

# A three-dimensional chemostat with quadratic yields

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A three-dimensional chemostat with two microorganisms which are both with quadratic yields is studied. The stability of the equilibrium 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 [3, 11–13, 19–22, 25, 28, 29]. 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 [24], and it is also useful in the study of the mammalian large intestine (see [9]). The basic analysis of the chemostat can be found in Levin and Stewart [27], Hsu et al. [11], Fredrickson and Stephanopoulos [8]. The book of Smith and Waltman [25] provides a detailed description of the chemostat and its properties.

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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. [7]). Crooke [4, 5] 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 ([23]) constructed a chemostat with variable yield and studied the multiple limit cycles in the model. It is interesting to notice that the model in [23] is exactly same as the one studied by Huang in fermentation [14]. The existence conditions, the relative position and the perimenter of the limit cycles are investigated there [14]. However, the model in [23] and [14] only considered one microorganism in the system.

A three-dimensional chemostat with two microorganisms which are both with linear yields was studied by Song and Li [26]. 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 [26] 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 Song and Li [26]. 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 [26].

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  $\tau$  with  $t$ , the system (1) becomes

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{x}{A + BS_0^2S^2} \left( \frac{m_1S}{k_1 + S} - L \right) - \frac{y}{C + DS_0^2S^2} \left( \frac{m_2S}{k_2 + S} \right) \\ \frac{dx}{dt} &= \left( \frac{m_1S}{k_1 + S} - L - 1 \right) x \\ \frac{dy}{dt} &= \left( \frac{m_2S}{k_2 + S} - 1 \right) y. \end{aligned} \tag{2}$$

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  $R_+^3 = \{ (S, x, y) \mid 0 \leq S \leq 1, x \geq 0, y \geq 0 \}$ .

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[30]),

- (i) if  $0 < m_i < 1, i = 1, 2,$  then  $\frac{dx}{dt} < 0, \frac{dy}{dt} < 0$  and  $\lim_{t \rightarrow \infty} x(t) = \lim_{t \rightarrow \infty} y(t) = 0;$
- (ii) if  $m_1 > L + 1$  and  $\lambda_1 \geq 1,$  then  $\frac{dx}{dt} < 0$  and  $\lim_{t \rightarrow \infty} x(t) = 0;$
- (iii) if  $m_2 > 1$  and  $\lambda_2 \geq 1,$  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

$$0 < \lambda_i < 1, \quad i = 1, 2 \tag{4}$$

(which implies  $m_1 > 1 + L, \quad m_2 > 1$ ). Let

$$\begin{aligned} R_1 &= \frac{(1 - \lambda_2) (2\lambda_2(k_2 + \lambda_2)^2 - m_2k_2\lambda_2^2) - \lambda_2^2(k_2 + \lambda_2)^2}{(k_2 + \lambda_2)^2 + (1 - \lambda_2) m_2k_2} S_0^2, \\ R_2 &= \frac{(1 - \lambda_1) (2\lambda_1(k_1 + \lambda_1)^2 - m_1k_1\lambda_1^2) - \lambda_1^2(k_1 + \lambda_1)^2}{(k_1 + \lambda_1)^2 + (1 - \lambda_1) m_1k_1} S_0^2. \end{aligned} \tag{5}$$

We have

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

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

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

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

where

$$\begin{aligned} a_1 &= \frac{m_1\lambda_2}{k_1 + \lambda_2} - L - 1, \\ b_1 &= 1 + (1 - \lambda_2) \left( \frac{-2DS_0^2\lambda_2}{C + DS_0^2\lambda_2^2} + \frac{m_2k_2}{(k_2 + \lambda_2)^2} \right), \\ c_1 &= (1 - \lambda_2) \frac{m_2k_2}{(k_2 + \lambda_2)^2} \quad (\text{which is } > 0), \end{aligned} \tag{7}$$

$$\begin{aligned} a_2 &= \frac{m_2\lambda_1}{k_2 + \lambda_1} - 1, \\ b_2 &= 1 + (1 - \lambda_1) \left( \frac{-2BS_0^2\lambda_1}{A + BS_0^2\lambda_1^2} + \frac{m_1k_1}{(k_1 + \lambda_1)^2} \right), \\ c_2 &= (1 - \lambda_1) \frac{m_1k_1}{(k_1 + \lambda_1)^2} \quad (\text{which is } > 0). \end{aligned} \tag{8}$$

When  $C/D > R_1$ ,  $b_1 > 0$ , the roots of  $r^2 + b_1r + c_1 = 0$  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  $C/D < R_1$ ,  $b_1 < 0$ ,  $E_1$  is always unstable. Similarly, when  $A/B > R_2$ ,  $b_2 > 0$ , the roots of  $r^2 + b_2r + c_2 = 0$  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

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - y \frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^2 S^2}, \\ \frac{dy}{dt} &= \left( \frac{m_2 S}{k_2 + S} - 1 \right) y. \end{aligned} \tag{9}$$

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

$$\begin{aligned} \frac{dx}{dt} &= x (g(y) - 1), \\ \frac{dy}{dt} &= 1 - y - \frac{g(y)}{F(y)} x. \end{aligned} \tag{10}$$

if let  $y = S$ ,  $g(y) = m_2 S / (k_2 + S)$ ,  $F(y) = C + DS_0^2 S^2$ , and  $x = y$ .

In the region  $\{(x, y) | 0 \leq x \leq 1, y \geq 0\}$ , the system (10) 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  $(0, 1)$  is globally asymptotically stable if  $g(1) < 1$ , a saddle if  $g(1) > 1$ . Denote

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

The following theorem is established [14].

**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  $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^2 \lambda_2^2))$ , 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

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{x}{A + BS_0^2 S^2} \left( \frac{m_1 S}{k_1 + S} - L \right), \\ \frac{dx}{dt} &= x \left( \frac{m_1 S}{k_1 + S} - L - 1 \right), \end{aligned} \tag{12}$$

which is also a special case of (10) with

$$y = S, \quad F(y) = A + BS_0^2S^2, \quad g(y) = \frac{M_1S}{k_1 + S} - L \quad \text{and } x = y. \quad (13)$$

In  $R_+^2 = \{(S, x) \mid 0 \leq S \leq 1, x \geq 0\}$ , the system (12) has equilibrium points:  $N_1(1, 0)$  which is a saddle, and  $N_2(\lambda_1, (1 - \lambda_1)(A + BS_0^2\lambda_1^2))$  if  $g(1) > 1$ .

Calculating  $p$  in (11) and  $R_2$  in (5) will result theorem 3.

**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  $N_2(\lambda_1, (1 - \lambda_1)(A + BS_0^2\lambda_1^2))$ .

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

$$r^2 + b_2r + c_2 = 0. \quad (14)$$

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

$$trJ(\mu) = 1 + (1 - \lambda_1) \left( \frac{-2S_0^2\lambda_1}{\mu + S_0^2\lambda_1^2} + \frac{m_1k_1}{(k_1 + \lambda_1)^2} \right). \quad (15)$$

Since

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

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

Since

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

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  $\mu$  increases. So (12) undergoes a Hopf 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

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

where  $D$  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  $D_1 = \{(S, x, y) \mid S < 0, x > 0, y > 0\}$  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

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

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

Regarding the multiple of limit cycles in the system (9), Pilyugin and Waltman[23] 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.

Denote  $(k_2 + S)/(C + DS_0^2S^2)/m_2S(1 - S)$  as  $F(S)$  and consider the following auxiliary system

$$\begin{aligned} \frac{dS}{dt} &= \frac{m_2S}{k_2 + S} \frac{1}{C + DS_0^2S^2} (F_i(S) - y), \\ \frac{dy}{dt} &= y \left( \frac{m_2S}{k_2 + S} - 1 \right), \\ S(0) &= S_0 > 0, y(0) = y_0 > 0, i = 1, 2. \end{aligned} \tag{18.1}$$

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

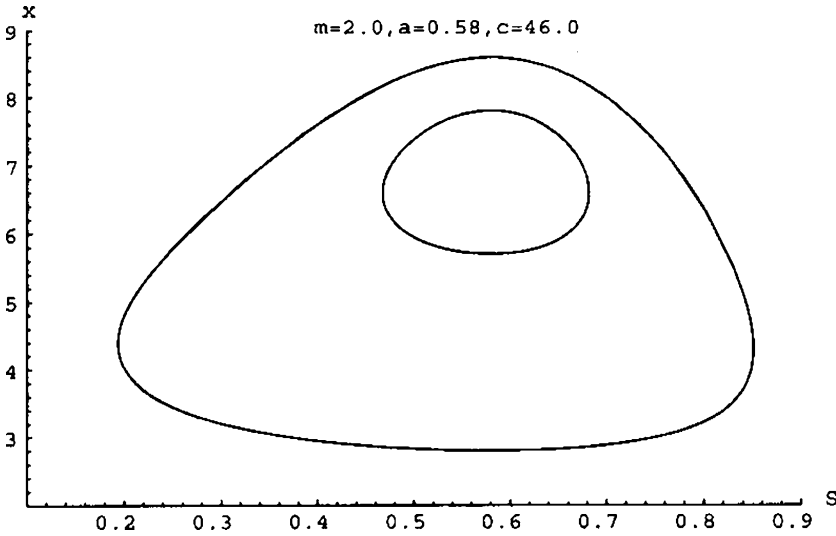


Figure 1. An example of two limit cycles in (9) for some particular values of the parameters ([23]).

Let  $(S_e, y_e)$  be the equilibrium point of (18.1), that is,

$$\begin{aligned} \frac{m_2 S_e}{k_2 + S_e} &= 1, \\ y_e &= F_1(S_e) = F_2(S_e). \end{aligned} \tag{18.2}$$

Let  $P_0 = (S_e, y_0)$ , with  $y_0 < y_e$ ,  $\Gamma_i$  be the orbit of the system (18.1) starting with  $P_0$ . Also, suppose that  $A_i, Q_i, B_i$  are the first points (in time spent) of 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 lemma 1.

**Lemma 1.** Suppose

$$\begin{aligned} F_1(S) &\leq F_2(S) \quad \text{for } S \in [0, S_e], \\ F_1(S) &\geq F_2(S) \quad \text{for } S \in [S_e, 1] \end{aligned} \tag{19}$$

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)  $y_{B_i} \leq F_i(S_{Q_i})$  if  $F'_i(S) \geq 0$  for  $0 \leq S \in S_e, i = 1, 2.$

*Proof.* Let the vector  $\bar{V}_i$  be defined as

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



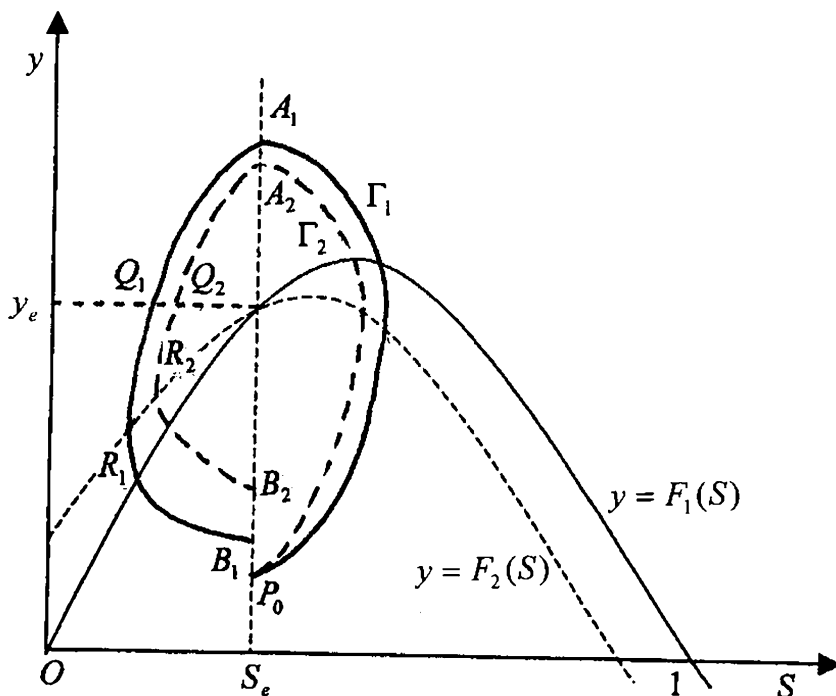


Figure 2. The flow of (18.1) is always directed outside with respect to the flow of (18.2).

Consider the cross product of  $\bar{V}_1$  and  $\bar{V}_2$

$$\bar{V}_1 \times \bar{V}_2 = \left( 0, 0, y \left( \frac{m_2 S}{k_2 + S} - 1 \right) \frac{m_2 S}{(k_2 + S)(C + DS_0^2 S^2)} (F_1(S) - F_2(S)) \right). \quad (21)$$

Since (19),

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

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

Then, since

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

we have

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

If  $F'_i(S) \geq 0$  for  $S \in [0, S_e]$ , then

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

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 (18.1), following the argument of the existence of limit cycles in [14,15], there exists  $\delta > 0$  such that

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

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  $\delta$  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  $(\lambda_2, y_0)$  with  $y_0 \in (\frac{\delta}{2}, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$  will be contained in the region  $\{(S, y) | y > 0, 0 < S < S_1\}$ . Moreover, by the boundedness of solutions with the initial values  $S(0) = \lambda_2, y(0) = y_0 \in (\frac{\delta}{2}, (1 - \lambda_2)(C + DS_0^2\lambda_2^2))$ , we can assume, if a limit cycle of the system (9) exists, it must be inside a circle. Suppose it is inside the circle

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

Let

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

Suppose  $F'(S^*) > 0$ . There exists  $S_2 \in [\lambda_2, S_1]$  such that  $F(S_2) = F(\lambda_2)$ , and  $F(S) \geq F(S^*)$  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

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

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

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

Further, consider the system

$$\begin{aligned} \frac{dS}{dt} &= \frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^2 S^2} (F_i(S) - y) \\ \frac{dx}{dt} &= y \left( \frac{m_2 S}{k_2 + S} - 1 \right) \end{aligned} \tag{27}$$

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

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

- (i)  $F'(S) \geq 0$  for  $0 \leq S \leq \lambda_2$  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

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

By lemma 1 and (ii),

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

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  $(\lambda_2, y_i), i = 1, 2$  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  $\delta = \text{const.}$ ,  $g(S) = m_2S/k_2 + S$ , 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  $\lim_{t \rightarrow \infty} S(t) = \lambda_2$ , and  $\lim_{t \rightarrow \infty} y(t) = 1 - \lambda_2$ . Similar situation happens to  $N_2$ .

*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 ( $n \geq 3$ )(see the counterexample given by D'Heedene[6]). 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 [10].

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

$$\begin{aligned}
 \frac{dy}{dS} &= \frac{y \left( \frac{m_2S}{k_2 + S} - 1 \right)}{\frac{m_2S}{k_2 + S} \frac{1}{C + DS_0^2\lambda_2^2} ((1 - \lambda_2)(C + DS_0^2\lambda_2^2) - y)} \\
 S(0) &= \lambda_2, y(0) = \bar{y}
 \end{aligned}
 \tag{34}$$

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

In section 2, 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, 3, 26], 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  $n = m = 2$ .

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