1'(S),\ j_{22} = g_1(S) - 1,\ j_{23} = j_{32} = 0,\\
j_{31} &= yg_2'(S),\ j_{33} = g_2(S) - 1.
\end{aligned}
$$

The corresponding characteristic equation for E_1 is

$$
(r - (g_2(\lambda_1) - 1))\left(r^2 + b_1r + c_1\right) = 0, \tag{4}
$$

where

$$
\begin{aligned}
b_1 &= 1 + (1-\lambda_1)\left(g_1'(\lambda_1) - \frac{A_1S_0 + 2A_2S_0^2\lambda_1 + \cdots + nA_nS_0^n\lambda_1^{n-1}}{A_0 + A_1S_0\lambda_1 + \cdots + A_nS_0^n\lambda_1^n}\right)\\
c_1 &= (1-\lambda_1)\,g_1'(\lambda_1) > 0.
\end{aligned}
$$

If $b_1 > 0$, or if $\frac{A_0}{Q_1} > R_1$ and $\lambda_1 < \lambda_2$, then the three roots of (4) are either negative or with negative real parts. Hence E_1 is locally asymptotically stable, and it is unstable if either of the inequality is reversed. Obviously, the plane $y = 0$ is a stable manifold of (2).

Similarly, we can prove the result (iii) for E_2.

When $\lambda_i > 1, i = 1, 2$, then E_1 and E_2 do not exist and E_0 is the only equilibrium, the global statement of (i) can be established by comparison theorems using (2) and the flow on each of the invariant sets $x = 0$ and $y = 0$. The same comparison argument and the Butler–MeGehee Theorem (see Smith and Waltman [15], p. 12) shows that if only one of E_1 and E_2 exists, that equilibrium point is globally asymptotically stable. The proof of Theorem 1 is completed. □

Theorem 2 *System (2) has a positive invariant set Ω which takes the form:*

$$
\begin{aligned}
&\{(S,x,y)|\ 0\le S\le M - x - y,\ 0\le x\le \left(A_0+A_1S_0\lambda_1+\cdots+A_nS_0^n\lambda_1^n\right)\\
&\quad(1-\lambda_1)+\varepsilon_0 0\le y\le \left(B_0+B_1S_0\lambda_2+\cdots+B_mS_0^m\lambda_2^m\right)\\
&\quad(1-\lambda_2)+\varepsilon_0,\ 0<M<+\infty,\ \varepsilon_0>0,\ const.\}.
\end{aligned}
$$

Proof We are going to show that any trajectory initiated at (S, x, y) in the open positive octant will enter into Ω as $t \to +\infty$. In fact, by the first equation of (2), any trajectory starting in $\{(S, x, y)|\, S < 0, x > 0, y > 0\}$ will cross the face $S = 0$ into the positive octant in R^3. But the reverse is not true.

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

$$\begin{aligned}\left.\frac{d\pi}{dt}\right|_{\pi=0} &= \left.\left(\frac{dS}{dt} + \frac{dx}{dt} + \frac{dy}{dt}\right)\right|_{S=M-x-y} \\ &= 1 - M - x\left(\frac{1}{A_0 + A_1 S_0(L - x - y) + \cdots + A_n S_0^n (M - x - y)^n} - 1\right) \\ &\quad \times g_1(M - x - y) \\ &\quad - y\left(\frac{1}{B_0 + B_1 S_0(M - x - y) + \cdots + B_m S_0^m (M - x - y)^m} - 1\right) \\ &\quad \times g_2(M - x - y).\end{aligned}$$

Since x, y, g_1, g_2 are bounded, and $A_i, B_j, i = 0, 1, \ldots, n, j = 0, 1, \ldots, m$ are positive, $\left.\frac{d\pi}{dt}\right|_{\pi=0} < 0$ for sufficiently large M. Therefore, the trajectory will cross the face $\pi = 0$ into Ω.

Moreover, $\left.\frac{dS}{dt}\right|_{S=0} = 1 > 0$, and both the faces $x = 0$ and $y = 0$ are the solutions of (2). Thus, Ω is positively invariant under (2). □

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. We recall the following result [11].

Consider the system

$$\begin{aligned}\frac{dx}{dt} &= x\,(g(y) - 1)\,, \\ \frac{dy}{dt} &= 1 - y - \frac{g(y)}{F(y)}x,\end{aligned} \tag{5}$$

where $g(0) = 0$, $g'(y) \geq 0$, $F(y) > 0$, $F'(y) \geq 0$.

In $\{(x, y)|0 \leq x \leq 1, y \geq 0\}$, system (5) has two equilibrium points $(0, 1)$, and (x^*, y^*) if $g(1) > 1$, where

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

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

Denote

$$p = 1 + x^* \frac{d}{dy}\left(\frac{g}{F}\right)\Big|_{y=y^*}\,. \tag{6}$$

The following theorem was established [11]. □

Theorem H *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 (5) surrounding the equilibrium* (x^*, y^*).

On the face $y = 0$, the two dimensional stable manifold, system (2) is reduced to

$$\frac{dS}{dt} = 1 - S - x\frac{1}{A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n} g_1(S)$$
$$\frac{dx}{dt} = x\left(g_1(S) - 1\right), \tag{7}$$

which is a special case of (5) if let $y = S$, $g(y) = g(S)$, $F(y) = A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n$. By Theorem H, it follows

Theorem 3 *If* $0 < \lambda_1 < 1$, *system (7) has two equilibrium points:* $M_1(1, 0)$, *and* $M_2(\lambda_1, (1 - \lambda_1)(A_0 + A_1 S_0 S + \cdots + A_n S_0^n S^n))$. M_1 *is a saddle, and* M_2 *is stable if* $\frac{A_0}{Q_1} > R_1$, *and unstable if* $\frac{A_0}{Q_1} < R_1$. *In the case when* M_2 *is unstable, there is at least one limit cycle of (7) surrounding* M_2 *on the face* $y = 0$.

Similarly, if $x = 0$,then the projection of (2) on the stable manifold $x = 0$, has two equilibrium points: $N(1, 0)$ and $N_2(\lambda_2, (1 - \lambda_2)(B_0 + B_1 S_0 \lambda_2 + \cdots + B_m S_0^m \lambda_2^m))$. We have

Theorem 4 *Assume* $0 < \lambda_2 < 1$. *If* $\frac{B_0}{Q_2} > R_2$, *then is stable; if* $\frac{B_0}{Q_2} < R_2$, *then* N_2 *is unstable and there exists at least one limit cycle on the stable manifold* $x = 0$ *surrounding* N_2.

Regarding the bifurcation on the two-dimensional stable manifolds, the following theorems are valid.

Theorem 5 *System (7) undergoes a Hopf bifurcation on the face* $y = 0$ *when* $\frac{A_0}{Q_1} = R_1$.

Proof Let $J(M_2)$ be the Jacobian at M_2. The corresponding characteristic equation is

$$r^2 + b_1 r + c_1 = 0. \tag{8}$$

Let $\frac{A_0}{Q_1} = \mu$. Denote b_1, the coefficient of r in the above equation, as $tr J\left(\frac{A_0}{Q_1}\right)$, or $tr J(\mu)$, where

$$tr J(\mu) = 1 + (1 - \lambda_1)\left(g_1'(\lambda_1) - \frac{1 + \frac{A_2 S_0 + 2A_3 S_0^2 \lambda_1 + \cdots + (n-1)A_n S_0^{n-1} \lambda_1^{n-2}}{A_1 + A_2 S_0 \lambda_1 + \cdots + A_n S_0^{n-1} \lambda_1^{n-1}}}{\mu + \lambda_1}\right). \tag{9}$$

Since

$$\frac{d}{d\mu} tr J(\mu)\,\Big|_{\mu = R_1} = (1 - \lambda_1)\frac{1 + \frac{A_2 S_0 + 2A_3 S_0^2 \lambda_1 + \cdots + (n-1)A_n S_0^{n-1} \lambda_1^{n-2}}{A_1 + A_2 S_0 \lambda_1 + \cdots + A_n S_0^{n-1} \lambda_1^{n-1}}}{(R_1 + \lambda_1)^2} > 0,$$

$tr\,J(\mu)$ is increasing at $\mu = R_1$, and the phase structure of M_2 changes from unstable to stable at R_1 as the parameter μ increases. So (7) undergoes a Hope bifurcation at $\frac{A_0}{Q_1} = R_1$ by the definition Zhang [18]. □

Theorem 6 *If $x = 0$, then for the equilibrium point N_2, the projecting system of (2) on the stable manifold $x = 0$ undergoes a Hopf bifurcation at $\frac{B_0}{Q_2} = R_2$.*

The stability of the periodic solution created by the bifurcation can be shown as follows. For the simplicity, we assume that the functional responses take the special form $g_i(S) = \frac{m_i S}{k_i + S}$, $i = 1, 2$ in the proof.

Theorem 7 *The periodic solution of system (7) created by the bifurcation at $\frac{A_0}{Q_1} = R_1$ is stable when $0 < \frac{A_0}{Q_1} - R_1 \ll 1$, and $g_3 < 0$ (where g_3 is defined as in (14)).*

Proof We first make the following transformation:

$$\bar{S} = S - \lambda_1, \bar{x} = x - (1 - \lambda_1)(A_0 + A_1 S_0 \lambda_1 + \cdots + A_n S_0^n \lambda_1^n).$$

Let

$$dt = (A_0 + A_1 S_0(\bar{S} + \lambda_1) + \cdots + A_n S_0^n (\bar{S} + \lambda_1)^n)(k_1 + \bar{S} + \lambda_1) d\tau,$$

and denote $a = A_0 + A_1 S_0 \lambda_1 + \cdots + A_n S_0^n \lambda_1^n$, $b = k_1 + \lambda_1$, $d = 1 - \lambda_1$, then drop the bars above the variables, system (7) now takes the form:

$$\begin{aligned}
\frac{dS}{dt} &= [a(d - b) + bd(A_1 S_0 + C_2^1 A_2 S_0^2 \lambda_1 + \cdots + C_n^{n-1} A_n S_0^n \lambda_1^{n-1}) - adm_1]S \\
&\quad -m_1 \lambda_1 x - m_1 x S \\
&\quad +[(d - b)(A_1 S_0 + C_2^1 A_2 S_0^2 \lambda_1 + \cdots + C_n^{n-1} A_n S_0^n \lambda_1^{n-1}) \\
&\quad +bd(A_2 S_0^2 + C_3^1 A_3 S_0^3 \lambda_1 + \cdots + C_n^{n-2} A_n S_0^n \lambda_1^{n-2}) - a]S^2 \\
&\quad +[(d - b)(A_2 S_0^2 + C_3^1 A_3 S_0^3 \lambda_1 + \cdots + C_n^{n-2} A_n S_0^n \lambda_1^{n-2}) \\
&\quad +bd(A_3 S_0^3 + C_4^1 A_4 S_0^4 \lambda_1 + \cdots + C_n^{n-3} A_n S_0^n \lambda_1^{n-3}) \\
&\quad -(A_1 S_0 + C_2^1 A_2 S_0^2 \lambda_1 + \cdots + C_n^{n-1} A_n] S_0^n \lambda_1^{n-2})]S^3 + \cdots \\
&\quad +[(d - b)(A_{n-1} S_0^{n-1} + C_n^1 A_n S_0^n \lambda_1) + bd A_n S_0^n \\
&\quad -(A_{n-2} S_0^{n-2} + C_{n-1}^1 A_{n-1} S_0^{n-1} \lambda_1 + C_n^2 A_n S_0^n \lambda_1^2)]S^n \\
&\quad +[(d - b) A_n S_0^n - (A_{n-1} S_0^{n-1} + C_n^1 A_n S_0^n \lambda_1)]S^{n+1} - A_n S_0^n S^{n+2}, \\
\frac{dx}{dt} &= (m_1 - 1)(xS + adS)(A_0 + A_1 S_0(S + \lambda_1) + A_2 S_0^2 (S + \lambda_1)^2 + \cdots \\
&\qquad +A_n S_0^n (S + \lambda_1)^n) \\
&= (m_1 - 1)(xS + adS)(a + A_1 S_0 + C_2^1 A_2 S_0^2 \lambda_1 + \cdots + C_n^{n-1} A_n S_0^n \lambda_1^{n-1})S \\
&\quad +(A_2 S_0^2 + C_3^1 A_3 S_0^3 \lambda_1 + \cdots + C_n^{n-2} A_n S_0^n \lambda_1^{n-2})S^2 \\
&\quad +(A_3 S_0^3 + C_4^1 A_4 S_0^4 \lambda_1 + \cdots + C_n^{n-3} A_n S_0^n \lambda_1^{n-3})S^3 + \cdots \\
&\quad +(A_{n-1} S_0^{n-1} + C_n^1 A_n S_0^n \lambda_1)S^{n-1} + A_n S_0^n S^n.
\end{aligned}$$

Note that, here $C_n^k = \frac{n!}{k!(n-k)!}, k = 0, 1, 2, \ldots, n$, the combination coefficients. Denote

$$\begin{aligned}
\bar{A}_1 &= A_1 S_0 + C_2^1 A_2 S_0^2 \lambda_1 + C_3^2 A_3 S_0^3 \lambda_1^2 + \cdots + C_n^{n-1} A_n S_0^n \lambda_1^{n-1},\\
\bar{A}_2 &= A_2 S_0^2 + C_3^1 A_3 S_0^3 \lambda_1 + C_4^2 A_4 S_0^4 \lambda_1^2 + \cdots + C_n^{n-2} A_n S_0^n \lambda_1^{n-2},\\
\bar{A}_3 &= A_3 S_0^3 + C_4^1 A_4 S_0^4 \lambda_1 + C_5^2 A_5 S_0^5 \lambda_1^2 + \cdots + C_n^{n-3} A_n S_0^n \lambda_1^{n-3},\\
&\cdots\\
\bar{A}_{n-1} &= A_{n-1} S_0^{n-1} + C_n^1 A_n S_0^n \lambda_1,\\
\bar{A}_n &= A_n S_0^n.
\end{aligned}$$

Write the above system in $A_i, i = 1, 2, \ldots, n$,

$$\begin{aligned}
\frac{dS}{dt} &= ((d-b)a + bd\bar{A}_1 - adm_1)S - m_1\lambda_1 x - m_1 x S\\
&\quad +((d-b)\bar{A}_1 + bd\bar{A}_2 - a)S^2 + ((d-b)\bar{A}_2 + bd\bar{A}_3 - \bar{A}_1)S^3 + \cdots\\
&\quad +((d-b)\bar{A}_{n-1} + bd\bar{A}_n - \bar{A}_{n-2})S^n + ((d-b)\bar{A}_n - \bar{A}_{n-1})S^{n+1} - \bar{A}_n S^{n+2},\\
\frac{dx}{dt} &= (m_1 - 1)(a(ad + x)S + \bar{A}_1(x + ad)S^2 + \cdots + \bar{A}_n(x + ad)S^{n+1}).
\end{aligned} \tag{10}$$

Note that the condition $\frac{A_0}{Q_1} = R_1$ is now equivalent to $a(d-b) + bd\bar{A}_1 - adm_1 = 0$. Then, system (10) is equivalent to

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{m_1 k_1}{m_1 - 1} x - m_1 x S + [(d-b)\bar{A}_1 + bd\bar{A}_2 - a)S^2 + \cdots\\
&\quad +((d-b)\bar{A}_n - \bar{A}_{n-1})S^{n+1} - \bar{A}_n S^{n+2},\\
\frac{dx}{dt} &= (m_1 - 1)a^2 d S + (m_1 - 1)(a x S + \bar{A}_1(x + ad)S^2\\
&\quad +\bar{A}_2(x + ad)S^3 + \cdots + \bar{A}_n(x + ad)S^{n+1}).
\end{aligned} \tag{11}$$

By another transformation: $S = \frac{\sqrt{m_1 k_1}}{a(m_1-1))\sqrt{d}}\bar{S}, x = \bar{x}, t = \frac{1}{a\sqrt{dm_1 k_1}}\bar{t}$, and drop the bars, system (11) becomes

$$\begin{aligned}
\frac{dS}{dt} &= -x + a_1 S^2 - a_2 x S + a_3 S^3 + a_4 S^4 + \cdots + a_{n+1} S^{n+1} - a_{n+2} S^{n+2},\\
\frac{dx}{dt} &= S + b_1 x S + b_2 x S^2 + \bar{b}_2 S^2 + b_3 x S^3 + \bar{b}_3 S^3 + \cdots + b_n x S^n + \bar{b}_n S^n\\
&\quad +b_{n+1} x S^{n+1} + \bar{b}_{n+1} S^{n+1},
\end{aligned} \tag{12}$$

where,

$$a_1 = \frac{(d-b)\bar{A}_1 + bd\bar{A}_2 - a}{(m_1 - 1)a^2 d},$$

$$
\begin{aligned}
a_2 &= \frac{m_1}{a\sqrt{dk_1m_1}},\\
a_3 &= \frac{((d-b)\bar{A}_2 + bd\bar{A}_3 - \bar{A}_1)\sqrt{m_1k_1}}{(m_1-1)^2a^3d\sqrt{d}}, \ldots,\\
a_{n+1} &= \frac{((d-b)\bar{A}_n - \bar{A}_{n-1})\left(\sqrt{m_1k_1}\right)^{n-1}}{(m_1-1)^n a^{n+1}\left(\sqrt{d}\right)^{n+1}},\\
a_{n+2} &= \frac{\bar{A}_n\left(\sqrt{m_1k_1}\right)^{n}}{(m_1-1)^{n+1} a^{n+2}\left(\sqrt{d}\right)^{n+2}};\\
b_1 &= \frac{1}{ad}, \quad b_2 = \frac{\bar{A}_1\sqrt{m_1k_1}}{(m_1-1)a^3d\sqrt{d}}, \quad \bar{b}_2 = \frac{\bar{A}_1\sqrt{m_1k_1}}{(m_1-1)a^2\sqrt{d}},\\
&\cdots\\
b_{n+1} &= \frac{\bar{A}_n\left(\sqrt{m_1k_1}\right)^{n}}{(m_1-1)^{n} a^{n+2}\left(\sqrt{d}\right)^{n+2}}, \quad \bar{b}_{n+1} = \frac{\bar{A}_n\left(\sqrt{m_1k_1}\right)^{n}}{(m_1-1)^{n} a^{n+1}\left(\sqrt{d}\right)^{n}}.
\end{aligned}
$$

Let $S = r\cos\theta$, $x = r\sin\theta$. Then, system (12) becomes

$$
\begin{aligned}
\frac{dr}{dt} &= \cos\theta(a_1S^2 - a_2xS + a_3S^3 + a_4S^4 + \cdots + a_{n+1}S^{n+1} - a_{n+2}S^{n+2})\\
&\quad + \sin\theta(b_1xS + b_2xS^2 + \bar{b}_2S^2 + b_3xS^3 + \bar{b}_3S^3 + \cdots + b_{n+1}xS^{n+1} + \bar{b}_{n+1}S^{n+1}),\\
\frac{d\theta}{dt} &= 1 - \frac{1}{r}[\sin\theta(a_1S^2 - a_2xS + a_3S^3 + a_4S^4 + \cdots + a_{n+1}S^{n+1} - a_{n+2}S^{n+2})\\
&\quad - \cos\theta(b_1xS + b_2xS^2 + \bar{b}_2S^2 + \cdots + b_{n+1}xS^{n+12} + \bar{b}_{n+1}S^{n+1})].
\end{aligned}
$$

Substituting by $S = r\cos\theta$, $x = r\sin\theta$, and cancel the time variable t. If expend $\frac{dr}{d\theta}$ as a power series in r, we have

$$
\begin{aligned}
\frac{dr}{d\theta} &= r^2[a_1\cos^3\theta + (\bar{b}_2 - a_2)\sin\theta\cos^2\theta + b_1\sin^2\theta\cos\theta]\\
&\quad + r^3\{[a_3\cos^4\theta + \bar{b}_3\cos^3\theta\sin\theta + \bar{b}_2\cos^2\theta\sin\theta] - [a_1\cos^3\theta\\
&\quad + (\bar{b}_2 - a_2)\cos^2\theta\sin\theta + b_1\cos\theta\sin^2\theta)]\,[\bar{b}_2\cos^3\theta\\
&\quad + (b_1 - a_1)\cos^2\theta\sin\theta + a_2\cos\theta\sin^2\theta]\} + \cdots.
\end{aligned} \tag{13}
$$

Assume that the solution of (13) takes the form $r = c + r_2(\theta)c^2 + r_3(\theta)c^3 + \cdots$, with $r_1(0) = r_2(0) = r_3(0) = \cdots = 0$. Then substituting this solution into (13) and comparing the coefficients of c^2, one has

$$
\frac{dr_2}{d\theta} = a_1\cos^3\theta + (\bar{b}_2 - a_2)\cos^2\theta\sin\theta + b_1\sin^2\theta\cos\theta.
$$

Integrating the above equation in $[0, \theta]$ will result in

$$r_2(\theta) = a_1 \sin\theta + \frac{1}{3}(b_1 - a_1)\sin^3\theta - \frac{\bar{b}_2 - a_2}{3}\cos^3\theta + \frac{\bar{b}_2 - a_2}{3}.$$

It is easy to see that $r_2(\theta)$ is a periodic function with the period 2π. Compare the coefficients of c^3, we have

$$\frac{dr_3}{d\theta} = 2r_2[a_1\cos^3\theta - (\bar{b}_2 - a_2)\sin\theta\cos^2\theta + b_1\sin^2\theta\cos\theta] + \{a_3\cos^4\theta$$
$$+\bar{b}_3\cos^3\theta\sin\theta + b_2\cos^2\theta\sin^2\theta - [a_1\cos^3\theta + (\bar{b}_2 - a_2)\cos^2\theta\sin\theta$$
$$+b_1\cos\theta\sin^2\theta]\,[\bar{b}_2\cos^3\theta + (b_1 - a_1)\cos^2\theta\sin\theta + a_2\cos\theta\sin^2\theta]\}.$$

Let $r_3(\theta) = g_3\theta + f_3(\theta)$, then

$$g_3 = \frac{1}{2\pi}\int_0^{2\pi}\left[\left(-\frac{4}{3}a_1\bar{b}_2 + \frac{4}{3}a_1a_2 - \frac{2}{3}b_1b_2 - \frac{1}{3}a_2b_1 + b_2\right)\cos^2\theta\right.$$
$$+\left(\frac{5}{3}a_1\bar{b}_2 - \frac{8}{3}a_1a_2 - \frac{4}{3}b_1\bar{b}_2 + \frac{7}{3}a_2b_1 + a_3 - b_2\right)\cos^4\theta$$
$$\left.+\,(-2a_1\bar{b}_2 + 2b_1\bar{b}_2 + 2a_1a_2 - 2a_2b_1)\cos^6\theta\right]d\theta,$$

that is,

$$g_3 = -\frac{2}{3}a_1\bar{b}_2 + \frac{7}{24}a_1a_2 - \frac{5}{24}b_1\bar{b}_2 + \frac{1}{12}a_2b_1 + \frac{1}{8}b_2 + \frac{3}{8}a_3. \tag{14}$$

$$f_3(\theta)$$
$$= \int_0^{\theta}\left[(2a_1^2 + \bar{b}_3)\sin\theta\cos^3\theta + \left(a_2^2 - b_1^2 - \frac{2}{3}a_1^2 + \frac{2}{3}a_1\bar{b}_2 - a_2\bar{b}_2 + a_1b_1\right)\right.$$
$$\times\cos^3\theta\sin^3\theta + \left(a_1^2 - \frac{1}{3}\bar{b}_2^2 + \frac{2}{3}a_2^2 - \frac{1}{3}\bar{b}_2a_2 - a_1b_2\right)\cos^5\theta\sin\theta$$
$$+\,2a_1b_1\sin^3\theta\cos\theta + \frac{2}{3}a_1(\bar{b}_2 - a_2)\cos^3\theta$$
$$\left.-\frac{2}{3}(\bar{b}_2 - a_2)^2\cos^2\theta\sin\theta + \frac{2}{3}(\bar{b}_2 - a_2)b_1\sin^2\theta\cos\theta\right]d\theta.$$

Obviously, $f_3(\theta)$ is a periodic function with the period 2π. If $g_3 < 0$, by the criteria of the successor function, M_2 is a first order stable focus, and if $\frac{A_0}{Q_1} < R_1$, M_2 is unstable, by the method of Friedrich (see [18]), the periodic solution surrounding M_2 is stable. We thus complete the proof of Theorem 6. □

4 Conclusion

We have showed it analytically that the limit cycle created by the bifurcation in the stable manifold $S - x$ face of system (2) is stable under certain conditions. This work is based on many numerical simulations [2,14]. As an example, Fig. 2, which is from Pilyugin and Waltman [14], Fig. 2, p. 159, shows that for some particular system parameters, system (7) can have two limit cycles. As shown in the figure, of the two periodic trajectories shown here, the outer is asymptotically stable and the inner is unstable. The asymptotically stable equilibrium E_1 or M_2 as in Theorem 3 (not shown) is located inside the inner cycle.

We would like to consider another example,

$$\begin{aligned}\frac{dS}{dt} &= 1 - S - x\frac{1}{1+c_1S^3}\frac{2S}{0.7+S} - y\frac{1}{120}\frac{m_2S}{6.5+S},\\ \frac{dx}{dt} &= x\left(\frac{2S}{0.7+S} - 1\right),\\ \frac{dy}{dt} &= y\left(\frac{m_2S}{6.5+S} - 1\right),\\ S(0) &= S_0 \geq 0,\ x(0),\ y(0) \geq 0.\end{aligned} \tag{15}$$

As shown in Fig. 1, the five stable limit cycles in the positive orthant correspond to $m_2 = 9.85+0.05k$, $k = 1, 2, \ldots, 5$. They were computed as numerical simulations of (15) with initial conditions: $S(0) = 0.4$, $x(0) = 2.0$, $y(0) = 0.01$ for $0 \leq t \leq 5000$. The figure shows the parametric plots of these solutions for $4500 \leq t \leq 5000$. The limit cycle in the $S - x$ plane is the trajectory of (2). It was computed by setting $S(0) = 0.4$, $x(0) = 2.0$, $y(0) = 0$.

These numerical simulations indicate that a further study of the system proposed in this paper is useful in describing the microbial growth dynamics in chemostat when

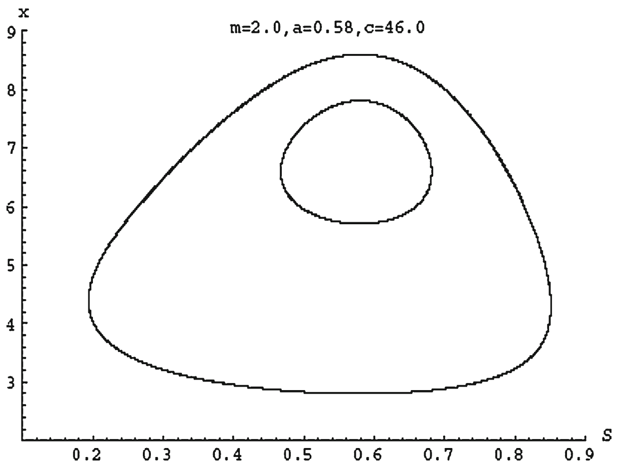

Fig. 2 Two limit cycles in the stable manifold $S - x$ face of system (2) (see [14], Fig. 2, p. 159)

the yield depends on the limiting nutrient concentration. For some particular choice of the system parameters, the variable yield models exhibit sustained oscillations and multiple limit cycles exist. The variable yield model conforms to the experimental data on microbial growth in continuous cultures that exhibit sustained oscillations (see [14] and its references).

Because many authors have already suggested some particular polynomials as the yield coefficients (see, for example [2–5,12–14,16,19]), it is of interests to use complete nth and mth order polynomials in analyzing the dynamical behavior of the chemostat. That helps to understand how the yield depends on the substrate and to incorporate the term correctly in the model.

Note that the conditions of the theorems are in terms of the system functions and parameters. This might be useful in reactor technology. The dynamical system on the stable manifold $y = 0$ (i.e. the $S - x$ face) is important when the microorganism x is a better competitor [10].

The existence of limit cycles in the three-dimensional system (2) has not been proved directly in the three-dimensional space, but in the two-dimensional stable manifold. However, the limit cycles on the face $y = 0$ are still the ones of the space. In general, proving the existence of periodic solutions of the n-dimensional differential system is always of interest in both theory and applications. This is because the situation of $n \geq 3$ is much complicated than the one of $n = 2$ and the powerful tools in the plane system like the Poincare-Bendixson theorem cannot be applied directly in the space. So any results regarding the 3-D limit cycles are welcome in this area.

Finally, we would like to mention, suggested by one of the referee, that a generalization of the Poincare-Bendixson theorem for higher dimensional cases with chemical application can be found in the last reference [17].

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