A three dimensional chemostat with quadratic yields

Xuncheng Huang* and Lemin Zhu

Yangzhou Polytechnic University, 20 Mountain Tiger Road, 2-403 Yangzhou 225002, China
E-mail: xh311@yahoo.com

A three dimensional chemostat with two microorganisms which are both with quadratic yields is studied. The stability of the equlibrium points, the existence of limit cycles, the Hopf bifurcation, and the positive invariant set for the system are discussed. We also prove the conditions that guarantee two limit cycles in the model.

KEY WORDS: Continuous culture, variable yield, limit cycles, Hopf bifurcation

AMS subject classification: 34A34, 92D25

1. Introduction

The basic chemostat is an interesting example of an open system with purely exploitative competition [2,10–12,18–21,24,27–28]. It consists of three vessels. The first contains the nutrient which is pumped at a constant rate into the second vessel which is called the culture vessel. This vessel is charged with microorganisms which compete, in a purely exploitative manner, for the nutrient. The contents of the second vessel is pumped, at a constant rate, into the third or overflow vessel. It is assumed that the culture vessel is well stirred, and the temperature, pH, etc., are kept constants and the turnover of the vessel is sufficiently fast, that no well growth occurs and that there is no buildup metabolic products.

In ecology the chemostat is a model of a simple lake but in chemical engineering it serves as a laboratory model of a bio-reactor used to manufacture products with genetically altered organisms. In waste water treatment it is often the starting point for construction of models (Schuler and Kargi [23]), and it is also useful in the study of the mammalian large intestine (see Freter [8]). The basic analysis of the chemostat can be found in Levin and Stewart [26], Hsu, Hubbell and Waltman [10], Fredrickson and Stephanopoulos [7]. The book of Smith and Waltman [24] provides a detailed description of the chemostat and its properties.

---

*Corresponding author.

Most of the models in chemostat assume that the yield coefficient is a constant. But the accumulation of experimental data suggest that a constant yield fails to explain the observed oscillatory behavior in the chemostat (see Dorofeev, et al. [6]). Crooke [3,4] once suggested a linear function instead of the constant for the yield coefficient and declared a limit cycle may exist in his model. Pilyugin and Waltman (2003 [22]) constructed a chemostat with variable yield and studied the multiple limit cycles in the model. It is interesting to notice that the model in [22] is exactly same as the one studied by Huang in fermentation (1990 [13]). The existence conditions, the relative position and the perimenter of the limit cycles are investigated there [13]. However, the model in [22] and [13] only considered one microorganism in the system.

A three dimensional chemostat with two microorganisms which are both with linear yields was studied by [25]. In the model the functional reaction functions were in the Monod type, and the yield coefficients were assumed linear functions of the concentration of nutrient. The stability of the solution was obtained. We are going to generalize the yield functions in [25] from linear to quadratic and study the stability of the solutions, the existence of limit cycles, the Hopf bifurcation, and the positive invariant set for the three dimensional system. We also obtain the conditions that guarantee two limit cycles in the model.

2.   The Model and Main Theorems

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

$$
\begin{aligned}
\frac{dS}{dt} &= (S_0 - S)Q - \frac{1}{\delta_1}\left(\frac{m_1 S}{k_1 + S} - L\right)x - \frac{1}{\delta_2}\frac{m_2 S}{k_2 + S}y \\
\frac{dx}{dt} &= x\left(\frac{m_1 S}{k_1 + S} - L - Q\right) \\
\frac{dy}{dt} &= y\left(\frac{m_2 S}{k_2 + S} - Q\right) \\
S(0) &= S_0 > 0, \quad x(0), \quad y(0) > 0,
\end{aligned}
\tag{1}
$$

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, and $\delta_i, i = 1, 2$, the yield coefficients. All these functions are positive. This is usually called the Monod model or the model with Michaelis Menten dynamics.

The system (1) with the yield coefficients $\delta_1 = A_1 + S, \delta_2 = A_2 + S$ was studied by [25]. Here we investigate the system (1) with $\delta_1 = A + BS^2, \delta_2 = C + DS^2$, which means that the production of the microbial biomasses is much sensitive to the concentration of the nutrient in the vessel than the case in [25].

Performing the standard scaling for the chemostat, let

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

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

$$\begin{aligned}
\frac{dS}{dt} &= 1 - S - \frac{x}{A + BS_0^2 S^2}\left(\frac{m_1 S}{k_1 + S} - L\right) - \frac{y}{C + DS_0^2 S^2}\left(\frac{m_2 S}{k_2 + S}\right) \\
\frac{dx}{dt} &= \left(\frac{m_1 S}{k_1 + S} - L - 1\right) x \\
\frac{dy}{dt} &= \left(\frac{m_2 S}{k_2 + S} - 1\right) y.
\end{aligned} \tag{2}$$

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 $R_+^3 = \{(S, x, y) \,|\, 0 \leqslant S \leqslant 1, \quad x \geqslant 0, \quad y \geqslant 0\}$.

Let $\lambda_1 = \frac{k_1(L+1)}{m_1 - (L+1)}$, $\quad \lambda_2 = \frac{k_2}{m_2 - 1}$. We have, (see Theorem 4.1, p. 167 [2]),

(i) if $0 < m_i < 1, i = 1, 2$, then $\frac{dx}{dt} < 0, \frac{dy}{dt} < 0$ and $\lim_{t \to \infty} x(t) = \lim_{t \to \infty} y(t) = 0$;

(ii) if $m_1 > L + 1$ and $\lambda_1 \geqslant 1$, then $\frac{dx}{dt} < 0$ and $\lim_{t \to \infty} x(t) = 0$; $\tag{3}$

(iii) if $m_2 > 1$ and $\lambda_2 \geqslant 1$, then $\frac{dy}{dt} < 0$ and $\lim_{t \to \infty} y(t) = 0$.

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

$$0 < \lambda_i < 1, \quad i = 1, 2 \text{ (which implies } m_1 > 1 + L, \quad m_2 > 1) \tag{4}$$

Let

$$\begin{aligned}
R_1 &= \frac{(1 - \lambda_2)\left(2\lambda_2(k_2 + \lambda_2)^2 - m_2 k_2 \lambda_2^2\right) - \lambda_2^2(k_2 + \lambda_2)^2}{(k_2 + \lambda_2)^2 + (1 - \lambda_2)m_2 k_2} S_0^2, \\
R_2 &= \frac{(1 - \lambda_1)\left(2\lambda_1(k_1 + \lambda_1)^2 - m_1 k_1 \lambda_1^2\right) - \lambda_1^2(k_1 + \lambda_1)^2}{(k_1 + \lambda_1)^2 + (1 - \lambda_1)m_1 k_1} S_0^2.
\end{aligned} \tag{5}$$

We have

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

$$E_0(1, 0, 0), \quad E_1\left(\lambda_2, 0, (C + DS_0^2 \lambda_2^2)(1 - \lambda_2)\right) \text{ and } E_2\left(\lambda_1, (A + BS_0^2 \lambda_1^2)(1 - \lambda_1), 0\right),$$

in which E_0 is a saddle; E_1 is stable if $C/D > R_1$ and $\lambda_1 > \lambda_2$; unstable if $C/D > R_1$ and $\lambda_1 < \lambda_2$, or $C/D < R_1$. E_2 is stable if $A/B > R_2$ and $\lambda_1 < \lambda_2$, unstable if $A/B > R_2$ and $\lambda_1 > \lambda_2$, or $A/B < R_2$.

Proof. We only prove the cases for E_1 and E_2. From the Jacobians at E_1 and E_2, the corresponding characteristic equations take the forms

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

where

$$a_1 = \frac{m_1 \lambda_2}{k_1 + \lambda_2} - L - 1$$

$$b_1 = 1 + (1 - \lambda_2)\left(\frac{-2DS_0^2\lambda_2}{C + DS_0^2\lambda_2^2} + \frac{m_2 k_2}{(k_2 + \lambda_2)^2}\right) \tag{7}$$

$$c_1 = (1 - \lambda_2)\frac{m_2 k_2}{(k_2 + \lambda_2)^2} \quad \text{(which is } > 0\text{)};$$

$$a_2 = \frac{m_2 \lambda_1}{k_2 + \lambda_1} - 1$$

$$b_2 = 1 + (1 - \lambda_1)\left(\frac{-2BS_0^2\lambda_1}{A + BS_0^2\lambda_1^2} + \frac{m_1 k_1}{(k_1 + \lambda_1)^2}\right) \tag{8}$$

$$c_2 = (1 - \lambda_1)\frac{m_1 k_1}{(k_1 + \lambda_1)^2} \quad \text{(which is } > 0\text{)}.$$

When $C/D > R_1$, $b_1 > 0$, 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 unstable if $\lambda_2 > \lambda_1$, stable if $\lambda_1 > \lambda_2$. When $C/D < R_1$, $b < 0$, E_1 is always unstable. Similarly, when $A/B > R_2$, $b_2 > 0$, the roots of $r^2 + b_2 r + c_2 = 0$ have negative real parts. The stability of E_2 is determined by the sign of $a_2 = m_2\lambda_1/(k_2 + \lambda_1) - 1$. Thus E_2 is unstable if $\lambda_1 > \lambda_2$, stable if $\lambda_1 < \lambda_2$. When $A/B < R_2$, $b_2 < 0$, E_2 is always unstable.

The proof of Theorem 1 is completed.

Regarding the dynamical system on the two dimensional faces $x = 0$ or $y = 0$, we have the following results.

On the face $x = 0$, the system (2) is reduced to

$$\frac{ds}{dt} = 1 - S - y\frac{m_2 S}{k_2 + S}\frac{1}{C + DS_0^2 S^2}$$

$$\frac{dy}{dt} = \left(\frac{m_2 S}{k_2 + S} - 1\right)y. \tag{9}$$

We would like to point out that the system (9) is a special case of the simple chemotat system:

$$\frac{dx}{dt} = x\left(g(y) - 1\right)$$

$$\frac{dy}{dt} = 1 - y - \frac{g(y)}{F(y)}x, \tag{10}$$

if letting $y = S$, $g(y) = m_2 S/(k_2 + S)$, $F(y) = C + D S_0^2 S^2$, and $x = y$.

In the region $\{(x, y)|0 \leqslant x \leqslant 1, \ y \geqslant 0\}$, the system (10) has two equilibrium pints $(0, 1)$, 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

$$p = 1 + x * \frac{d}{dy}\left(\frac{g}{F}\right)\bigg|_{y=y^*}. \tag{11}$$

The following theorem is established [13].

Theorem A. 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 (10) surrounding the equilibrium (x^*, y^*).

Then, we have

Theorem 2. Assume (4) (which implies that $m_2 > k_2 + 1$). The system (9) has two equilibrium points: $M_1(1, 0)$, which is a saddle, and $M_2(\lambda_2, (1 - \lambda_2)(C + D S_0^2 \lambda_2^2))$, which is stable if $C/D > R_1$, and unstable if $C/D < R_1$. In the case when M_2 is unstable, there is at least one limit cycle in (9) surrounding M_2.

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

$$\begin{aligned}
\frac{ds}{dt} &= 1 - S - \frac{x}{A + B S_0^2 S^2}\left(\frac{m_1 S}{k_1 + S} - L\right) \\
\frac{dx}{dt} &= x\left(\frac{m_1 S}{k_1 + S} - L - 1\right),
\end{aligned} \tag{12}$$

which is also a special case of (10) with

$$y = S, F(y) = A + B S_0^2 S^2, g(y) = \frac{M_1 S}{k_1 + S} - L \text{ and } x = y. \tag{13}$$

In $R_+^2 = \{(S, x)\,|0 \leqslant S \leqslant 1, x \geqslant 0\}$, the system (12) has equilibrium points: $N_1(1, 0)$ which is a saddle, and $N_2(\lambda_1, (1 - \lambda_1)(A + B S_0^2 \lambda_1^2))$ if $g(1) > 1$.

Calculating p in (11) and R_2 in (5) will result the following theorem.

Theorem 3. Assume (4), or $m_1 > (k + 1)(L + 1)$. If $A/B > R_2$, then N_2 is stable; if $A/B < R_2$, then N_2 is unstable and there exists at least one limit cycle in (12) surrounding $N_2(\lambda_1, (1 - \lambda_1)(A + B S_0^2 \lambda_1^2))$.

Note that if N_2 is stable, it is also globally asymptotically stable.

Theorem 4. The system (12) undergoes a Hopf bifurcation at $A/B = R_2$ and so does the system (9) at $C/D = R_1$.

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

$$r^2 + b_2 r + c_2 = 0. \tag{14}$$

Let $A/B = \mu$. Denote b_2, the coefficient of r in the above equation, as $trJ(A/B)$, or $trJ(\mu)$, where,

$$trJ(\mu) = 1 + (1 - \lambda_1)\left(\frac{-2S_0^2\lambda_1}{\mu + S_0^2\lambda_1^2} + \frac{m_1 k_1}{(k_1 + \lambda_1)^2}\right). \tag{15}$$

Since

$$\left.\frac{\mathrm{d}}{\mathrm{d}\mu}trJ(\mu)\right|_{\mu=R_2} = (1 - \lambda_1)\frac{2S_0^2\lambda_1}{\left(R_2 + S_0^2\lambda_1^2\right)^2} > 0,$$

the function $trJ(\mu)$ is increasing at $\mu = R_2$.
    Since

$$trJ(\mu) \begin{cases} < 0 & \text{if } \mu < R_2 \\ = 0 & \text{if } \mu = R_2 \\ > 0 & \text{if } \mu > R_2, \end{cases} \tag{16}$$

the phase structure of $N_2(\lambda_1, (1 - \lambda_1)(A + BS_0^2\lambda_1^2))$ changes from unstable to stable at R_2 as the parameter μ increases. So (12) undergoes a Hope bifurcation at $A/B = R_2$ by the definition.
    Similarly, for the equilibrium point $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^2\lambda_0^2))$, we can prove the bifurcation theorem for the system (9).

Theorem 5. Let

$$D = \{(S, x, y) \mid 0 \leqslant S \leqslant l - x - y, 0 \leqslant x \leqslant (A + BS_0^2\lambda_1)(1 - \lambda_1) + \varepsilon_0,$$
$$0 \leqslant y \leqslant (C + DS_0^2\lambda_2)(1 - \lambda_2) + \varepsilon_0, 0 < l < \infty, \varepsilon_0 > 0, \text{constant,}\}.$$

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

Proof. By the first equation of (2), any trajectory in $D_1 = \{(S, x, y) \mid S < 0, x > 0, y > 0\}$ 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

$$
\begin{aligned}
\frac{\mathrm{d}W}{\mathrm{d}t}\bigg|_{W=0} &= \left(\frac{\mathrm{d}S}{\mathrm{d}t} + \frac{\mathrm{d}x}{\mathrm{d}t} + \frac{\mathrm{d}y}{\mathrm{d}t}\right)\bigg|_{S=l-x-y} \\
&= 1 - l - x\left(\left(\frac{1}{A + BS_0^2(l-x-y)^2} - 1\right)\left(\frac{m_1(l-x-y)}{k_1 + l - x - y} - L\right) + 1\right) \\
&\quad - y\left(\left(\frac{1}{C + DS_0^2(l-x-y)^2} - 1\right)\frac{m_2(l-x-y)}{k_2 + l - x - y} + 1\right).
\end{aligned}
\tag{17}
$$

Since x, y are bounded and $A, B, C, D, S_0, m_i, k_i$ $i = 1, 2$ are all positive, $\frac{\mathrm{d}w}{\mathrm{d}t}\big|_{W=0} < 0$ 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 5 is completed.

Regarding the multiple of limit cycles in the system (9), Pilyugin and Waltman [22] used the Hopf bifurcation technique to produce two limit cycles for some particular parameters (see figure 1). Here we prove analytically that the multiple limit cycles do exist in the system.
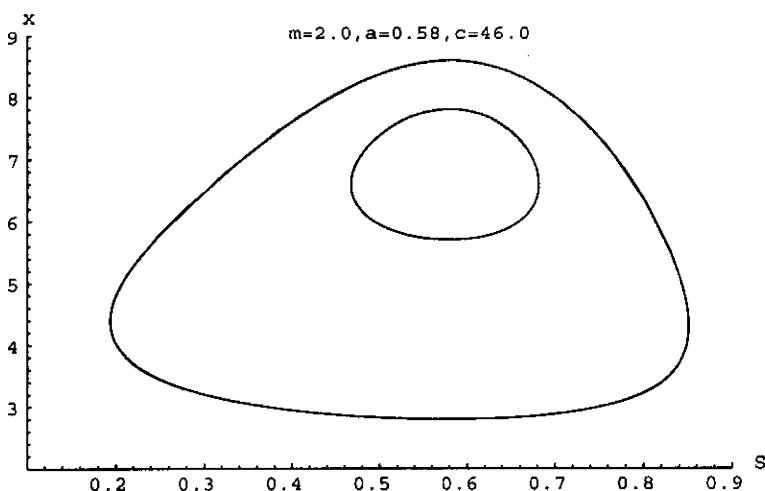

Figure 1. An example of two limit cycles in (9) for some particular values of the parameters [22].

Denote $(k_2 + S)(C + DS_0^2 S^2)/m_2 S(1 - S)$ as $F(S)$ and consider the following auxiliary system

$$
\begin{aligned}
\frac{dS}{dt} &= \frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^2 S^2}(F_i(S) - y) \\
\frac{dy}{dt} &= y\left(\frac{m_2 S}{k_2 + S} - 1\right), \\
S(0) &= S_0 > 0, \quad y(0) = y_0 > 0, \quad i = 1, 2.
\end{aligned}
\tag{18i}
$$

We will determine the functions $F_i(S)$ late.

Let (S_e, y_e) be the equilibrium point of (18i), that is,

$$
\begin{aligned}
\frac{m_2 S_e}{k_2 + S_e} &= 1 \\
y_e &= F_1(S_e) = F_2(S_e).
\end{aligned}
$$

Let $P_0 = (S_e, y_0)$, with $y_0 < y_e$, Γ_i be the orbit of the system (18i) starting with P_0. Also, suppose that A_i, Q_i, B_i are the first points (in time spent) of Γ_i intersecting with the rays $S = S_e, y > y_e, S < S_e, y = y_e$, and $S = S_e, y < y_e$, respectively (as shown in figure 2).

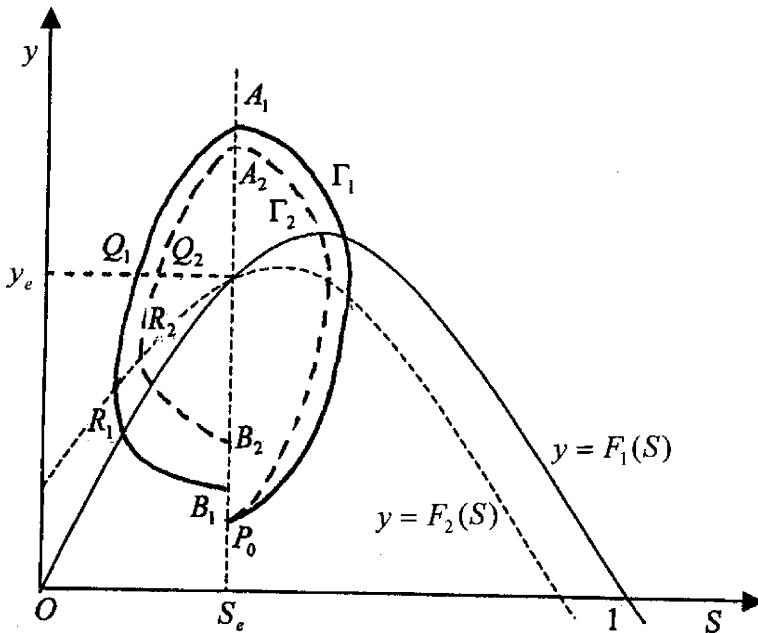Denote (S_p, y_p) as the coordinates of P. Then, we have the following Lemma 1.

Figure 2. The flow of (18.1) is always directed outside with respect to the flow of (18.2).

Lemma 1. Suppose

$$F_1(S) \leqslant F_2(S) \quad \text{for } S \in [0, S_e]$$
$$F_1(S) \geqslant F_2(S) \quad \text{for } S \in [S_e, 1]' \tag{19}$$

with strict inequality for some $S \in [0, S_e]$ and $[S_e, 1]$, respectively. Then

(i) $y_{A_1} > y_{A_2}$, (ii) $y_{B_1} < y_{B_2}$, (iii) $S_{Q_1} < S_{Q_2}$,

(iv) $y_{B_i} \leqslant F_i(S_{Q_i})$ if $F_i'(S) \geqslant 0$ for $0 \leqslant S \in S_e$, $i = 1, 2$.

Proof. Let the vector $\overline{V_i}$ be defined as

$$\overline{V_i} = \left(\frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^2 S^2}(F_i(S) - y), \ y \left(\frac{m_2 S}{k_2 + S} - 1 \right), 0 \right), \quad i = 1, 2. \tag{20}$$

Consider the cross product of $\overline{V_1}$ and $\overline{V_2}$

$$\overline{V_1} \times \overline{V_2} = \left(0, 0, \ y \left(\frac{m_2 S}{k_2 + S} - 1 \right) \frac{m_2 S}{(k_2 + S)(C + DS_0^2 S^2)}(F_1(S) - F_2(S)) \right). \tag{21}$$

Since (19),

$$y \left(\frac{m_2 S}{k_2 + S} - 1 \right) \frac{m_2 S}{k_2 + S} \cdot \frac{1}{C + DS_0^2 S^2}(F_1(S) - F_2(S)) \geqslant 0, \quad \text{for } 0 \leqslant S \leqslant 1.$$

Hence, the flow of (18.1) is always directed outside with respect to the flow of (18.2). Therefore (*i*)–(*iii*) hold. Now suppose Γ_i intersects with the isocline $y - F_i(S) = 0$ $(0 \leqslant S \leqslant S_e)$ at R_i.

Then, since

$$\frac{dy}{dt} < 0 \quad \text{for } 0 < S < S_e$$
$$\frac{dS}{dt} < 0 \quad \text{for } 0 < S < S_e \text{ and } F_i(S) - y < 0$$
$$\frac{dS}{dt} = 0 \quad \text{for } F_i(S) - y = 0 \tag{22}$$
$$\frac{dS}{dt} > 0 \quad \text{for } 0 < S < S_e \text{ and } F_i(S) - y > 0,$$

we have

$$S_{R_i} \leqslant S_{Q_i} \quad i = 1, 2.$$

If $F_i'(S) \geqslant 0$ for $S \in [0, S_e]$, then

$$y_{B_i} \leqslant y_{R_i} = F_i(S_{R_i}) \leqslant F_i(S_{Q_i}).$$

Thus (*iv*) is valid and the proof of Lemma 1 is completed.

Now for the system (9) with the equilibrium point $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$, which corresponds to (S_e, x_e) in (18i), following the argument of the existence of limit cycles in [13, 14], there exists $\delta > 0$ such that

$$y_0 - y_{B_1}(x_0) < 0 \text{ for all } y_0 \in (0, \delta). \tag{23}$$

Here B_1 is the intersection of the orbit $\Gamma_1(\lambda_2, y_0)$ and the line segment $S = \lambda_2$, $0 < y < (1 - \lambda_2)(C + DS_0^2\lambda_2^2)$, and $y_{B_1}(x_0)$, the y coordinate of B_1, is a continuous function of y_0.

Also, fix δ and find an $S_1 \in (\lambda_2, 1)$ such that $F(S) > 0$ for $S \in [\lambda_2, S_1]$ and the orbits starting at (λ_2, y_0) with $y_0 \in \left(\frac{\delta}{2}, (1 - \lambda_2)(C + DS_0^2\lambda_2^2)\right)$ will be contained in the region $\{(S, y) \,|\, y > 0, 0 < S < S_1\}$. Moreover, by the boundedness of solutions with the initial values $S(0) = \lambda_2$, $y(0) = y_0 \in \left(\frac{\delta}{2}, (1 - \lambda_2)(C + DS_0^2\lambda_2^2)\right)$, we can assume, if a limit cycle of the system (9) exists, it must be inside a circle. Suppose it is inside the circle

$$(S - \lambda_2)^2 + (y - (1 - \lambda_2)(C + DS_0^2\lambda_2^2))^2 = r_0, r_0 \in (0, (1 - \lambda_2)(C + DS_0^2\lambda_2^2)). \tag{24}$$

Let

$$\alpha_1 = \min_{S \in [\lambda_2, S_1]} \{F(S)\}, \alpha_2 = (1 - \lambda_2)\left(C + DS_0^2\lambda_2^2\right). \tag{25}$$

Suppose $F'(S^*) > 0$. There exists $S_2 \in [\lambda_2, S_1]$ such that $F(S_2) = F(\lambda_2)$, and $F(S) \geqslant F(S^*)$ for all $S \in [\lambda_2, S_2]$. Moreover, since $F(1) = 0$, there exist $S_3 \in [S_2, S_1]$ and $S_4 \in [S_1, 1]$ such that

$$F(S_3) = F(S_4) = \alpha_1.$$

Define $F_i(S)$ $(i = 1, 2)$ as

$$F_1(S) = F(S),$$

$$F_2(S) = \begin{cases} \alpha_2 & 0 \leqslant S \leqslant S_2 \\ F(S) & S_2 \leqslant S \leqslant S_3 \\ \alpha_1 & S_3 \leqslant S \leqslant S_4 \\ F(S) & S_4 \leqslant S \leqslant 1. \end{cases} \tag{26}$$

Clearly, $F_i(S)$ is continuous and satisfies Lipschitz's condition.

Further, consider the system

$$\begin{aligned} \frac{\mathrm{d}S}{\mathrm{d}t} &= \frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^2 S^2} (F_i(S) - y) \\ \frac{\mathrm{d}x}{\mathrm{d}t} &= y\left(\frac{m_2 S}{k_2 + S} - 1\right) \end{aligned} \tag{27i}$$

and denote its orbit starting at (λ_2, y_0) as $\Gamma_i(\lambda_2, y_0)$, $i = 1, 2$. We are in a position to prove the following theorem.

Theorem 6. In addition to the existence of limit cycles, if the system (9) satisfies

(i) $F'(S) \geqslant 0$ for $0 \leqslant S \leqslant \lambda_2$ and $F'(\lambda_2) > 0$;

(ii) there exists $\bar{y} \in (0, (1 - \lambda_2)(C + DS_0^2\lambda_2^2) - r_0)$ such that $\bar{y} > F(S_{Q_2}(\bar{y}))$,

where Q_2 is the intersection of $\Gamma_2(\lambda_2, \bar{y})$ and the line segment $y = (1 - \lambda_2)(C + DS_0^2\lambda_2^2)$, $0 < S < \lambda_2$; then the system (9) has at least two limit cycles around $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$.

Proof. Define a function of y_0 as

$$\rho(y_0) = y_0 - y_{B_1}(y_0) \tag{28}$$

where B_1 is the intersection of $\Gamma_1(\lambda_2, y_0)$ and the segment $S = \lambda_2$, $0 < y < (1 - \lambda_2)(C + DS_0^2\lambda_2^2)$.

Since $(\lambda_2, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$ is unstable, if $y_0 < (1 - \lambda_2)(C + DS_0^2\lambda_2^2)$ and y_0 is sufficiently close to $(1 - \lambda_2)(C + DS_0^2\lambda_2^2)$,

$$\rho(y_0) > 0. \tag{29}$$

By Theorem A, the system (9) has at least one limit cycle around $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$. Thus, we can find a

$$y_1 \in ((1 - \lambda_2)(C + DS_0^2\lambda_2^2) - r_0, (1 - \lambda_2)(C + DS_0^2\lambda_2^2)),$$

such that

$$\rho(y_1) = 0. \tag{30}$$

The stability of the above limit cycle implies that there exists $\delta_1 > 0$ such that

$$\rho(y_0) < 0 \quad \text{for } y_0 \in (y_1 - \delta_1, y_1). \tag{31}$$

By Lemma 1 and (*ii*),

$$\begin{aligned}
y_{B_1}(\bar{y}) &\leqslant F_1\left(S_{R_1}(\bar{y})\right) \\
&\leqslant F_1\left(S_{Q_1}(\bar{y})\right) \\
&\leqslant F_2\left(S_{Q_2}(\bar{y})\right) \\
&< \bar{y}.
\end{aligned} \tag{32}$$

Thus

$$\rho(\bar{y}) > 0. \tag{33}$$

Since $\rho(y_0)$ is continuous with respect to y_0, there exist $y_2 \in (\bar{y}, y_1)$ such that

$$\rho(y_2) = \rho(y_1) = 0.$$

Clearly each orbit starting at (λ_2, y_i), $i = 1, 2$ is a limit cycle of the system (9). We thus complete the proof of Theorem 6.

3.   Remarks and conclusion

Before we end our article, we would like to make the following remarks.

Remark 1. If $F = 1$, or, if $\delta =$ constant, $g(S) = \frac{m_2 S}{k_2 + S}$, it always has $p > 0$. That is, if the yield is a constant, the corresponding system has no limit cycle.

Remark 2. In the case when the equilibrium point M_2 is stable, it is globally asymptotically stable with $\lim_{t \to \infty} S(t) = \lambda_2$, and $\lim_{t \to \infty} y(t) = 1 - \lambda_2$. Similar situation happens in N_2.

Remark 3. The Poincare–Bendixson annular region theorem is very powerful in discussing the existence of limit cycles in the plane autonomous differential equations but doesn't work directly in the systems of higher dimensions ($n \geqslant 3$) (see the counterexample given by D'Heedene [5]). However, the positively invariant set D in Theorem 5 is still useful in proving the existence of periodic solutions in the space, see Grasman theorem [9].

Remark 4. The condition (*ii*) in Theorem 6 is not difficult to check. This is because by the uniqueness of solutions the separable equation

$$\frac{dy}{dS} = \frac{y\left(\dfrac{m_2 S}{k_2 + S} - 1\right)}{\dfrac{m_2 S}{k_2 + S}\dfrac{1}{C + DS_0^2\lambda_2^2}((1 - \lambda_2)(C + DS_0^2\lambda_2^2) - y)}$$
$$S(0) = \lambda_2, \quad y(0) = \bar{y} \tag{34}$$

in $0 \leqslant S \leqslant \lambda_2$ is easy to solve, and then $S_{Q_2}(\bar{y})$ can be determined easily.

In the previous section, we introduce a three dimensioned chemostat with quadratic yields. We use the qualitative analysis and bifurcation theory to study the properties of the equilibrium points, existence of the limit cycles. We prove that if there is an asymptotically stable equilibrium points, there also can be, at least, two limit cycles surrounds it. We show that the quadratic yields lead to oscillatory coexistence of the microorganisms in the continuous culture. Our result is a generalization of the previously published results [1,4,25], and is useful

in the further study of the coexistence of competing populations in the chemostat.

The methods in this paper can be used in analyzing the system (1) with more general yield functions like $\delta_1 = A + BS^n, \delta_2 = C + DS^m$. We are very interested to notice that all the formulas and parameters in the general cases has almost exactly same structure as in the case of $n = m = 2$.

References

[1] R. Agrawal, C. Lee, H.C. Lim and D. Ramkrishna, Theoretical investigations of dynamic behavior of isothermal continuous stirred tank biological reactors, Chem. Eng. Sci. 37 (1982) 453.

[2] J.B. Clark, in: *Sphere-rod transitions in Arthrobacter,* (ed.) J.H. Parish (Developmental Biology of Prokaryotes, University of California, Berkeley and Los Angeles, 1979) p. 73.

[3] P.S. Crooke, C.-J. Wei and R.D. Tanner, The effect of the specific growth rate and yield xpressions on the existence of oscillatory behavior of a continuous fermentation model, Chem. Eng. Commun. 6 (1980) 333.

[4] P.S. Crooke and R.D. Tanner, Hopf bifurcations for a variable yield continuous fermentation model, Int. J. Eng. Sci. 20 (1982) 439.

[5] D'Heedene R.N., A third order autonomous differential equation with almost periodic solutions, J. Math. Anal. Appl. 3 (1961) 344.

[6] A.G. Dorofeev, M.V. Glagolev, T.F. Bondarenko and N.S. Panikov, Observation and explanation of the unusual growth kinetics of Arthrobacter globiforms, Microbiology 61 (1992) 33.

[7] A.G. Fredrickson and G. Stephanopoulos, Microbial competition, Science 218 (1981) 972.

[8] R. Freter, Mechanisms that control the microflora in the large intestine, Hunan Intestinal Microflora in Health and Disease, ed. D.J. Hentges, (Academic press, New York, 1983).

[9] W. Grasman, Periodic solutions of autonomous differential equations in higher dimension 1 space, Rocky Mountain J. Math. 7:3 (1977) 457.

[10] S.B. Hsu, S.P. Hubbell and P. Waltman, A mathematical theory for single nutrient competition in continuous cultures of micro-organisms, SIAM J. Appl. Math. 32 (1977) 366.

[11] D. Herbert, Some principles of continuous culture, in: *Recent Progress in Microbiology*, ed. G. Tunevall (Almqvist and Wiksell, Stockholm, 1959) p. 381.

[12] D. Herbert, R. Elsworth and R.C. Telling, The continuous culture of bacteria: a theoretical and experimental study, J. Gen. Microbiol. 4 (1956) 601.

[13] X. Huang, Limit cycles in a continuous fermentation model, J. Math. Chemistry 5 (1990) 287.

[14] X. Huang, Stability of a general predator-prey model, J. Franklin Institute, 327:5 (1990) 751.

[15] X. Huang and L.M. Zhu, A study of a general Kolmogorov system, J. Yangzhou Polytechnic University, 8:1 (2004) 20.

[16] X. Huang and L.M. Zhu, Limit cycles in a general Kolmogorov model, Nonlinear Analysis: Theory, Methods and Applications, 60:8(2005) 1393.

[17] I.H. Lee, A.G. Frederickson and H.M. Tsuchia, Damped oscillations in continuous culture of Lactobacillus plantarum, J. Gen. Microbiol. 93 (1976) 204.

[18] J. Liu and S.N. Zheng, Qualitative analysis of a kind of model with competition in microorganism continuous culture, J. Biomath. 17:4 (2002) 399.

[19] A. Matin and H. Veldkamp, Physiological basis of the selective advantage of Spirillum in a carbon-limited environment, J. Gen. Microbiol. 105 (1978) 187.

[20] A. Novick and L. Szilard, Description of the chemostat, Science 112 (1950) 715.

[21] N.S. Panikov, *Microbial Growth Kinetics* (Chapman and Hall, London, 1995).

[22] S.S. Pilyugin and P. Waltman, Multiple limit cycles in the chemostat with variable yield, Math. Biosci. 182 (2003) 151.

[23] M.L. Schuler and F. Kargi, *Bioprocess Engineering Basic Concepts* (Prentice Hall, Engelwood Cliffs, 1992).

[24] H.L. Smith and P. Waltman, *The Theory of the Chemostat* (Cambridge University, Cambridge, UK, 1995).

[25] G. Song and X. Li, Stability of solution to the chemostat system with non-constant consuming rate, J. Biomath. 14:1 (1999) 24.

[26] F.M. Stewart and B.R. Levin, Partitioning of resources and the outcome of interspecific competition: A model and some general considerations, Am. Nat. 107 (1973) 171.

[27] B. Tang and G.S. Wolkowicz, Mathematical models of microbial growth and competition in the chemostat regulated by cell-bound extra-cellular enzymes, J. Math. Biol. 31 (1992) 1.

[28] H. Veldkamp, Ecological studies with the chemostat, Adv. Microb. Ecol. 1 (1977) 59.

[29] L.S. Chen and J. Chen, *Nonlinear Dynamic System in Biology* (Science Press, Beijing, 1993).