

# Bifurcation in a Three Dimensional Continuous Fermentation Model

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**Abstract:** A three dimensional continuous fermentation model with variable yields is proposed in this paper. The properties of the equilibrium points, the global stability, the existence of limit cycles and the Hopf bifurcation in the two dimensional stable manifold of one microorganism while the other is going to vanish in the competition are investigated by qualitative analysis of differential equations.

**Keywords:** continuous culture; variable yield; limit cycles; Hopf bifurcation.

## 1. Introduction

The continuous fermentation model is an interesting example of an open system with purely exploitative competition. 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 continuous fermentation model serves to model a simple lake but in chemical engineering it is a laboratory model of a bio-reactor to manufacture products with genetically altered organisms. In waste water treatment it is often the starting point for con-

struction of models (Schuler and Kargi [10]), and it is also useful in the study of the mammalian large intestine (see Freter [11]). The basic analysis of the chemostat can be found in the book of Smith and Waltman [1].

Most of the models in continuous fermentation assumes that the yield coefficient is a constant [1, 5-7]. But the accumulation of experimental data suggests that a constant yield fails to explain the observed oscillatory behavior in the vessel (see Dorofeev, et al. [2, 7]). Crooke [3, 4] suggested a linear function for the yield coefficient and declared a limit cycle may exist in his model. Huang(1990[8], [15, 16]), and Pilyugin and Waltman (2003[7]) constructed the model with a general variable yield, and studied the limit cycles and the Hopf bifurcation for the model. However, all these models considered only one microorganism in the system. In Liu and Zheng [12], a three dimensional chemostat with two microorganisms was studied. In the model the

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functional reaction functions were in the Monod type, and one of the yield coefficients was assumed a particular function of the concentration of nutrient and the other still constant. The properties of the equilibrium points, the existence of limit cycles were discussed there [12].

In this paper, we study a three dimensional continuous fermentation model of which both the yield coefficients are functions of the nutrient. The model is useful in modeling the case when the microorganism is very sensitive to the nutrient. We are going to analyze the equilibrium points, global stability, the existence of limit cycles and the Hopf bifurcation in the two dimensional stable manifold of one microorganism when the other is going to vanish in the competition. The model and our main theorems are in the next section.

## 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

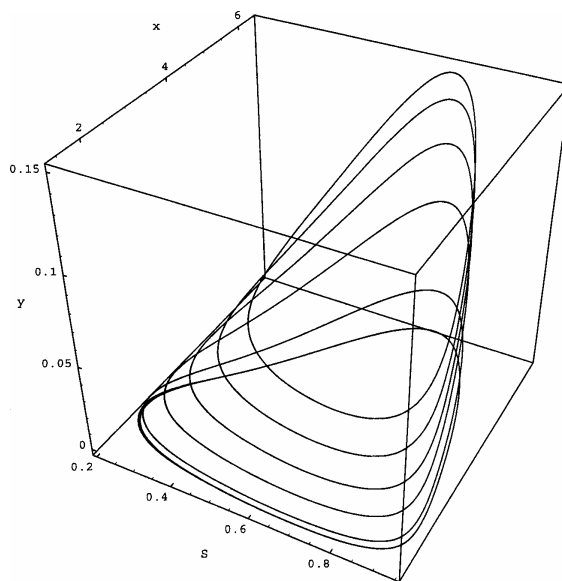
$$\begin{aligned} \frac{dS}{dt} &= (S_0 - S)Q - \frac{1}{\delta_1} \left( \frac{m_1 S}{k_1 + S} - L \right) x - \frac{1}{\delta_2} \frac{m_2 S}{k_2 + S} y \\ \frac{dx}{dt} &= x \left( \frac{m_1 S}{k_1 + S} - L - Q \right) \\ \frac{dy}{dt} &= y \left( \frac{m_2 S}{k_2 + S} - Q \right) \\ S(0) &= S_0 >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

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,

which are all positive.  $L$  is the intrinsic consumption rate for the first microorganism,

which is also positive. This is usually called the Monod model or the model with Michaelis-Menten dynamics.

System (1) with the yield coefficients  $\delta_1 = A + BS^2$ ,  $\delta_2 = const.$  was discussed in [12]. Here we investigate system (1) with  $\delta_1 = A + BS^3$ ,  $\delta_2 = C + DS^4$ . The relationships of the microorganisms and the nutrient in this model are different from all the previous models in the literature, which certainly is interesting in dealing with the nonlinear oscillatory phenomena in the continuous fermentation. In [18], a two predator-one prey ecosystem was studied using the above chemostat setting, which is similar to system (1) with our assumptions. And in [7], Pilyugin and Waltman even provided a numeric example with the yields of the first microorganism  $\delta_1 = 1 + 50S^3$ , and the second  $\delta_2 = 120$ , and obtained multiple limit cycles in computer simulating (see Figure 1).



**Figure 1.** More limit cycles of the chemostat with a cubic yield  $\delta_1 = 1 + 50S^3$  and a constant yield  $\delta_2 = 120$ .

It is easy to note that the above numerical example is a special case of our system when

$A = 1, B = 50, C = 120$  and  $D = 0$ . Thus, a further mathematical analysis of such model with cubic and/or quadratic yields is of course necessary.

Performing the standard scaling for the continuous fermentation, let

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

and then drop the bars and replace  $\tau$  with  $t$ , system (1) becomes

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{x}{A + BS_0^3 S^3} \left( \frac{m_1 S}{k_1 + S} - L \right) - \frac{y}{C + DS_0^4 S^4} \left( \frac{m_2 S}{k_2 + S} \right) \\ \frac{dx}{dt} &= \left( \frac{m_1 S}{k_1 + S} - L - 1 \right) x \\ \frac{dy}{dt} &= \left( \frac{m_2 S}{k_2 + S} - 1 \right) y. \end{aligned} \tag{2}$$

The parameters have been scaled by the operating environment of the continuous fermentation, which are determined by  $S_0$  and  $Q$ . The variables are non-dimensional and the discussion is in

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

$$\text{Let } \lambda_1 = \frac{k_1(L+1)}{m_1 - (L+1)}, \quad \lambda_2 = \frac{k_2}{m_2 - 1}.$$

It is easy to see that

$$(i) \text{ if } 0 < m_i < 1, i=1,2, \text{ then } \frac{dx}{dt} < 0, \frac{dy}{dt} < 0$$

$$\text{and } \lim_{t \rightarrow +\infty} x(t) = \lim_{t \rightarrow +\infty} y(t) = 0;$$

$$(ii) \text{ if } \lambda_1 \geq 1, \text{ then } \frac{dx}{dt} < 0 \text{ and } \lim_{t \rightarrow +\infty} x(t) = 0;$$

$$(iii) \text{ if } \lambda_2 \geq 1, \text{ then } \frac{dy}{dt} < 0 \text{ and } \lim_{t \rightarrow +\infty} y(t) = 0.$$

(3)

Note that if  $\lambda_1 \geq 1$ , the first microorganism in the chemostat goes to vanish, and so does the second one if  $\lambda_2 \geq 1$ . Thus, in order to avoid the microorganisms vanishing, we need to make certain arrangement between the growth rates  $m_i$ , the Menton constants  $k_i$ , and the organism parameter  $L$  before the experiment or bio-reactor starts. We now assume that

$$0 < \lambda_i < 1, i=1,2 \text{ (which imply } m_1 > L+1, m_2 > 1).$$

Let

$$R_1 \equiv \frac{(1-\lambda_1)(3\lambda_1^2(k_1+\lambda_1)^2 - m_1 k_1 \lambda_1^3) - \lambda_1^3(k_1+\lambda_1)^2}{(k_1+\lambda_1)^2 + (1-\lambda_1)m_1 k_1} S_0^3, \tag{4}$$

$R_2 \equiv$

$$\frac{(1-\lambda_2)(4\lambda_2^3(k_2+\lambda_2)^2 - m_2 k_2 \lambda_2^4) - \lambda_2^4(k_2+\lambda_2)^2}{(k_2+\lambda_2)^2 + m_2 k_2 (1-\lambda_2)} S_0^4. \tag{5}$$

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

$$E_0(1, 0, 0), \quad E_1(\lambda_1, (A + BS_0^3 \lambda_1^3)(1 - \lambda_1), 0) \text{ and } E_2(\lambda_2, 0, (C + DS_0^4 \lambda_2^4)(1 - \lambda_2)),$$

in which  $E_0$  is unstable (saddle);  $E_1$  is asymptotically stable if  $\frac{A}{B} > R_1$  and  $\lambda_1 < \lambda_2$ ,

unstable if either inequality is reversed;  $E_2$  is asymptotically stable if  $\frac{C}{D} > R_2$  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 system (2) at  $E_1$  and  $E_2$ , the corresponding characteristic equations takes the form

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

where

$$\begin{aligned} a_1 &= \frac{m_2 \lambda_1}{k_2 + \lambda_1} - 1 \\ b_1 &= 1 + (1 - \lambda_1) \left( \frac{-3BS_0^3 \lambda_1^2}{A + BS_0^3 \lambda_1^3} + \frac{m_1 k_1}{(k_1 + \lambda_1)^2} \right) \\ c_1 &= (1 - \lambda_1) \frac{m_1 k_1}{(k_1 + \lambda_1)^2}, \quad (\text{which is } > 0); \end{aligned} \quad (7)$$

$$\begin{aligned} a_2 &= \frac{m_1 \lambda_2}{k_1 + \lambda_2} - L - 1 \\ b_2 &= 1 + (1 - \lambda_2) \left( \frac{-4DS_0^4 \lambda_2^3}{C + DS_0^4 \lambda_2^4} + \frac{m_2 k_2}{(k_2 + \lambda_2)^2} \right) \\ c_2 &= (1 - \lambda_2) \frac{m_2 k_2}{(k_2 + \lambda_2)^2}, \quad (\text{which is } > 0). \end{aligned} \quad (8)$$

When  $\frac{A}{B} > R_1$ ,  $b_1 > 0$ , 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  $\frac{A}{B} < R_1$ ,  $b_1 < 0$ ,  $E_1$  is always unstable. Similarly, when  $\frac{C}{D} > R_2$ ,  $b_2 > 0$ , 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  $a_2 = \frac{m_1 \lambda_2}{k_1 + \lambda_2} - L - 1$ . Thus  $E_2$  is unstable if  $\lambda_1 > \lambda_2$ , stable if  $\lambda_1 < \lambda_2$ . When  $\frac{C}{D} < R_2$ ,  $b_2 < 0$  is always unstable.

The proof of Theorem 1 is completed.

**Theorem 2.** (i) If  $\lambda_1 < \lambda_2$ , and  $\frac{A}{B} > R_1$ , the equilibrium point  $E_1$  is globally asymptotically stable in  $R_+^3$ ; (ii) if  $\lambda_1 > \lambda_2$ , and

$\frac{C}{D} > R_2$ , the equilibrium point  $E_2$  is globally asymptotically stable, too.

**Proof.** Let

$$\begin{aligned} \Theta &= \{(S, x, y) \mid 0 \leq S \leq l - x - y, \\ &0 \leq x \leq (1 - \lambda_1)(A + BS_0^3 \lambda_1^3) + \varepsilon_0, \\ &0 \leq y \leq (1 - \lambda_2)(C + DS_0^4 \lambda_2^4) + \varepsilon_0, \\ &0 < l < +\infty, \varepsilon_0 > 0\}. \end{aligned}$$

We first prove that  $\Theta$  is a positively invariant set of (2).

Consider the face  $S = 0$ , and by Eq.(2),  $\frac{dS}{dt} \Big|_{S=0} = 1 + \frac{Lx}{A} > 0$ . Thus, any trajectory in  $\{(S, x, y) \mid S < 0, x > 0, y > 0\}$  will go through  $S = 0$  into  $R_+^3$ , but the reverse is not true. For the face  $M = S + x + y - l = 0$  ( $0 < l < +\infty$ ),

$$\begin{aligned} \frac{dM}{dt} \Big|_{M=0} &= 1 - l - x \left( \frac{1}{A + BS_0^3(l-x-y)^3} - 1 \right) \left( \frac{m_1(l-x-y)}{k_1 + (l-x-y)} - L \right) \\ &\quad - y \left( \frac{1}{C + DS_0^4(l-x-y)^4} - 1 \right) \frac{m_2(l-x-y)}{k_2 + (l-x-y)}. \end{aligned}$$

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

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

For  $E_2$ , in the solution plane of  $x = 0$ ,

system (2) is reduced to

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - y \frac{m_2 S}{k_2 + S} \frac{1}{C + DS_0^4 S^4} \\ \frac{dy}{dt} &= \left( \frac{m_2 S}{k_2 + S} - 1 \right) y. \end{aligned} \quad (9)$$

We would like to point out that (9) is a special case of the following system (Huang[8])

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

with

$$y = S, \quad g(y) = \frac{m_2 S}{k_2 + S}, \quad F(y) = C + DS_0^4 S^4,$$

and  $x = y$ .

System (10) has two equilibrium points  $(0, 1)$ , and  $(x^*, y^*)$ , where

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

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

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

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

The following theorem is proved in [8].

**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 3.** Assume  $m_2 > k_2 + 1$ . System (9) has two equilibrium points:  $M_1(1, 0)$ , which is a saddle, and  $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^4 \lambda_2^4))$ , which is stable if  $\frac{C}{D} > R_2$ , and unstable if  $\frac{C}{D} < R_2$ . In the case when  $M_2$  is unstable, there is at least one limit cycle in Eq. (9) surrounding  $M_2$ .

**Remark 1.** If  $F = 1$ ,  $g(S) = \frac{m_2 S}{k_2 + S}$ , it al-

ways has  $p > 0$ . That is, if the yield is a constant, the corresponding system has no limit cycle.

**Remark 2.** The equilibrium point  $M_2$  is globally asymptotically stable with  $\lim_{t \rightarrow \infty} S(t) = \lambda_2$ , and  $\lim_{t \rightarrow \infty} y(t) = 1 - \lambda_2$ .

For  $E_1$ , we study the phase portrait in the solution plane  $y = 0$ . In this case (2) is reduced to

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{x}{A + BS_0^3 S^3} \left( \frac{m_1 S}{k_1 + S} - L \right) \\ \frac{dx}{dt} &= x \left( \frac{m_1 S}{k_1 + S} - L - 1 \right), \end{aligned} \quad (12)$$

which is also a special case of (10) with

$$y = S, \quad F(y) = A + BS_0^3 S^3, \quad g(y) = \frac{M_1 S}{k_1 + S} - L$$

and  $x = y$ .

In  $\left\{ (S, x) \mid 0 \leq S \leq 1, x \geq 0 \right\}$ , system (12)

has two equilibrium points:  $N_1(1, 0)$ , which is a saddle, and  $N_2(S^*, x^*)$ , where

$$S^* = \frac{k_1(L+1)}{m_1 - (L+1)}, \quad x^* = (1 - S^*) (A + BS_0^3 S^{*3}) \quad (13)$$

Calculating  $p$  as in Eq. (11) and  $R_1$  as in Eq. (4) will result the following theorem.

**Theorem 4.** Assume  $m_1 > (k_1 + 1)(L + 1)$ . If  $\frac{A}{B} > R_1$ , then  $N_2(S^*, x^*)$  is stable; if  $\frac{A}{B} < R_1$ , then  $N_2$  is unstable and there exists at least one limit cycle in Eq. (12) surrounding  $N_2(S^*, x^*)$ .

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

**Theorem 5.** System (12) undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$ .

**Proof.** Let  $J(S^*, x^*)$  be the Jacobian of Eq. (12) at  $N_2$ . The corresponding characteristic equation is

$$r^2 + b_1 r + c_1 = 0. \tag{14}$$

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

$$trJ(\mu) = 1 + (1 - \lambda_1) \left( \frac{-3S_0^3 \lambda_1^2}{\mu + S_0^3 \lambda_1^2} + \frac{m_1 k_1}{(k_1 + \lambda_1)^2} \right). \tag{15}$$

Since

$$\left. \frac{d}{d\mu} trJ(\mu) \right|_{\mu=R_1} = (1 - \lambda_1) \frac{3S_0^3 \lambda_1^2}{(R_2 + S_0^3 \lambda_1^2)^2} > 0,$$

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

Notice that

$$trJ(\mu) \begin{cases} < 0 & \text{if } \mu < R_1 \\ = 0 & \text{if } \mu = R_1 \\ > 0 & \text{if } \mu > R_1. \end{cases} \tag{16}$$

The sign of the real parts of the roots for Eq. (14) has been changed from positive to negative. That means the phase structure of  $N_2(S^*, x^*)$  changes from unstable to stable at  $R_2$  as  $\mu$  increases. Thus, Eq. (12) undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$  by the definition [13].

Similarly, for the equilibrium point  $M_2(\lambda_2, (1 - \lambda_2)(C + DS_0^4 \lambda_2^4))$ , we can prove the bifurcation theorem for system (9).

**Theorem 5.** In system (9), a Hopf bifurcation occurs at  $\frac{C}{D} = R_2$ .

Finally, we would like to use the following remark to conclude our article.

**Remark 3.** It is interesting to note that the

structure of the solutions of system (1) with the yields  $\delta_1 = A + BS^n$ ,  $\delta_2 = C + DS^m$  has quite similar property. A further study will be very necessary and useful in the study of the continuous fermentation.

## References

- [ 1 ] Smith, H. L. and P. Waltman. 1995. "The Theory of the Chemostat". Cambridge University, Cambridge, UK.
- [ 2 ] Dorofeev, A. G., M. V. Glagolev, T. F. Bondarenko, and N. S. Panikov. 1992. Observation and explanation of the unusual growth kinetics of *Arthro bacter globiforms*. *Microbiology*, 61:33-42.
- [ 3 ] Crooke, P. S., C.-J. Wei, and R. D. Tanner. 1980. The effect of the specific growth rate and yield expressions on the existence of oscillatory behavior of a continuous fermentation model. *Chemical Engineering Communications*, 6: 333-339.
- [ 4 ] Crooke, P. S. and R. D. Tanner. 1982. Hopf bifurcations for a variable yield continuous fermentation model, *International Journal of Engineering Science*, 20:439-443.
- [ 5 ] Panikov, N. S. 1995. "Microbial Growth Kinetics". Chapman and Hall, London.
- [ 6 ] Tang, B. and G. S. Wolkowicz. 1992. Mathematical models of microbial growth and competition in the chemostat regulated by cell-bound extra-cellular enzymes. *Journal of Mathematical Chemistry*, 31: 1-23.
- [ 7 ] Pilyugin, S. S. and P. Waltman, 2003. Multiple limit cycles in the chemostat with variable yield. *Mathematical Biosciences*, 182: 151-166.
- [ 8 ] Huang, X. C. 1990. Limit cycles in a continuous fermentation model. *Journal of Mathematical Chemistry*, 5: 287-296.
- [ 9 ] Huang, X. C. and Zhu, L.M. 2005. Limit cycles in a general Kolmogorov model. *Nonlinear Analysis: Theory, Methods*

- and Applications*, 60, 8: 1393-1414.
- [10] Schuler, M. L. and F. Kargi, 1992. "Bioprocess Engineering Basic Concepts". Prentice Hall, Engelwood Cliffs.
- [11] Freter, R. 1983. Mechanisms that control the microflora in the large intestine. *Hunan Intestinal Microflora in Health and Disease* (ed. D. J. Hentges). Academic press, New York.
- [12] Liu, J. and S.N. Zheng. 2002. Qualitative analysis of a kind of model with competition in microorganism continuous culture. *Journal of Biomechanics*, 17, 4: 399-405.
- [13] Zhang, J. 1987. "The Geometric Theory and Bifurcation Problem of Ordinary Differential Equation". Peking University Press, Beijing.
- [14] Wolkowicz, G. S. K. and Z. Lu, 1992. Global dynamics of a mathematical model of competition in the chemostat: general response functions and differential death rates. *SIAM Journal on Applied Mathematics*, 32: 222-233.
- [15] Zhu, L. and X.C. Huang. 2005. Relative positions of limit cycles in the continuous culture vessel with variable yields. *Journal of Mathematical Chemistry*, 38, 2: 119-128.
- [16] Zhu, L. and X.C. Huang. 2005. Multiple limit cycles in a continuous culture vessel with variable yield. *Nonlinear Analysis: Theory, Methods and Applications*. (accepted)
- [17] Bulter, G. and P. Waltman. 1981. Bifurcation from a limit cycle in a two predator-one prey ecosystem modeled on a chemostat. *Journal of Mathematical Biology*, 12: 295.

